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Natural disturbances and benthic communities in Monterey Canyon Head

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Natural disturbances and benthic communities in Monterey Canyon head

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San Jose State University, 1993

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NATURAL DISTURBANCES AND BENTHIC COMMUNITIES IN MONTEREY CANYON HEAD

A Thesis
Presented to
The Faculty of Moss Landing Marine Laboratories
and The Department of Biology
San Jose State University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science in Marine Science

by
Thomas A. Okey
August, 1993

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ABSTRACT

NATURAL DISTURBANCES AND BENTHIC COMMUNITIES IN MONTEREY CANYON HEAD

by Thomas A. Okey

Seasonal sediment flushing, earthquakes, and sunken drift algae influence the abundance and distribution of benthic macrofauna in Monterey Canyon's head. Each contributes to the canyon's overall disturbance regime. Large scale (> 100 m^2) sediment flushing may occur in the axis with the first fall storm. A year of monthly sampling revealed fluctuating polychaete worm populations at the axis station. Two un-flushed reference stations harbored less variable populations.

The Loma Prieta earthquake triggered slumping on the canyon walls, but not axis flushing. All taxa were numerically reduced in earthquake slumps, except for the newly recruited polychaete *Prionospio pygmaea.*

Comparative sampling and field experimentation with sunken algae revealed that crustaceans and polychaetes generally exhibited opposite numerical patterns. More crustaceans were found in algal patches in the spring, more polychaetes in the fall. Amphipods rapidly colonized experimental alga patches in all seasons and habitats. Polychaetes colonized more slowly, and in particular seasons and habitats.

DEDICATION

I thank my mother, Joan, for her Love
and my dear ol' dad, Frank, for enjoying the good game.
Thank you both for always supporting me on my unusual path.

ACKNOWLEDGEMENTS

This study could not have been accomplished without the help of many outstanding people. I thank Dr. John Oliver for conceptualizing much and taking credit for little, for polychaete taxonomy, and for never hesitating to offer his tremendous perspective. I thank Peter Slattery for crustacean taxonomy, and for reminding me that nature is infinitely simple as well as infinitely complex. I am thankful to Dr. James Nybakken and Dr. Mike Foster for their support, and their reviews that made me stop and think. I thank Jim Oakden for help with data processing and sediment analysis, and for recognizing the humor in every situation. I appreciate the generosity of Lynn McMasters who provided her expertise with figures. The heroic assistance in sample processing by Heather Ross and Melissa Wilson was as crucial as the extraordinary talents of our librarians at Moss Landing Marine Laboratories, Sheila Baldridge and Sandi O'Neil. I am most grateful for the reliability and enthusiasm of my companions at Moss Landing Marine Laboratories who made the extensive field work achievable and fun: Cassandra Roberts, Amy Wagner Nicole, Diana Steller, Hunter Lenihan, Tony Bennett, Matt Burd, Dean Antonio, Kim Burdett, Brenda Konar, Nicole Crane, Joan Gardner-Taggart, Bev Hanna, James Downing, Phil Barrington, Guerrmo Moreno, Frank Roddy, Linda Browne, Pat Conroy, Lawrence Honma, Kim Kiest, Ken Isreal, Sheila Bowman, Jenifer Levitt, John Levitt, Allen Andrews, Donna Kline, Daniella Maldini, Carrie Bretz, Aaron King, Bill Hayden, Eric Johnson, Rich San Filippo, Thomas Burks, Dr. Rikk Kvitek, John Douglas, Sandy Zeiner, Steve Osborn, Nancy Black, Tom Kiekhefer, Tom Norris, Sal Cerchio, Mike Feinholz, Diane Carney, Dion Oxman, and Paul Balogna (from the University of Maine). We are fortunate to have a diving safety officer like John Heine, whose competence, wisdom, and amiability have launched a program that is safe, as well as conducive to science. The helpfulness and cooperation of Mike Prince, Nedra Shutts, and Tracy Thomas at MLML Marine Operations was also crucial. I thank Dr. Greg Cailliet, Dr. Jim Barry, Dr. Andrew De Vogelaere, Dr. Chris Harrold, Dr. Bill Broenkow, Dr. Mike Ledbetter, and Dr. Gary Greene for their encouragement and helpful criticism of my writings. A special thanks to Dr. Bill Broenkow and Richard Reaves for the use of their unpublished weather and oceanographic data. Dr. Mike Ledbetter was confident enough in this research to share valuable ship time. Cindy Armstrong, Eric Johnson, Aldo DeRose, Richard Shutts, and Andy Heard helped design and build sampling gear for deep water which was successfully deployed with the help of Captain Steve Bliss and his crew on the R/V Point Sur and Tracy Thomas, captain of the R/V Ed Ricketts. Sandy Yarbrough, Irene Chung, and Gail Johnston made this project more enjoyable by skillfully humanizing administrative details. I regret that I am late in thanking Dr. John Martin, who always offered me his enthusiasm, support, and humor. But perhaps most of all, I thank Melinda the Beautiful for believing. This work was further supported by the Earl and Ethel Meyers Marine Biology and Oceanographic Trust, and National Science Foundation Grant OCE 9005970.

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Chapter 1

SEDIMENT FLUSHING OBSERVATIONS AND BENTHIC COMMUNITY CHANGES IN MONTEREY CANYON HEAD

Chapter 1

SEDIMENT FLUSHING OBSERVATIONS AND BENTHIC COMMUNITY CHANGES IN MONTEREY CANYON HEAD

Thomas A. Okey
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Abstract: A large area of axis sediment (> 100 m^2) may be annually removed from the head of Monterey Submarine Canyon with the first onshore storm of the fall/winter storm season. In this scenario, flushing events are followed by net accumulation of sediment and organic debris—especially macro-algae—in the shallow axis. This continues throughout the remainder of the year until the next fall-flushing. The benthic community at a canyon axis station was characterized by highly fluctuating populations of opportunistic polychaete worms, primarily *Capitella* spp. and *Armandia brevis*. The canyon axis community was very different from communities living at adjacent sloping-wall and sandflat stations where sudden sediment flushing does not occur. Sloping-wall and sandflat stations harbored more and longer-lived species, larger individuals, and a less variable population structure during a year of sampling.

The Loma Prieta earthquake triggered small sediment slumps on the canyon walls, and did not cause the axis to flush. Two weeks after the quake, the usual seasonal slumping of the axis occurred with the arrival of the first storm. Benthic communities were reduced in abundance inside earthquake-induced slumps; however, the slumped areas were rapidly colonized by *Prionospio pygmaea*, a polychaete opportunist common to the sandflat. Surprisingly, the physical and biological impacts of the earthquake were much less severe than the seasonal axis-flushing associated with storms.

INTRODUCTION

Erosion of the sea floor, or mass wasting, occurs on all continental shelves and slopes. Mass wasting processes encompass a variety of types and scales of sea-floor disturbance ranging from the movement of a few sediment grains to slides and flows of hundreds of square kilometers (*see* Coleman and Prior 1988). Submarine cables, even oil platforms, can be destroyed or disappear as large blocks of sediment slide down slopes of as little as 0.25°, or flow down steeper angles of repose (Inman et al 1976, Prior and Coleman 1978, Field et al. 1982). The frequency of these events may be as varied as their magnitudes and areal extents. Little is predictable about mass wasting processes, but they are certainly widespread on continental margins.

Almost nothing is known about the effects of mass wasting on benthic communities. Despite this paucity of data, several researchers have speculated about the ecological effects of slides and flows (Griggs et al. 1969, Jumars and Hessler 1976, Hecker 1982, Jumars and Wheatcroft 1989), but only VanBlaricom (1978) quantified direct effects of mass wasting on soft bottom communities. He showed that large numbers of opportunistic polychaetes colonized, then rapidly declined, after a large-scale, storm-induced sediment slump in a tributary of Scripps Canyon in La Jolla, California. However, he did not fully discuss the ecological implications of this large-scale event. Later, Hecker (1982) speculated that submarine landslides destroy existing communities, make new space available, select for mobile over sedentary species, and transport organically rich sediment to deep water habitats.

Mass wasting of large magnitude occurs more often in submarine canyons than in other areas along the continental margin (Shepard and Dill 1966, Coleman and Prior 1988). The heads of many submarine canyons are known to be active sites of downward sediment transport (Shepard 1951, Chamberlain 1964, Shepard and Reimnitz 1981, Eittreim et al.

1982, Hothckiss and Wunsch 1982, Baker and Hickey 1986, Stanley et al. 1986, Dingler and Anima 1989, Gardner 1989, Venec-Peyre 1990). In Scripps Canyon-head at La Jolla, California, a 9 m-thick layer of sediment (~172, 000 m^3), mostly between 15 and 60 m depths, can be removed during a discrete flushing event that occurs once per year (Shepard 1951, Chamberlain 1964, Dill 1964, Shepard and Dill 1966, Shepard and Marshall 1973, Inman et al. 1976). Because submarine canyon heads extend shoreward to within scuba depths they provide an opportunity for thorough ecological studies of mass wasting; they are the best starting point to construct a useful ecological model of mass wasting on continental margins.

I designed a sampling program to assess the responses of the benthic community to the expected large-scale (> 100 m^2), storm-induced, sediment-flushing in Monterey Canyon's shallow head (< 40 m depth). Such sediment deepenings were observed by Arnal et al. (1975) and Oliver (1979 and personal communication). I compared the infaunal macro-invertebrate assemblages among three stations: the canyon-axis station, which is subjected to flushing, and the sloping-wall and sandflat stations, which do not suddenly flush like an axis. The following hypotheses were formulated: (1) There will be more opportunistic species at the axis station than at the sloping wall and sandflat stations; (2) Assemblages of macrofauna will fluctuate more at the axis station than at the other two stations. A less formal question was, how does the canyon-axis pattern compare to patterns found at the other stations? For example, do long-lived and large-bodied, later-successional species colonize the axis station after short-lived and small-bodied, opportunistic colonists, as in terrestrial landslides (Flaccus 1959, Garwood et al. 1979, Veblen 1985, Mark et al. 1989) and disturbances in general (MaCarthur and Wilson 1967, Odum 1969, Pianka 1970, Connell 1978, Sousa 1984, Pickett and White 1985)? Alternately, are opportunistic species continuously favored over later successional species at the highly disturbed axis station, as in forests and grasslands that are subjected to frequent fires (Daubenmire 1968, Algren 1974, Komerek 1974, Vogl 1974, Romme 1981, Veblen 1985, Lawesson 1988), and in other marine soft-bottoms that are frequently disturbed by storms (Rees et al. 1977, Wolff et al. 1977)?

The big surprise of the study came when the Loma Prieta earthquake of 17 October 1989 (magnitude 7.1) did not trigger the expected axis flushing, but caused several small slumps along the sloping-walls in the shallow head of Monterey Canyon. The geological and biological consequences of the earthquake contributed to an up-to-date assessment of the physical model of axis flushing, and they provided novel insights into the responses of the benthic community to sediment disturbances.

METHODS

Study location

The head of Monterey Canyon extends to within five meters of the sea surface just ten meters offshore of Moss Landing in Monterey Bay, California, USA (121° 47' W, 36° 48' N). It incises California's narrow continental shelf and cuts into lagoonal clay at its most headward reaches (Shepard 1948, Martin 1964, Shepard and Dill 1966). The Monterey Canyon system extends 500 km west to ~128° W, 36° N, where it reaches 4600 m depth (Martin 1964). The steep axial and wall gradients of the canyon's shallow head (< 30 m depth) contrasts with the gradual slope of the surrounding sandflats on this semi-protected outer coast (Shepard 1948, Martin 1964; Fig. 1). The shallow sea floor within 20 km North and South of the canyon head is predominantly covered with soft sediment. The mouth of Elkhorn Slough, a coastal embayment, is adjacent to the north branch of the shallow head's three tributaries.

A 30 m^2 sampling station was located at 24 m depth in each of the three topographically distinct, canyon head habitats: the axis of its southern tributary, an adjacent sloping-wall, and an adjacent sandflat (Fig. 1); they were in use from October 1988 through June of 1991. The axis station's slope was measured at 10° from horizontal with a clinometer (a protractor attached to a cork-float with a string). The sloping-wall station was 35° from horizontal, and the sandflat station was < 2°. The sampling and observations were carried out by divers using SCUBA (over 150 dives). All depth measurements are relative to MLLW.

Sediment disturbances

Axis flushing, sloping-wall, and sandflat - Timing and extent of large sediment movements were assessed with measurements of grain-size parameters, and with observations of changes in topography and sediment characteristics during frequent diver surveys from October 1988 to June 1991. Grain size distribution of sediment was measured from a single 10 cm^2 core taken at each station on 1 and 22 November 1989 and quarterly from 25 July 1990 to 26 April 1991. Sediment was analyzed using sieve and hydrometer analyses (Folk and Ward 1957).

To determine whether axis flushing coincided with intense waves or wind, canyon observations and sediment measurements were compared to continuous wave and wind data from a nearby Monterey station (Broenkow and Reaves unpublished data). Data on local and regional precipitation, local and regional currents, tides, and internal waves were also compared to canyon observations and measurements.

Slumping caused by the Loma Prieta earthquake - Extensive before-and-after surveys of the shallow canyon head's upper sloping-walls left little doubt that the sudden wall-slumping resulted from the 17 October 1989 earthquake. During the weeks prior to the earthquake exceptionally clear water provided a rare window-of-opportunity to survey the canyon head. These surveys were repeated during the weeks following the quake to examine its effects. Sediment slumps and scarps were mapped and measured with surveyors tape. The gradual disappearance of these scarps as well as observations of changes in sediment consolidation in slumped areas was charted during the following three months using bi-weekly surveys.

Community changes

General protocol - Diver-operated corers (120 cm^2) were inserted 10 cm into the substratum to sample benthic macro-invertebrates (> 0.5 mm). Samples were washed over a 0.5 mm screen, preserved in 4% formaldehyde solution and later transferred to 40%

isopropyl alcohol. Macrofauna were separated from sediment and debris, identified to species, and counted (32,471 total individuals). Biomass of total fauna was measured wet. Observations of mega-invertebrates and fishes associated with sediment disturbances were also recorded.

General taxonomic categories, biomass, and the ten to fifteen most abundant species were then considered for hypothesis testing. Normality was assumed, not tested, because of small sample sizes. Analysis of variance is known to be extremely robust to departures from normality (Underwood 1981). Homogeneity of variances was tested with F-tests or Cochran's tests (Underwood 1981, Day and Quinn 1989). Square-root transformations were used to remove the relationship between the variances and the means in cases where heterogeneity of variances was detected (Underwood 1981). Nonparametric tests were used with the original data if they remained heteroscedastic after transformations. In general, parametric statistics were used only when sample sizes were equal or near equal and when the assumption of homogeneity of variances was not violated. Most taxonomic categories were analyzed with ANOVA, and some with their non-parametric equivalents. All factors were considered to be fixed (model-one tests). Methods specific to each hypothesis are included in the following sections.

Axis, sloping-wall, and sandflat - Macrofauna at each 24 m-deep, 30 m^2 station were sampled with six 120 cm^2 cores every month from 28 October 1988 to 21 September 1989. Samples were collected haphazardly because deep diving in poor-visibility prevented sampling with a formal random method. Haphazard and formal random samples of benthic communities were indistinguishable from a similar sedimentary environment (Fager 1968). The three stations were not replicated because only one shallow axis of Monterey Canyon is clearly pristine (i.e. not directly influenced by the tidal currents facilitated by the 1946 opening of the Elkhorn Slough/Moss Landing harbor mouth). All fauna were sampled during the day near the end of flooding tides.

Kruskal-Wallis tests and their associated H statistics were used to compare the fluctuation among taxonomic categories at the axis station (eleven monthly sampling dates). Quarterly samples from the wall and sandflat stations were then compared with the same quarterly dates from the axis station using parametric and non-parametric two-factor ANOVAs. Specifically, these were used to test whether assemblages differed among the three stations, and among the four sampling dates. Protected Tukey tests were then used to compare pairs of stations or sampling dates. Games-Howell tests were used in cases where variances were unequal (Day and Quinn 1989). The hypothesis of differences in faunal change among stations was evaluated with tabular presentation of mean numbers of individuals at each station and date, and with comparisons of H-values from separate Kruskal-Wallis analyses at each station (H or H_c was used as a coefficient of variation). H-values were compared to the X^2 distribution because *n,* or *k,* or both were adequately large.

Effects of earthquake-induced slumping - To evaluate the effects of earthquake-induced slumps on high-wall assemblages of Monterey Canyon, one 120 cm^2 core was taken at 18 m depth from each of five replicate natural slumps, and five similar but un-slumped areas, all toward the west end of a 15 m-deep bench that projects into the canyon head (Fig. 1). Samples were taken from the slumped and un-slumped areas both one and four months after the 17 October 1989 earthquake. One-tailed Mann-Whitney U tests were used to compare the assemblages from slumped and un-slumped areas for each sampling date; they were one-tailed because abundances were expected to be lower in slumped areas, and they were non-parametric because of heteroscedasticity.

RESULTS

Sediment disturbances

Axis flushing - Evidence of sudden flushing events in the axis of Monterey Canyon consists only of limited sediment samples, diver observations of changes in topography and sediment composition, and an observation from shore of a sediment re-suspension event. This evidence is presented chronologically, with concurrent wind and wave data from 1988-1991.

1988 - On 29 November I recorded that axis topography and sediment had changed since the last axis dive on 28 October. The transverse profile of the axis had changed from wide and bowl-shaped to deeper (~2 m) with newly-exposed, vertical, clay walls (both buoys and a nearby ship-anchor served as horizontal and vertical reference points). Axis sediment was a black and gelatinous mud with decomposing drift algae and percolating gasses on 28 October, but on 29 November clean, sandy sediment was present instead.

On 24 November, daily maximum wave heights reached 2.54 m (Fig 3), the highest since 18 January. All four events of high daily maximum wind velocity of the fall of 1988 occurred during November (Fig 3). Wind velocity on 6 November reached 41.7 km/hr. from 304°, and on 13 November it reached 51.9 km/hr. from 220°. These were each the highest daily maximums since 26 September. Wind velocity on 17 November reached 58.3 km/hr. from 313°, the highest since 27 March. On 23 November it reached 47.7 km/hr. There was no unusual precipitation or tide during this period.

1989 - Course sand comprised 1% of the sediment, and the mean grain size was .16 mm, in the single sample from the axis station on 1 November 1989. In contrast, course sand was 30% and mean grain size was .29 mm in the sample from the axis station on 22

November. Such differences were not found between the two corresponding samples from the sloping-wall station (Table 1).

On 22 November, I recorded that axis topography had changed dramatically since the month began (1 November 1989). I noted changes in topography and sediment composition similar to those observed the previous year.

On 3 November, daily maximum wave heights reached 1.79 m, the highest since 26 March (Fig. 2). Daily maximum wind velocity peaked on 23 October at 69.1 km/hr. from 179°. This was the highest wind since 30 April 1988. A smaller event occurred on 25 November at 52.0 km/hr from 196° (Fig. 2). Again, there were no unusual tidal or precipitation events during this fall.

1990 - There were considerable differences among the four (quarterly) sediment samples from the axis station, some differences among those from the sloping-wall station, and very small differences among those from the sandflat station (Table 1). Increases in sediment parameter values occurred only between 28 October and 11 February in these un-replicated samples.

A large, black, sediment plume was observed from shore during high onshore winds in the late afternoon of 31 October 1990. This plume was localized over the canyon head and mistaken for a sewage spill by marine-lab staff because of the strong hydrogen sulfide odor. Closer inspection revealed that clumps of semi-decomposed *Enteromorpha* spp. had floated to the surface with the black sediment; the plume was photographed. After a diver survey on 2 December, I recorded that the axis substratum had changed since a survey on the morning of 31 October. Course sand—presumably from the beach—was now found in the axis, where gelatinous sediment had been on 31 October. Deepening of the axis, relative to the ship anchor, was also apparent.

The Loma Prieta earthquake - A number of new slumps were observed along the upper walls (15-20 m) of the shallow head of Monterey Canyon after the 17 October 1989 earthquake (diver surveys on 2 November). These surveys also revealed that the earthquake did not trigger flushing of the presumably unstable axis-fill, a poorly consolidated, gelatinous mud, permeated with decaying algae and gas.

Community changes

Canyon axis - Populations of benthic macrofauna fluctuated considerably at the axis station between October of 1988 and September of 1989 (Fig. 3). Significant differences among the eleven sampling dates were detected in all tested categories ($p < .05$, Kruskal-Wallis tests; $n = 6$). These categories follow, with their Kruskal-Wallis test statistics (H_c = H corrected for ties) presented for comparison to the chosen chi-squared value ($X^2_{0.05,10} = 18.3$): total fauna ($H_c = 54.7$), total polychaetes ($H_c = 54.7$), total crustaceans ($H_c = 28.9$), total molluscs ($H_c = 23.3$), number of species ($H_c = 50.2$), and in descending order of abundance, the ten numerically dominant taxa: the opportunistic polychaetes *Capitella* spp. ($H_c = 39.2$) and *Armandia brevis* ($H_c = 44.6$), the lysianassid amphipod *Orchomene pacifica* ($H_c = 34.9$), the polychaetes *Prionospio pygmaea* ($H_c = 31.6$), *Eteone dilatae* ($H_c = 37.3$), and *Nephtys cornuta* ($H_c = 31.2$), nemerteans ($H_c = 30.0$), and the polychaetes *Phyllodoce* sp. ($H_c = 31.9$), *Spiophanes* spp. ($H_c = 32.7$), and *Magelona sacculata* ($H_c = 23.4$). H_c, in this case, is a measure of variability among sampling dates. Note that H_c are the same for total fauna and total polychaetes.

The densities of *Capitella* spp., *A. brevis*, and *O. pacifica* increased and then rapidly declined at the axis station after the flushing of 1988 (Fig. 3). Assemblages remained comparatively low after this decline and throughout the calm summer months. *Capitella* spp. began its prolific increase by 28 January, two months after the major wind and wave events of November. *A. brevis* and *O. pacifica* began increasing one and two months later respectively. These three opportunists, along with total molluscs, and number of species, reached maximum abundance on 19 April, when patches of drift *Enteromorpha* spp. were present on the axis substratum and in three of the six cores (Fig. 3, Fig. 4). Of the less numerous polychaetes, *Spiophanes*. spp. were most abundant on 28 January. *E. dilatae, N. cornuta,* Nemertea, and *Phyllodoce* sp. peaked on 25 February. *P. pygmaea* was most abundant on 28 October. *M. sacculata* was most abundant on 29 November. Faunal changes relative to presumed flushing events of 1989 and 1990 are unknown because these stations were sampled for one year only.

Sunken patches of the green, macro-alga *Enteromorpha* spp. were associated with the high abundance of macrofauna in April. *Enteromorpha* spp. and large numbers of polychaetes and crustaceans were observed in three of the six axis-samples from 19 April 1989. These six samples were extracted from the overall design and split into two groups—three with *Enteromorpha* spp. and three with none. The three most abundant species that were captured illustrate that some species were much more abundant in algae, while others were not (Fig. 4). Total fauna, total polychaetes, total molluscs, total crustaceans, *Capitella* spp., *O. pacifica, N. cornuta,* and *Mysella* sp. were significantly more abundant in *Enteromorpha* spp.-patches than away from them ($p < .05$, Mann-Whitney U tests; $n = 3$). But, significant differences were not detected for *A. brevis, P. pygmaea, E. dilatae, Phyllodoce* sp., nemerteans, and the ophiuroid *Amphiodia urtica* (the ten most abundant taxa were tested). Density of macrofauna in sunken *Enteromorpha* spp. was 238,917 individuals per m^2 (2,867 ± 480 S.E. individuals per core).

Sloping-canyon-wall and adjacent sandflat comparisons - Total polychaetes were temporarily much more abundant at the axis station than at the sloping-wall and sandflat stations (19 April 89). Even when data from all seasons were pooled, total polychaetes were still much more abundant at the axis station than at the other stations. This is largely due to the high abundance of the opportunistic polychaetes *Capitella* spp. and *A. brevis* on 19 April (Table 2, Fig. 3, previous discussion). Significant differences among stations were detected for total crustaceans, *Capitella* spp., *P. pygmaea, Dendraster excentricus, Spiophanes* spp., and *E. dilatae* ($p < .05$, non-parametric two-factor ANOVAs; $n = 6$, except for *P. pygmaea;* two-factor ANOVA). Total crustaceans, *Capitella* spp., and *E. dilatae* were most abundant at the axis station; *Spiophanes* spp. was most abundant at the wall-station; and *P. pygmaea* and *D. excentricus* were most abundant at the sandflat station. *O. pacifica,* which made up the bulk of the crustaceans, was also very abundant in the axis on 19 April, yet only two individuals were found at the sloping-wall station, and none were found at the sandflat station (Fig. 3, Table 2). Significant interaction between station and sampling date was detected for most other taxonomic categories.

Overall macrofauna abundance and biomass fluctuated most at the axis station, less at the sloping-wall station, and still less at the sandflat station. This is apparent when comparing changes in mean abundances among stations (Table 2), and further illustrated by comparing variability (H or H_c) among stations: total fauna H-values were 16.9 at the axis station, 14.2 at the sloping-wall station, and 13.5 at the sandflat station. Likewise, polychaete H-values were 16.8, 15.2, and 11.9, and crustacean H-values were 10.6, 9.1, and 1.3. This trend of highest fluctuations at the axis station and lowest at the sandflat station mimics that of the sediment parameters (Table 1). Data from the four-season sampling dates were used in this comparison ($X^2_{0.05, 3} = 7.8$).

Sloping-wall and sandflat assemblages had more large-bodied species than the axis station where small bodied opportunists dominated. Grand-mean biomass (wet) per individual (total biomass / total # of individuals) was 9.0 mg at the sloping wall station, 5.7 mg at the sandflat station, and 1.7 mg at the axis station. Larger polychaete species, *Mediomastus californiensis, Lumbrineris luti,* and *Nothria elegans* were more abundant at the sloping-wall (respectively: 6.7 individuals per core ± 1.6 SE; 5.3 ± .9; 1.2 ± .4) and sandflat (3.2 ± .6; 2.4 ± .4; .9 ± .2) stations than in the axis (.1 ± .1; .6 ± .2; .1 ± .1). *Spiophanes* spp., another large polychaete species, was more abundant on the sloping-wall (7.2 ± 1.2) than in the axis (2.1 ± 1.1), but it was least abundant on the sandflat (.4 ± .2; *see* Hartman 1968 and 1969 *for polychaete sizes*). Nemerteans were more abundant at the the sandflat (2.2 ± .4) and axis (1.5 ± .6) stations than at the sloping-wall (.6 ± .2).

The axis station always had fewer species than the sloping-wall station, which in turn always had fewer species than the sandflat station (Table 2); however, these differences were not always statistically significant. Only in July, when low-oxygen conditions in the axis were apparent, did the axis station have significantly fewer species than the sloping-wall or the sandflat station ($p < .05$, Tukey tests after two-factor ANOVA; $n = 6$). The sandflat station had significantly more species than both the wall and axis stations in January. During the other three months tested, the sandflat station had significantly more species than the axis station, but not the wall station.

The most species occurred in the spring at all three stations while the least occurred in the winter at the more wave-exposed sloping-wall and sandflat stations (Table 2). At the axis station, however, the least species were present during the low-oxygen, late-summer. There were significantly more species in April than in January at every station ($p < .05$, Tukey tests; $n = 6$). At the axis station there were significantly more species in April than both January or July. At the wall station October had significantly more species than January.

Opportunists were also occasionally present at the sloping-wall and sandflat stations, but they comprised a much smaller proportion of faunal assemblages than did opportunists at the axis station. The deposit feeding polychaetes *N. cornuta* and *A. brevis* were seasonally present (mostly in the spring) at the sloping-wall station. *P. pygmaea* was abundant on the sandflat station in October, significantly more so than in January or July ($p < .05$, Tukey tests after two-factor ANOVA on square root transformed data; $n = 6$). Newly settled sand dollars, *D. excentricus,* were also abundant at the sandflat station in October.

Earthquake slumping and community change - Sediment slumped in small hanging-channels in the upper canyon walls (18 m depth) coincident with the 17 October 1989 Loma Prieta earthquake. Infaunal abundances were much lower in slumped areas compared to similar un-slumped areas (Fig. 5). The slumped areas were subsequently colonized by *P. pygmaea* (Fig. 5). Forty-two days after the earthquake most groups (total fauna, total polychaetes, *Capitella* spp., *A. brevis,* and *N. cornuta)* were significantly less abundant in slumps than in un-slumped areas ($p < .05$, Mann-Whitney U tests; $n = 5$), but *P. pygmaea* was significantly more abundant in slumps. By February, four months after the earthquake, there were no significant numerical differences between slumped and un-slumped areas. However, note that fauna in February samples were almost an order of magnitude less abundant than the presumably impacted areas of November (Fig. 5).

DISCUSSION

Scope and limitations

Community structure measurements were emphasized in this study in the hopes of providing a needed biological complement to the evolving geological and physical knowledge of submarine canyons. This work was also intended to contribute an uncommon example of the ecology of large-scale disturbances on soft-bottoms. The simplified message is that a dynamic and weedy fauna existed at a highly-disturbed canyon axis station while the fauna at stations in less-disturbed habitats were more stable and steady. Inferences by the reader should be made cautiously, not only because sampling stations were small and un-replicated, but also because they were sampled for one year only. Evidence presented in this paper suggests, but does not demonstrate, a cause-effect relationship between observed seasonal sediment flushing and benthic community changes. Two additional years of sampling and observations during a companion study in Monterey Canyon (Chapter 2) indicate both regular cycles and apparently stochastic changes in fauna.

This study was not designed to thoroughly evaluate whether onshore storms cause canyon-axis flushing. Thus, causality between onshore storms and sediment flushing goes un-demonstrated. Although it is likely that such causation does exist, evidence herein is correlative in nature and quantitatively limited. Furthermore, these sediment disturbances were not thoroughly measured with respect to aerial extent and frequency. Multiple lines of evidence, rather than quantitative rigor, make a storm-flushing mechanism likely. Evidence that onshore storms are a reasonable cause of canyon head flushing include diver observations of topographic and sediment changes, measurements of changes in sediment parameters, and a surface-plume observation, all coincident with onshore storms. This evidence is persuasive because climatic, tidal, and current data failed to support alternative explanations. A review of canyon literature revealed three things: a pre-existing model of storm-induced canyon head flushing, some less reasonable explanations for canyon head flushing, and some reasonable explanations that are not applicable. The former lines of evidence and the latter review of flushing literature are both presented after the following discussion of benthic community changes.

Community changes and axis flushing

Considerable monthly variation of benthic macrofauna abundance and composition at the canyon axis station is indicated by consistently high Kruskal-Wallis H-values, as well as by Figure (3). Identical H_c-values for total fauna and total polychaetes indicate that the two are not independent at the axis station; the former is driven by the latter (*also see* Table 2). The axis was colonized by a number of opportunistic species throughout the year, but especially in the spring; they settled in large numbers and rapidly declined in abundance. The large storms of the fall and winter are suspect, not only as agents of disruption and removal of macrofaunal assemblages, but also in transporting new resources and re-oxygenating the habitat. It is likely that storms and associated flushing influence Monterey Canyon head's benthic community throughout much of the year.

This colonization-mortality pattern of opportunistic species has also been documented after marine benthic disturbances in several other settings (Grassle and Grassle 1974, McCall 1977, Pearson and Rosenberg 1878, Rhoads et al 1978, Rhoads and Boyer 1982). Furthermore, numerical dominance by opportunists may persist in frequently disturbed settings. Wolff et al. (1977) attributed the persistence of opportunistic species to frequent storm-wave events, suggesting that regular disturbance continuously created new resource opportunities. Later-successional species did not increase during the development of that shallow benthic ecosystem. Santos and Simon (1980) found that a pioneering assemblage was eliminated annually by anoxia disturbances. They, too, found no shift to an equilibrium community, contending that opportunists predominated because the annual catastrophic disturbance was too frequent to allow later-successional species to become established. Similarly, opportunists predominated in the Monterey Canyon axis station where sediment flushings apparently occur annually. This flushing-opportunist scenario sounds simple and logical. However, there are other factors—albeit sometimes related to flushing—-that influence benthic community structure in this complex setting. Speculation herein on the myriad physical and biological factors are unfortunately limited to those that are most obvious.

Sunken drift algae may be as much, if not more, of an influence on Monterey Canyon head community structure than physical sediment disturbance. Sunken patches of *Enteromorpha* spp. clearly accounted for high abundances of the opportunists *Capitella* spp. and *O. pacifica* in the 19 April axis samples (Fig. 4). After the peak and rapid decline of these opportunists at the disturbed axis station, all groups became suppressed during the summer; there was no increase in later-successional species during or after the decline of opportunists. This may be due to a low summer dissolved oxygen concentration at the axis station, indicated by observations and limited samples (4.5 mg/l taken 2 to 10 cm above bottom, compared with winter: 8.2 mg/l, and fall and spring: 7.3 mg/l and 7.4 mg/l; *see* Chapter 2 *for a discussion of the limitations of these data*). This also makes sense, because the few opportunists present throughout the summer (ie. *Capitella* spp.) are known to be associated with enrichment conditions such as accumulations of drift algae and low dissolved oxygen concentrations (Reish 1971, Pearson and Rosenberg 1978).

The swarming gammarid amphipod, *O. pacifica*, was very abundant at the axis station in April (Fig. 3), and was almost never found at the sloping-wall and sandflat stations. This is a similar pattern to that of the opportunistic polychaetes in the axis. Amphipods do not have opportunistic life cycles, per se, because they brood their young, but their high adult mobility allows behavioral opportunism. *O. pacifica,* and other species in this widespread genus, are known to be voracious and abundant scavengers of food resources on the sea floor (Slattery and Oliver 1986). This species, like many amphipods, can actively seek out resources and be highly selective of habitat.

Macrofaunal assemblages fluctuated less at the sloping-wall station than at the axis station, and still less at the sandflat station. This is illustrated by corresponding decreases in Kruskal-Wallis statistics, and by Table (2). Because this gradient of faunal fluctuation mimics the gradient of sediment-parameter fluctuation (Table 1), the most obvious conjecture is that the faunal patterns are influenced by differences in disturbance regime (ie. sediment disturbances at the wall and sandflat are not as severe as axis flushing). This is reasonable, and probably true. However, it leads to a broad simplification, and there may be other reasons for these fluctuation gradients (ie. sedimentation is influenced by many factors). Or, these patterns may simply be an artifact of chance; the sampling stations were not replicated, and sediment samples were not replicated. Moreover, deductions of causality are limited because the design was comparative (correlative), and not experimental.

Biomass trends also followed the sediment-parameter trends (fluctuating more at the axis station, less at the sloping-wall station, and still less at the sandflat station). However, it might be reckless to consider the difference between axis and sloping-wall biomass fluctuations biologically significant, based on the limited data herein (Table 1, Table 2).

Differences in sediment-disturbance regimes also serve as a reasonable explanation for the higher abundance of large-bodied and long-lived species at the sloping-wall and sandflat stations. The sloping-wall station may be exposed to some slow deformational creep (Oliver et al. 1980, Greene et al. 1991, personal observations), but it does not undergo massive flushing or collect algae, overlying water is less likely to stagnate there, and it is hardly exposed to wave-surge. This more benign setting might explain the presence of these later-successional species at the sloping-wall station. The sandflat disturbance regime also appeared to be less severe and punctuated than that of the axis. Surge at the sandflat's benthic boundary layer varied on a daily, weekly, and seasonal scale, but this type of disturbance may never be severe at 24 m depth where the sandflat-station was located (*see* Oliver et al. 1980).

The sandflat station always had the most species, followed by the sloping-wall station, and then the axis station which always had the least species. Fluctuations in sediment parameters would not be expected to reliably characterize *overall* disturbance regime because some disturbances are constant, like the ever-present wave surge on the sandflat. Although divers might consider the sandflat station to be intermediately disturbed, a useful way of quantitatively comparing overall disturbance regimes was elusive. This makes conjecture about relatedness to diversity/disturbance paradigms little more than that.

Community changes and earthquake slumping

Numbers of benthic infauna were reduced within the distinct earthquake-induced slumps 42 days after the earthquake. Only *P. pygmaea* was found to colonize new space provided by these earthquake-induced slumps (Fig. 5). This species was also most abundant at the sandflat station during the axis, wall, sandflat comparison. This suggests that *P. pygmaea* is, perhaps, more of a sediment-disturbance opportunist than an opportunist of calm, enriched settings, like *Capitella* spp.

Infaunal assemblages were not different between slumped and un-slumped areas four months after the earthquake (Fig. 5). This indicates only that the community level effects of the earthquake were no longer apparent at four months. Note that total fauna was a full order of magnitude lower than even the slumped areas three months earlier (Fig. 5). This enormous temporal variability indicates that earthquake-induced effects were smaller than other natural changes in this setting. In fact, this temporal variability makes patterns of earthquake-induced effects less compelling. The likely reason for such change is that the second sampling (21 February 90) took place after several large storms (Fig. 2). The 15-18 m deep upper reaches of this protruding canyon bench were probably disturbed by wave-surge between sampling dates. This does not severely conflict with previous measurements and observations that the sloping-wall station is hardly exposed to the surge, for that station was 24 m deep and within the wave-shadow of the canyon head (*see* Dayton et al. 1989). Implications of earthquake-slumping observations, with respect to storm-induced axis flushing, are discussed later in the following section.

Evaluation of the Shepard-Inman model of sediment flushing in canyon heads

Although the present study was not originally intended to evaluate models of canyon sediment transport, the observations and limited sediment data herein should be compared to evidence suggesting that seasonal storms may cause sediment-fill removals from Monterey Canyon head. This will provide a limited evaluation of the Shepard-Inman model's generality.

Massive removal of axis fill has been noted after large storms of every fall/winter season that the Monterey Canyon has been studied by diving researchers. During the present study, I observed a synchronism of fall storm events with major changes in topography and sediment characteristics. The large black sediment plume observed over the canyon head on windy 31 October 1990 also supports the storm-trigger mechanism. Sudden increases in percent coarse sand or percent sand, mean grain size, and sorting coefficients (Table 1) concurrent with onshore storms indicate that these events replaced fine axis-sediment with coarse beach-sand. The absence of sediment flushing at the sloping-wall and sandflat stations is supported by more constant sediment characteristics in the samples from these stations (Table 1), as well as diver observations. These data, however, provide limited confidence in inferring causation or estimating real-world conditions because values are from one station per date, and because there are some changes during non-storm months. Nevertheless, sediment characteristics are relatively homogeneous within subtidal topographic/exposure units (Bascom 1964), and changes measured in non-storm months were decreases, not increases, in grain size parameters. These decreases were probably due to deposition of fine sediment from the water column. Increases in grain-size parameters during stormy months could have been due to slow creep of beach sand into the axis, rather than sudden flushing. This is reasonable; in fact, the arrival of beach sand in the axis is probably due to a combination of sudden flushing and slow creep. Removal of the fine, gelatinous fill is more probably sudden, as indicated by its cohesiveness and the sudden depth increases.

Previous evidence of Monterey Canyon flushing also exists. Oliver and Slattery (unpublished data) measured a 10 m wide, > 2 m high deepening after a fall 1972 storm, with a cross-axis profile in Monterey Canyon head (Fig. 6). Martin (1964) identifies the canyon's shallow head as the most active area of turbidity current erosion, when discussing mass-movement in the axis as a major factor in the erosion of Monterey Canyon. Fifteen years of semi-annual measurements in the canyon head show sediment-depth increases during summer and decreases during winter (Broenkow et al. unpublished data). Several more researchers contend that storms cause axis-flushing in Monterey Canyon seasonally (Shepard and Emery 1941, Shepard 1948, Arnal et al. 1975, Oliver 1979). Dill (1964) observed a sediment plume in Scripps Canyon head, similar to the one I observed in Monterey Canyon head. It extended a half-mile from shore during a storm, and it too, had clumps of algae floating throughout. More recently, Dayton et al. (1989) observed that a single storm caused extensive erosion of the shoreward rim of La Jolla Canyon.

"Spontaneous liquefaction" was proposed by Chamberlain (1964) as the likely mechanism of mass sediment transport in Scripps Canyon head. In this scenario, differential vertical compaction of sedimentary facies, and lateral strain on seaward organic detritus causes the collapse of the unstable sediment structure. This produces excess pore water pressure and reduces sediment shearing resistance. His insights regarding biologically influenced geophysical changes can still be considered relevant to the axis flushing mechanism, but his straw-that-broke-the-camel's-back triggering-mechanism falls short. Although his statistical analyses revealed no significant relationships between the deepenings and onshore wind velocities, earthquakes, or precipitation, Chamberlain's data do reveal a relationship between the deepenings and onshore wind velocities; ten of eleven annual bottom deepenings in Scripps Canyon coincided with high onshore winds. His data, in fact, support storm-induced axis flushing.

Buried macro-algae appeared to influence the stability of the sediment fill in the axis of Monterey Canyon. Layers of algae accumulated in the axis throughout the spring and summer of each year, and were incorporated into the bottom as flocculent sediment buried them. Pore gasses accumulated in the axis sediment as algae decomposed. By the fall of each year, gas bubbles percolated out of the gelatinous and unstable sediment when prodded by divers. Also, intertwined plant material appeared to contribute lateral cohesiveness to the fill.

Organic debris has long been believed to influence sediment stability in Scripps Canyon and elsewhere (Shepard 1951, Chamberlain 1964, Dill 1964, Shepard and Dill 1966, Whelan et al. 1976, Rhoads and Boyer 1982, Aller 1982, Coleman and Prior 1988). Accumulations of sediment and algae were first observed in the shallow axes of Scripps and La Jolla Canyons during diver surveys (Shepard 1949). Canyon heads trap much of the sand and drifting vegetation that is carried by alongshore currents (Shepard 1951, Chamberlain 1964), and deposition rates in canyon heads are particularly high because they underlie a shelf nepheloid layer (Baker and Hickey 1986). Thus, macro-algae are quickly buried by sediment in canyon heads. Numerous deepenings have been documented, and buried, decomposing algae has been repeatedly suggested as a cause of instability leading to mass sediment-removal in Scripps Canyon head (Shepard 1951, Chamberlain 1964, Dill 1964, Shepard and Dill 1966). Microbial decomposition of this buried plant material lubricates layers of sediment fill by producing pore gasses such as methane (Rhoads and Boyer 1982, Aller 1982, Coleman and Prior 1988). Whelan et al. (1976) found that sediment sheer strength was decreased in areas with high concentrations of this gas. Also, layers of intertwined plant material provide lateral strength (Dill 1964, Shepard and Dill 1966), which promotes more decomposition by holding the fill in place. The eventual result of this combination of lubrication and reinforcement is that the bulk of this increasingly unstable, agglomerated fill moves as a single unit when triggered by storm events (Emery and Hulsemann 1963, Shepard and Dill 1966).

A more comprehensive model of canyon-head flushing emerged when Inman et al. (1976) showed that surface waves and high onshore winds caused strong down-axis currents in a shallow zone of Scripps Canyon. In this scenario, onshore wind or waves pile-up less water over the steeper canyon head than along the adjacent shoreline creating converging pressure gradients and alongshore currents. High incident waves create increasingly intense down-canyon pulses of water that become sustained when combined with converging currents and suspended sediment (*also see* Shepard et al. 1975). During a typical Monterey Bay storm, alongshore currents converge at the head of Monterey Canyon (Weigel 1964, *and* personal observations), creating a net down-canyon flow when wind is onshore (Gatje and Pizinger 1965). A contention of Inman et al. (1976), that this flushing mechanism occurs generally in submarine canyons, is supported by the evidence and descriptions here.

The Loma Prieta earthquake provided a test for the canyon-flushing model in addition to providing an opportunity to study benthic community effects of earthquake-induced slumping. This earthquake (magnitude 7.1) did not trigger flushing of the unstable axis-fill, even though it was locally powerful enough to destroy the nearby marine-lab buildings and cause extensive liquefaction of other sediments both onshore and offshore of Moss Landing (Greene et al. 1991, personal observations). Axis-fill was presumably ready to give way; flushing likely occurred just 20 days after the earthquake during the storm wave event of 3 November 1989 (daily maximum wave height = 1.79 m). Instead, I observed that a number of small sediment slumps were triggered on the high walls of the 15 m deep bench. The physical changes created by the earthquake in the shallow canyon head were apparently much less severe than storm flushing. On the deeper walls of Monterey Canyon (to 100 m), many new scarps and slumps were observed after the earthquake (Schwing et al. 1990, Greene et al. 1991), and there is some evidence that this deeper wall sliding triggered down-axis flows in that zone (Garfield et al. in prep.). Still, the timing of the observed axis deepenings in Monterey Canyon's shallow head corresponded to high waves and wind, not to earthquakes, seismic sea waves (Schwing et al. 1990), high precipitation (USNOAA climatological data), or extreme tidal exchange (Broenkow and Reeves unpublished data).

Earthquakes are widely recognized as a trigger for mass wasting on continental margins (Barnard 1978, Hampton and Bouma 1978, Karlsrud and Edgers 1980, von Huene and Arthur 1982, Carlson et al. 1982, Stow et al. 1984, Coleman and Prior 1988, Klaus and Taylor 1991). Others recognize that earthquakes trigger mass wasting on canyon walls, but not mass-movements of the accumulated fill in shallow axes (Shepard 1951, Chamberlain 1964, Shepard and Dill 1966, Shepard and Marshall 1978). Shepard (1951) attributed a massive slump on the wall of Scripps Canyon to an earthquake that shook La Jolla, but mass-movements of axis fill in Scripps Canyon were triggered by storms and not earthquakes (Emery and Huslemann 1963, Shepard and Dill 1966). These findings are intriguing because axis fill can be unstable, and because earthquake induced failures can occur on very low-angle slopes in other settings. For example, Field et al. (1982) concluded that an earthquake caused a 20 km long sediment flow on a river delta slope of 0.25° (*see also* Prior and Coleman 1978). Earthquake-induced mass-sidewall-slumping is discussed by Klaus and Taylor (1991) as a mechanism for widening and branching of a canyon, only after it is formed and deepened by pervasive types of mass wasting. Shepard and Marshall (1978) re-assert that turbidity flows in shallow canyon heads result from onshore storms and high swell, and that there is no evidence that they are triggered by earthquakes.

Storm-induced currents remain the most reasonable explanation for sediment movement in shallow west-coast canyon heads (Chamberlain's 1964 data, Shepard and Marshall 1973, Shepard et al. 1974 and 1975, Inman et al. 1976, Baker and Hickey 1986). Internal waves may be the major mechanism for re-suspending sediment in east-coast submarine canyons, which do not extend to within 85 km of shore or above 90 m depth (Keller and Shepard 1978, Gardner 1989, *but see* Lavelle et al. 1975, *and* Hotchkiss and Wunsch 1982). And, in deep zones of Monterey and other west-coast canyons it is likely that internal waves re-suspend sediment continually (Shea and Broenkow 1982, Breaker and Broenkow 1989, Heard 1992). Thus, internal waves should not be separated from any hydrographic event in submarine canyons. However, it is unlikely that continuously present internal waves are responsible for such discrete events as shallow axis flushing, since their periodicity and amplitude is controlled by tides, and extreme tidal exchange did not coincide with axis flushing (Broenkow and Reaves unpublished data).

When Inman et al. (1976) solidified the storm-flushing model, they separated submarine canyons into a shallow zone, where currents are influenced by surface waves and wind, and a deeper zone, where currents are influenced by internal waves and regional currents (*also see* Hotchkiss and Wunch 1982). More recent findings by Baker and Hickey (1986) and Hickey et al. (1986) conform to this model. They found that sediment from storm re-suspensions in two shallow canyon heads created nepheloid layers that detached from the slope at mid-depths rather than continuing as deep turbidity flows.

CONCLUSIONS

The data in this study indicate considerable monthly fluctuation of benthic macrofauna during one year at a station in the axis of Monterey Canyon, which was observed to undergo seasonal sediment flushing. The densities of opportunistic polychaetes, *Capitella* spp. and *A. brevis,* and the crustacean *O. pacifica,* increased then rapidly declined after the presumed date of flushing. The data also indicate that assemblages at the apparently less disturbed sloping-wall and axis stations fluctuated less, harbored less opportunists, more species, longer-lived species, and larger individuals. Axis flushing disturbances may largely account for the biological differences presented herein. However, neither causation nor correlation was established between axis flushing and changes in benthos, due to the nature of the Monterey Canyon setting and to the limited measurements of sediment disturbance. Also, other factors like sunken drift algae may be as much, or more, of an influence on the benthic community than axis flushing. Slumping caused by the Loma Prieta earthquake briefly influenced benthic community structure, reducing densities of most groups and apparently allowing larval recruitment of another opportunistic polychaete, *P. pygmaea.* However, the earthquake did not trigger expected axis flushing. Finally, the observations and data in this study not only contributed biological information to existing geological and physical knowledge of submarine canyons, but they also strengthened the generality of the Shepard-Inman model of sediment flushing in canyon heads.

Surely, physical disturbances that influence benthic community structure are everywhere on the continental margin. I looked only at the shallow heads of submarine canyons because the processes there are the most tractable. The ecological implications of mass wasting processes are probably very different in deeper water. In fact, the implications of canyon head flushing may have little relevance to mass wasting in general because of the enormous ranges of type, scale, and regime of sea-floor disturbance on continental margins. Nevertheless, the only ecological model of mass wasting we now have is from the heads of submarine canyons.

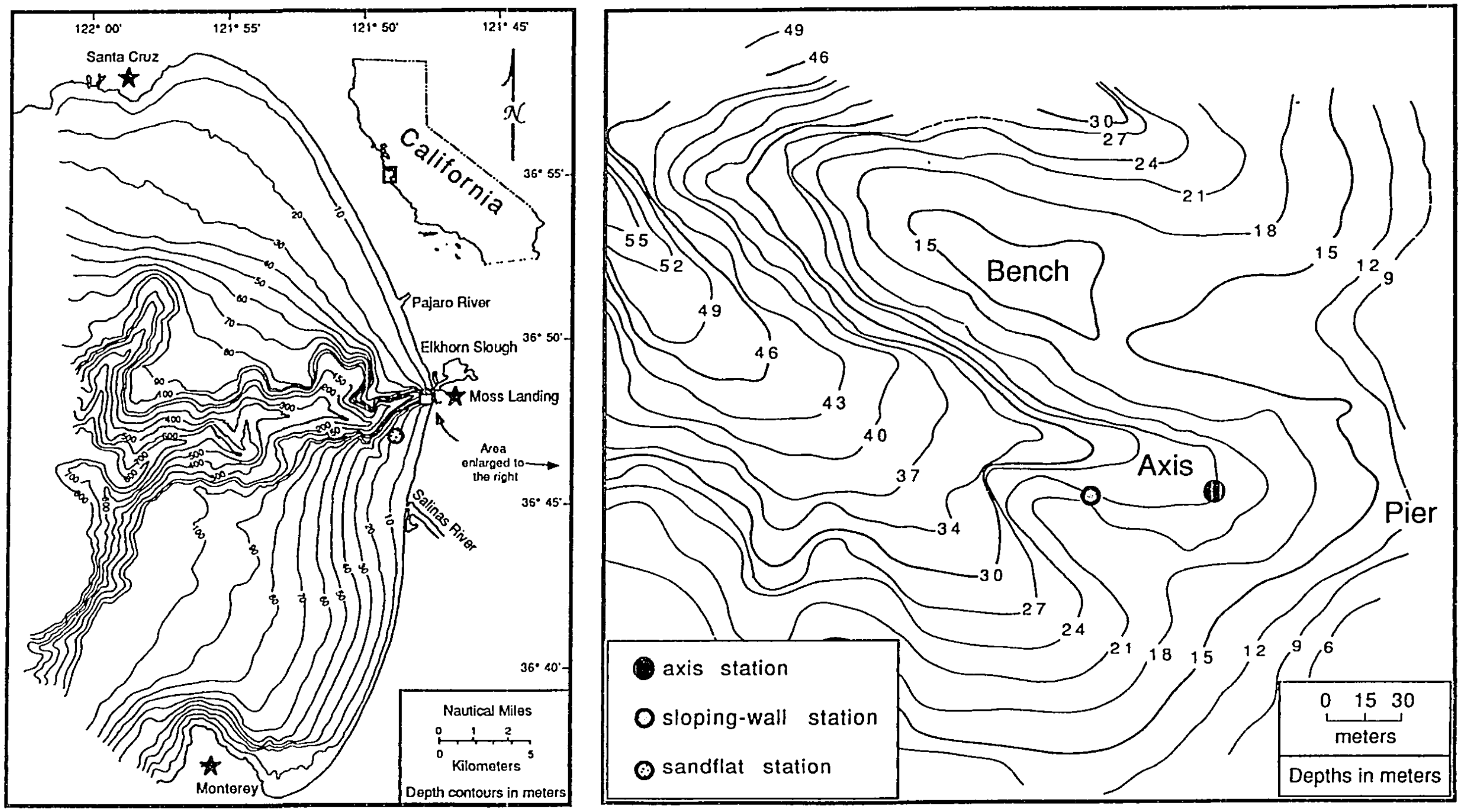

Fig. 1. Location of study area and axis, wall, and sandflat stations (dots). The Monterey Bay bathymetry is from NOAA chart N365121W, N365122W. Canyon head bathymetry was surveyed and plotted with the aid of Scientific Services, inc.

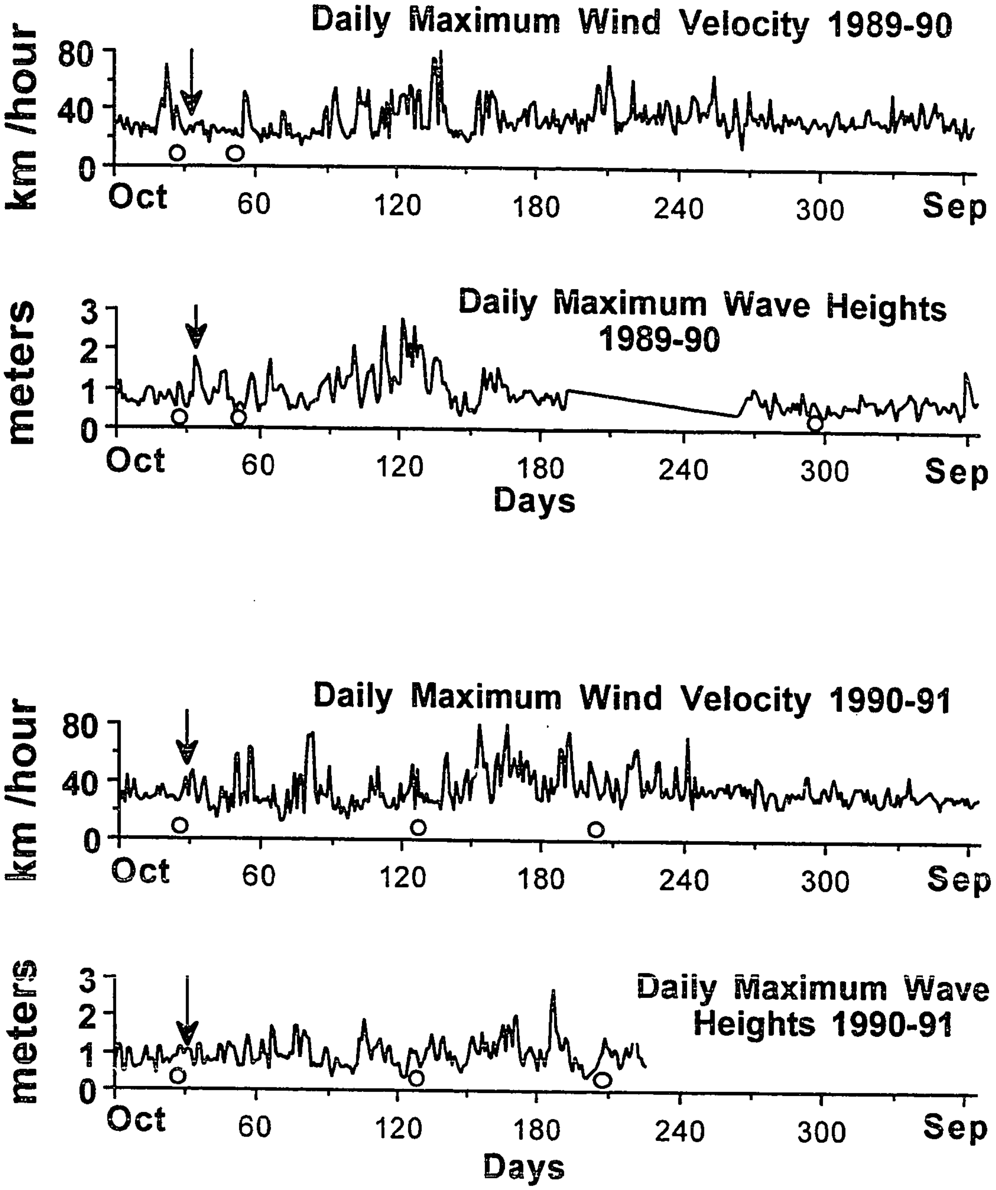

Fig. 2. Daily maximum wind velocities and daily maximum wave heights from October 1989 to May 1991, during which sediment sampling (denoted by hollow circles*) occurred. The upper solid arrow denotes inferred timing of 1989 flushing based on diver observations; the lower two denote timing of the observed flushing in 1990. Years begin in October for purposes of later presentation. Courtesy of Broenkow and Reaves (unpublished data). *See Table 1 for results of sediment analyses.

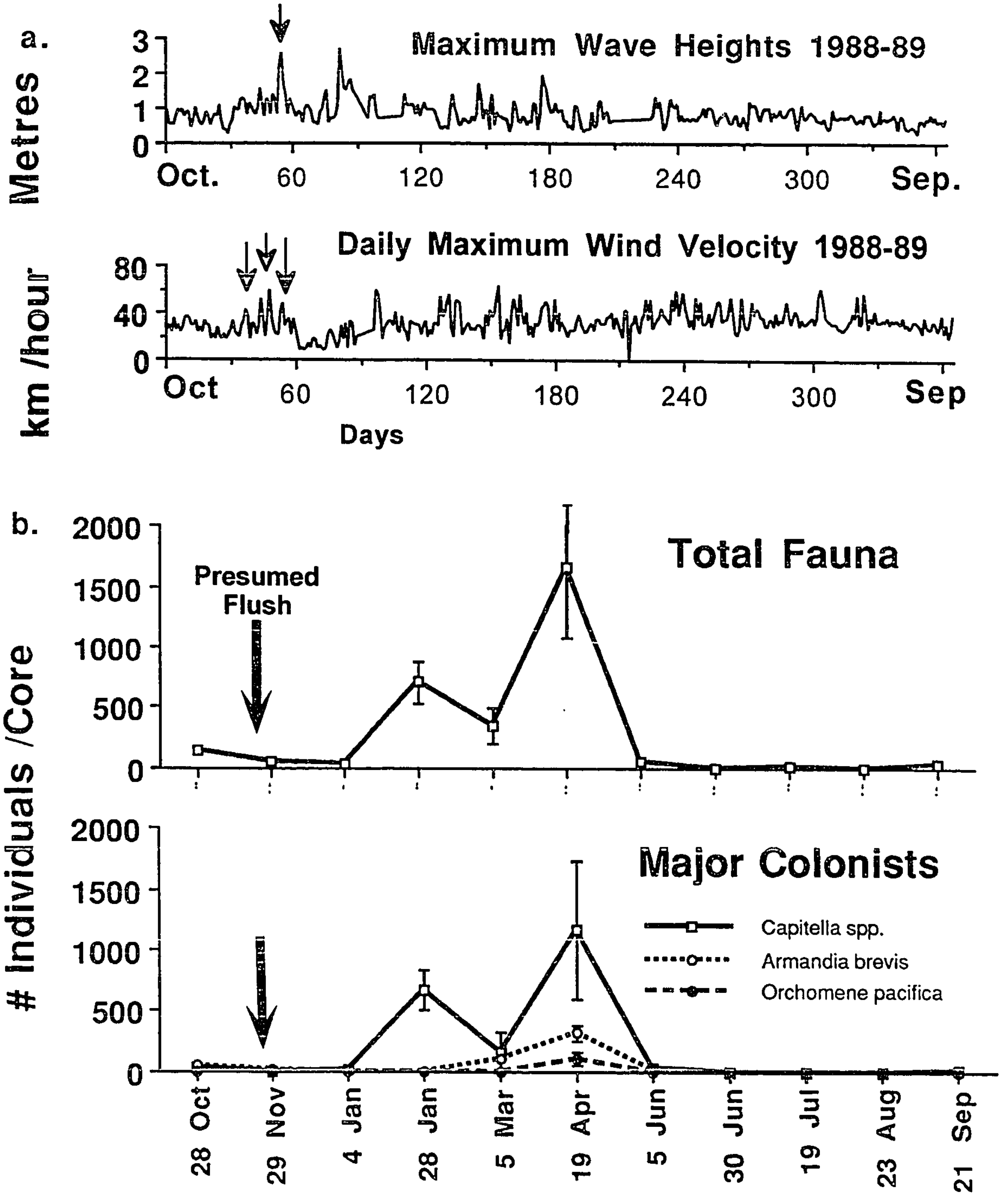

Fig. 3. Daily maximum wind velocities and daily maximum wave heights from October 1988 to September 1989 (a.), and changes in abundances of total fauna and the numerically dominant species at a 24 m deep station in the axis of Monterey Canyon (b.). Mean number of individuals per 120 cm^2 core ± standard error ($n = 6$ cores per datum).

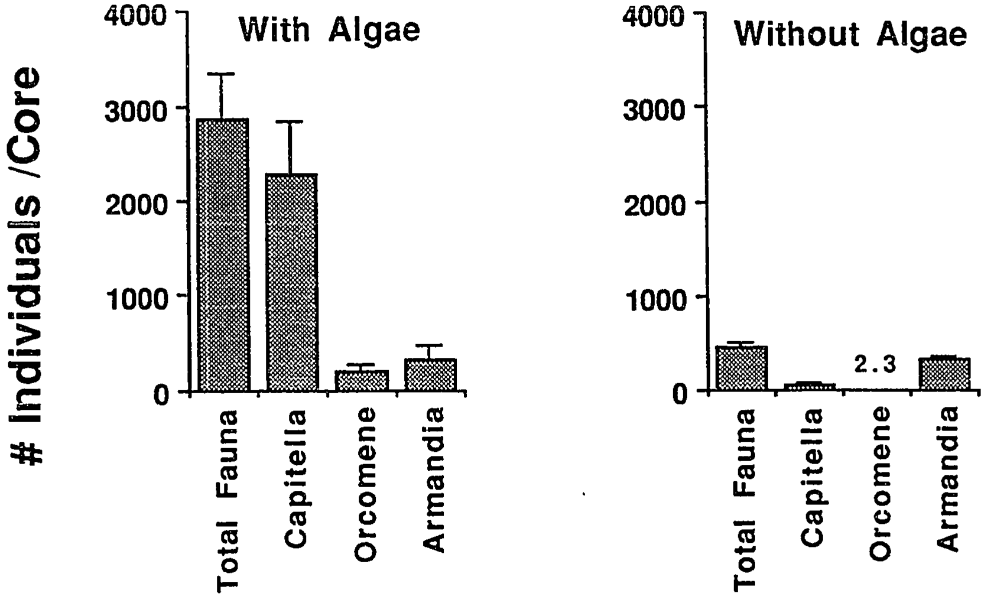

Fig. 4. Differences in total fauna and numerically dominant species between cores which contained *Enteromorpha* sp. and those which contained no algae. Mean number of individuals per 120 cm^2 core ± standard error ($n = 3$). From the six cores taken from the 24 m axis station on 19 April 1989.

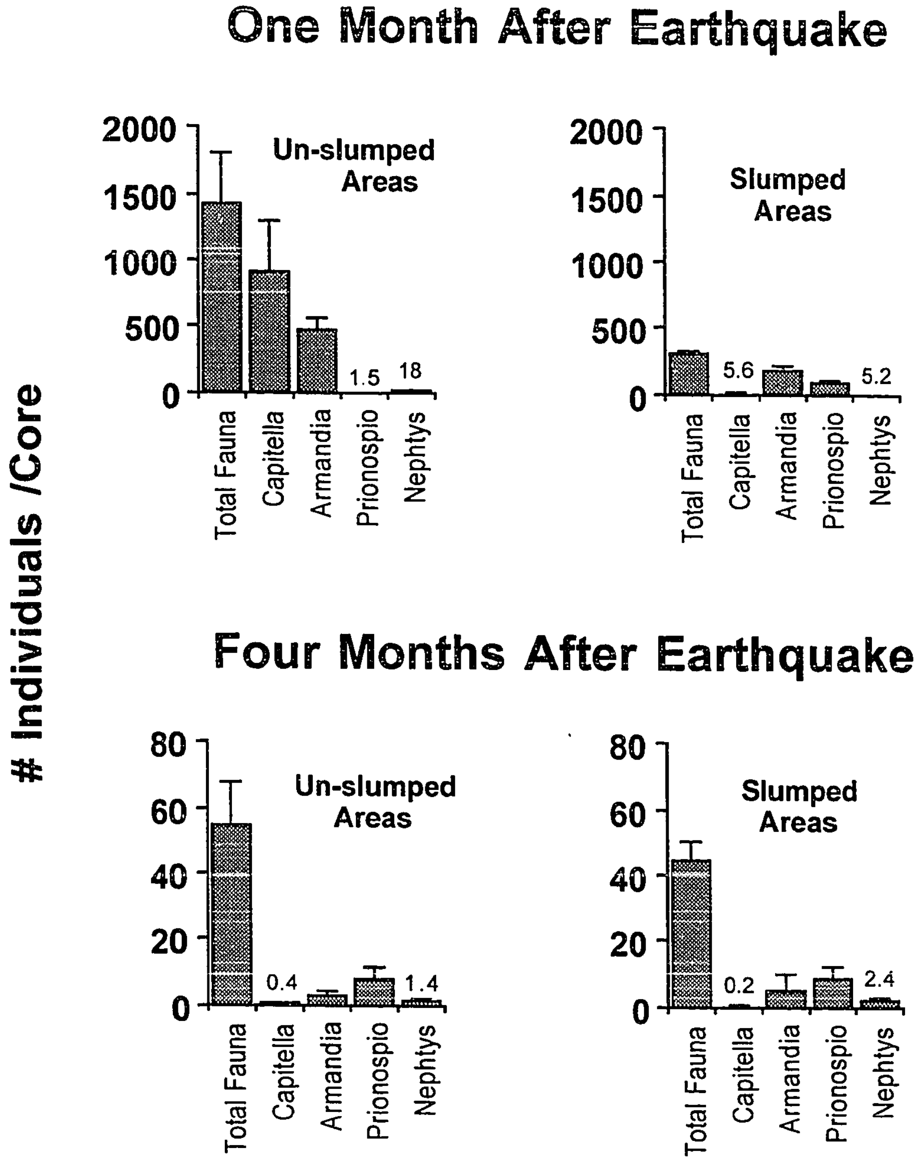

Fig. 5. Changes in abundances of total fauna and the numerically dominant species in slumps that were triggered by the 17 October 1989 Loma Prieta earthquake. Patterns in these slumps were the same as background assemblages by February, after winter storms. Mean number of individuals per 120 cm^2 core ± standard error (n = 5 cores per datum).

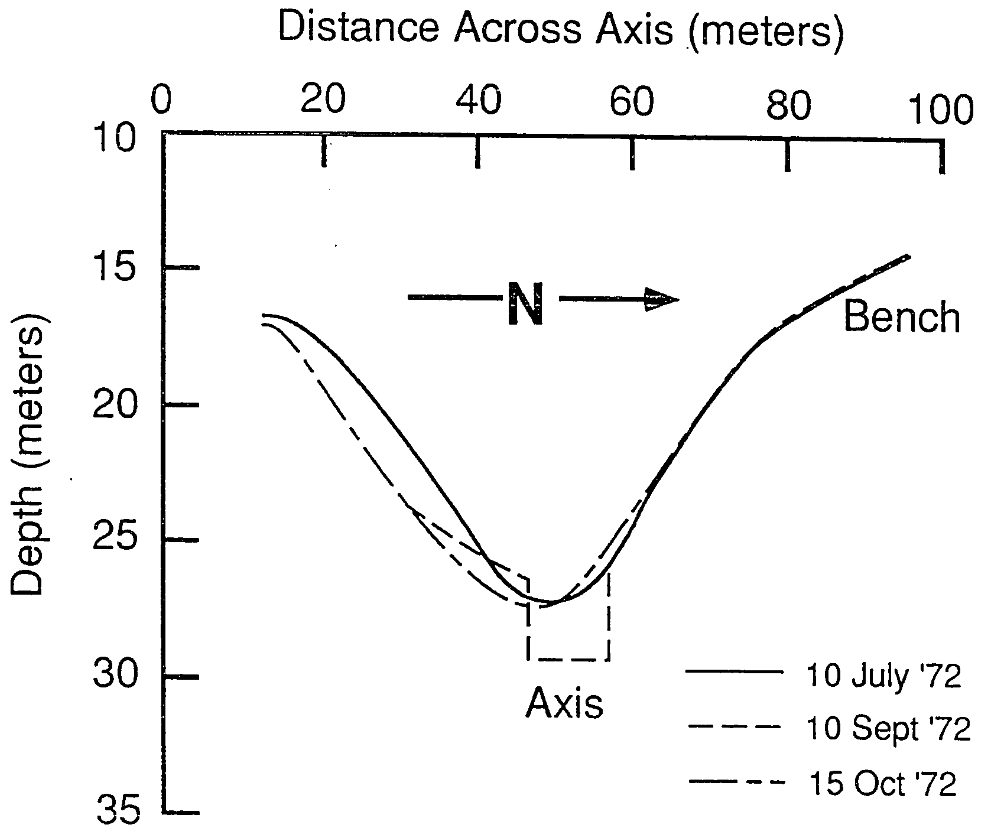

Fig. 6. Topographic changes in the south axis of Monterey Canyon in the fall of 1972 (Oliver and Slattery unpublished data).

Table 1. Differences in sediment characteristics at the 24 m-deep axis station before and after sediment flushing events of November 1989 and 31 October 90. Comparisons are provided from sloping wall and sandflat stations, which did not undergo severe flushing. Sorting coefficient is a measure of grain size distribution; a small value indicates less variation in size (Folk and Ward 1958).

	1 Nov '89		22 Nov '89	25 July '90	28 Oct '90		11 Feb '91	26 Apr '91
Axis		Presumed Flush →				Presumed Flush →		
% coarse sand	1.0		29.9	1.1	0.8		3.4	0.9
% sand	96.4		98.6	100.0	56.7		95.3	57.9
mean grain size (mm)	0.16		0.29	0.18	0.05		0.17	0.05
sorting coeficient (mm)	0.71		0.66	0.74	0.37		0.63	0.25
Sloping Wall								
% coarse sand	0.3		0.3	0.3	0.2		0.3	0.0
% sand	86.5		85.3	96.7	89.4		95.4	46.1
mean grain size (mm)	0.12		0.12	0.14	0.12		0.14	0.03
sorting coeficient (mm)	0.48		0.46	0.72	0.54		0.69	0.23
Sandflat								
% coarse sand	no data		no data	0.4	0.1		0.2	0.6
% sand	no data		no data	89.6	86.4		92.0	92.0
mean grain size (mm)	no data		no data	0.10	0.09		0.10	0.10
sorting coeficient (mm)	no data		no data	0.68	0.61		0.62	0.66

Table 2. Changes in abundances of major groups at three stations (all 24 m depth) in Monterey Canyon habitats: axis, sloping wall, and sandflat. Mean number of individuals per 120 cm 2 core ± standard error (n = 6 cores per datum).

	28 October '88	28 January '89	19 April '89	19 July '89
Canyon Axis				
Total Fauna	140.0 ± 32.9	33.5 ± 6.4	1657.5 ± 582.5	17.4 ± 3.5
Polychaetes	129.0 ± 33.5	29.5 ± 6.9	1524.8 ± 525.9	11.2 ± 2.0
Crustaceans	4.8 ± 2.4	3.0 ± 0.6	120.5 ± 56.0	4.6 ± 1.4
Species	14.2 ± 1.8	9.8 ± 0.7	19.3 ± 1.8	7.4 ± 0.5
Biomass (g wet wt.)	0.26 ± 0.16	0.38 ± 0.09	3.70 ± 1.60	0.05 ± 0.01
Sloping Wall				
Total Fauna	88.8 ± 8.7	69.6 ± 5.4	364.0 ± 38.3	72.2 ± 11.7
Polychaetes	77.2 ± 6.5	59.4 ± 4.9	348.3 ± 36.1	58.3 ± 8.6
Crustaceans	0.7 ± 0.4	5.0 ± 0.8	2.7 ± 1.2	4.0 ± 1.0
Species	19.8 ± 1.1	12.4 ± 1.0	23.2 ± 1.7	19.5 ± 2.7
Biomass (g wet wt.)	0.96 ± 0.16	0.15 ± 0.07	2.46 ± 1.01	1.79 ± 0.58
Sandflat				
Total Fauna	157.0 ± 10.6	69.3 ± 18.1	97.8 ± 7.5	69.7 ± 7.8
Polychaetes	92.3 ± 10.9	40.3 ± 9.8	78.7 ± 6.6	49.8 ± 6.3
Crustaceans	7.2 ± 3.6	10.3 ± 4.4	7.2 ± 0.8	9.0 ± 2.9
Species	25.5 ± 10.4	21.2 ± 2.7	30.2 ± 1.4	23.7 ± 2.2
Biomass (g wet wt.)	0.50 ± 0.17	0.83 ± 0.36	0.48 ± 0.20	0.42 ± 0.07

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Chapter 2

BENTHIC COMMUNITY RESPONSES TO SUNKEN DRIFT ALGAE IN MONTEREY CANYON HEAD

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Abstract: The shallow heads of submarine canyons are catchments of sediment and organic material as well as avenues for the transport of such material to deep water. Comparative sampling and field experiments revealed that accumulations of sunken drift-algae were a major influence on the abundance and distribution of benthic macrofauna in Monterey Canyon's axis. Crustaceans and polychaetes in sunken drift algae attained high densities ($5 \cdot 10^5$ per m^2), but these two taxonomic groups exhibited opposite seasonal, habitat, and colonization patterns. Naturally-occurring patches of sunken drift-algae were numerically dominated by motile crustaceans in the spring, and by an enrichment polychaete, *Capitella* spp., in the fall. Motile amphipods responded rapidly (< 5 days), and abundantly, to experimental patches of the alga *Enteromorpha* spp. in all four seasons, but not to *Macrocystis pyrifera* treatments. No significant cage effect was demonstrated. Statistical differences in crustacean abundances were detected between *Enteromorpha* spp. and control treatments, but not among habitats or seasons. In contrast, polychaetes were abundant only in particular habitats and seasons; most did not colonize drift algae. Emergence-trap sampling indicated habitat, depth, and seasonal trends in swarming crustaceans, even though the statistical resolution of the algal experiments was not adequate to detect such crustacean patterns. Accumulations of sunken drift algae contribute to the disturbance regime in the head of Monterey Canyon by disrupting community structure, changing habitat characteristics, and providing resources. Contrasting abundance patterns of polychaetes and crustaceans likely reflect differences in mobility and life-history.

INTRODUCTION

Sunken drift vegetation provides food and refuge for animals living in, on, or above the sea floor (Moore 1963, Gore et al. 1981, Hacker and Steneck 1990, Duffy and Hay 1991). Such vegetation influences the abundance and biomass of benthic fauna, and faunal distribution in time and space (Kleiver 1976, Wolff 1979, Gore et al. 1981, Bedford and Moore 1984, Josselyn et al. 1983, Levin and Smith 1984, Suchanek et al. 1985, Thrush 1986, Grassle and Morse-Porteous 1987, Virnstein and Howard 1987). Nekton falls have a similar effect (Smith 1985a, Smith 1986, Smith et al. 1989). Deposition of drift vegetation acts as a biogenic disturbance by disrupting the structure of benthic communities and changing resources as well as the physical and chemical environment (Thrush 1986, Grassle and Morse-Porteous 1987, Smith and Brumsuckle 1989). Interestingly, Pearson and Rosenberg (1978) found that most of the macrofaunal species responding to organic enrichment also responded to types of sediment disturbance where enrichment was not present. But a few ubiquitous species, including the polychaete *Capitella* spp., were identified specifically as enrichment species. Grassle and Grassle (1974) attribute this species' success at exploiting organic enrichment to its opportunistic life-history and its short-term genetic selection. Pearson and Rosenberg (1978) consider organic input to be one of the main causes of faunal change in nearshore benthic environments, and they conclude that a highly predictable gradient of faunal change exists in both time and space in relation to natural and anthropogenic enrichment.

Kelp forests and estuaries are conspicuous locations of plant production and export along coasts. Historically, estuaries have received the highest productivity ranking among ecosystems (Teal and Teal 1969). Large amounts of estuarine and terrestrial plant material flow into the ocean with tidal and lotic currents. More recently, several estimates establish kelp forests as the most productive ecosystem (Mann 1973, Estes et al. 1974, Duggins

1980, Mann 1982, Foster and Schiel 1985). Using areal photographs and extrapolations from Gerard's (1976) drift-algae estimates, Harrold and Lisin (1989) estimated that at least 130,000 tons of drift algae are exported yearly from the kelp forests of Monterey Peninsula. Most kelp forest algae are detached during storms (Kitching 1937, Johnston 1971, Bedford and Moore 1984, Ebeling et al. 1985, Thrush 1986, Tegner and Dayton 1987, Seymour et al. 1989). Much of the estuarine and kelp forest vegetation lingers on the continental shelf where variations in bathymetry, hydrography, and coastal production determine its temporal and spatial distribution. Even the small proportion of this material that makes it to the deep-sea floor is widely distributed (Moore 1963, Menzies et al. 1973, Wolff 1976, Menzies and Rowe 1979, Wolff 1979).

Submarine canyons are avenues for the transport of drift vegetation into deeper water (Emery and Hulsemann 1963, Chamberlain 1964, Shepard and Dill 1966, Cailliet and Lea 1977, Josselyn et al. 1983). But also, nearshore canyon heads are natural catchments where non-transported drift accumulates (Chamberlain 1964, Dill 1964, Shepard and Dill 1966). Zobell (1959) estimated—by measuring changes in topography—that during a single two day storm, 400 m^3 of drift seaweeds were deposited in Scripps Canyon head.

Macrofaunal communities are virtually unexplored in submarine canyons. Furthermore, there are few published studies of macrofaunal utilization of drift-algae in protected subtidal settings (Muus 1967, Bedford and Moore 1984, Thrush 1986, Hull 1987), and, to my knowledge, none in the exposed subtidal.

The head of Monterey Canyon is nearly adjacent to the mouth of Elkhorn Slough—a seasonal estuary that is a source of drifting macroalgae (personal observation). Kelp forests located 20 km away, north and south of the canyon head, are also a source of drift-algae (Fig. 1). Longshore currents, laden with drift-algae, often converge at the canyon head (Wiegel 1964, Gatje and Pizinger 1965, Inman et al. 1976, personal observation).

Sunken drift-algae in the canyon's axis influences the abundance and distribution of macrofauna. I found high densities of benthic macrofauna (2,867 individuals per 120 cm^2 core ± 480 S.E.) in *Enteromorpha* spp. patches, and significantly fewer (448 ± 57 S.E.) away from algae (Chapter 1, Fig. 4). This was not terribly surprising in light of Thrush's (1986) demonstration that sunken drift algae influenced the spatial distribution of benthic macrofauna in Lough Hyne, Ireland, and the other literature cited above. But, I also observed that physical conditions in the Monterey Canyon varied on seasonal and other scales, as did the presence of different categories of drift algae. Bedford and Moore (1984) showed that benthic macrofauna in sunken drift algae fluctuated seasonally, peaking in the late-fall/early-winter and declining in the summer. Thrush (1986) documented short term macrofaunal changes in patches of laminarian algae newly arrived on the floor of Lough Hyne; certain species increased while others decreased. Hull (1987) also documented opposite numerical responses to an alga (*Enteromorpha* spp.) by different species. Zimmerman et al. (1979), Hacker and Steneck (1990), Duffy and Hay (1991), and Denton and Chapman (1991) have all demonstrated preferential orientation, by phytal amphipods, to particular algal species or morphologies.

The above observations and literature review led to the following general hypotheses: (1) Abundances of macrofauna in drift algae are seasonally variable in Monterey Canyon's axis, (2) Different macrofaunal species, or guilds, have different numerical responses to drift algae there, (3) Different types of algae elicit different responses by macrofauna in Monterey Canyon, and, (4) Colonization of experimental algal patches differs among species, among seasons, between short-term sampling dates, and among Monterey Canyon habitats.

METHODS

Study location and drift-algae

Sampling and experimental stations were located in the southern branch of the canyon head, on the adjacent beach, on the sandflat south of the canyon head, and in the deeper axis of the canyon (Fig. 1). Most of the observations, sampling, and manipulations were carried out by divers using SCUBA (over 200 dives). All depth measurements are relative to MLLW.

To provide an example of the spatial distribution and percent cover of macroalgae in the axis, patch lengths of each species were recorded along a 50 m transect tape that was placed along the axis at depths between 9 m and 27 m. This axis survey was done only once, on 21 June 1990. Because the relative abundance of a macroalgal species in the axis generally coincided with its relative abundance on the adjacent beach (personal observation), changes in abundances of each prominent species were monitored on the beach to provide an indication of the temporal distribution of drift algae in the axis. On each of sixteen biweekly beach-sampling dates from February through September of 1990, ten 2 m^2 quadrats were placed randomly along a permanent 100 m transect line parallel to the shoreline. The center of each quadrat was then placed at the center of the drift-algae strand line, by aligning with its general course along the beach. The percent cover of each alga in each quadrat was visually estimated. Measurements and observations of beach algae were made concurrently with observations of algae in the canyon axis whenever possible. Sediment burial of algae-patches in the axis was also noted.

Community structure

General protocol - Benthic macro-invertebrates were sampled with diver-operated, sharpened corers inserted through benthic algae and ~8 cm into the substratum. Core area was 120 cm^2 except where high densities of invertebrates called for smaller core sizes (75 cm^2 or 24 cm^2). In these cases, raw data were converted to density per 120 cm^2. Samples were washed over a 0.5 mm screen, preserved in 4% formaldehyde solution and later transferred to 40% isopropyl alcohol. Macrofauna (46,754 total individuals) were separated from sediment and debris, identified to species, and counted. Notes were also made of mega-invertebrates, fishes, birds, and mammals associated with drift algae or experimental structures.

General taxonomic categories, biomass, and the ten to fifteen most abundant species were then considered for hypothesis testing in each experiment or comparison. Normality was not tested because of small sample sizes; data were assumed to have normal frequency distributions. Occasional departures from normality probably did not bias tests because analysis of variance is known to be extremely robust with respect to such departures (Underwood 1981). Homogeneity of variances was tested with F-tests and Cochran's tests (Underwood 1981, Day and Quinn 1989). Square-root transformations were used only in cases where heterogeneity of variances was detected (Underwood 1981). Results from square-root (x+1) transformations were favored over square-root (x) transformations only in cases where many zeros were present (Underwood 1981; p. 537), and when it made the difference between homo- and heteroscedasticity. Nonparametric tests were used with the original data if they remained heteroscedastic after transformations. In general, parametric statistics were used only when sample sizes were equal or near equal and when the assumption of homogeneity of variances was not severely violated (> 30 % above Cochran's critical value). In the typical comparison most taxonomic categories were analyzed with ANOVA and only a few with their non-parametric equivalents. All factors were considered to be fixed (model-one tests). In this paper the word *significant* refers to differences that are both statistically significant and biologically important. Other differences are mentioned because they are considered biologically important, though the design may have been inadequate to show statistically significant differences. Methods specific to each hypothesis are included in the following sections.

Seasonal variations in natural alga-patch fauna - Naturally-occurring patches of drift-algae in Monterey Canyon's axis were core-sampled on quarterly sampling dates from May 1990 to February 1991 at depths between 24 m and 30 m. Because of low visibility, the ephemeral nature of patches, and patch-marking constraints, each patch was opportunistically sampled as it was discovered on each of the four dates. Macrofauna abundances were compared using Kruskal-Wallis tests followed by Games-Howell tests.

Algae experiments

The overall experimental design addressed short-term population responses of benthic macrofauna to sunken patches of different alga species. These responses were compared among four seasons, and three habitats. Algae were collected from a Monterey kelp forest and an Elkhorn Slough mudflat; they were sunken to the offshore substratum and placed in separate corral-structures. The circular 0.25 m^2 corrals were constructed of 'two-squares per inch' wire mesh, with anchor legs of reinforcement bar. The anchor legs were implanted in the sediment so that the bottom of the corral wall reached ~3 cm below the substratum (Fig. 7). After algae were added to the corrals *in situ,* the corrals were covered with removable mesh lids. A single core was taken from each corral treatment and control both five and 19 days after emplacement of algae. Non-independence effects of the day-19 sample from the day-5 sample were reduced by taking the samples from opposite sides of corrals.

Spring algae experiment - To test the null hypothesis that there was no difference in species density among four alga-patch treatments placed 7 May 1990, samples from *Enteromorpha spp, M. pyrifera*, empty-corral, and no-corral treatments in 21 m deep hanging channels were compared after 5 and 19 days using randomized block one-factor ANOVAs (hanging channels are tributaries that terminate on the high canyon walls over the deeper canyon axis, like hanging glacial valleys). Treatments were blocked together in each of the four separate channels; their relative position within each channel was randomly assigned. These channels are located near the end of the 15 m deep bench that separates the south branch of the canyon head from the middle and north branches. A single 120 cm^2 faunal-core was taken from within the two filled corrals, from the empty-corral, and away from the corrals. This was repeated in each channel so that samples totaled 16 per date. To minimize the effects of temporal non-independence, samples were taken from the right side of the corral treatments on day-5 and from the left side on day-19. Overall, (32) samples were taken in the spring experiment: (1) sample per corral, (4) corral treatments per block (channel), (4) blocks per date, and (2) dates.

These randomized block, one-factor ANOVAs were also used to evaluate the similarity of the four channels following the protocol of Sokal and Rohlf (1981; pages 344-354). Friedman's tests were used when data were heteroscedastic. Tukey tests were used to test for differences between pairs of treatment means after the ANOVAs.

Alga experiments at four times during the year - To test the null hypotheses that there were no differences in macrofaunal density at four different times during the year, or between *Enteromorpha* spp. and empty-corral treatments, the above experiment was repeated in June and September of 1990 and February of 1991. Treatments were reduced to *Enteromorpha* spp. and empty-corrals only, because the spring experiment demonstrated no cage effects and little faunal response to *M. pyrifera*. Corrals were sampled after five days in June, September, and February to compare with the day-5 samples from May. Overall, (32) samples would be used in the "seasonal" experiment: (1) sample per corral, (2) corral treatments per block (channel), (4) blocks per date, and (4) dates. The factors season and alga-treatment were tested with two-factor ANOVAs followed by protected Tukey tests. When data were heterogeneous, non-parametric, two factor ANOVAs (Zar 1984) were followed by Games-Howell tests.

The September experiment was also sampled on day-19 to provide a fall complement of the time component of the spring experiment. (32) samples would also be used for this comparison: (1) sample per corral, (2) corral treatments per block (channel), (4) blocks per date, (2) dates per season, and (2) seasons. Two-factor, repeated-measures ANOVAs were used to compare macrofauna abundances between *Enteromorpha spp.* and empty corral treatments and between day-5 and day-19 (repeated measure) sampling dates. Spring and fall experiments were analyzed separately and the results were then compared.

Alga experiment in different habitats - To test the null hypotheses that there were no numerical differences in macrofaunal colonization at the three habitats, day-5 samples from the June 1990 *Enteromorpha* spp. and empty-corral treatments in 21 m channels were compared with concurrent experimental samples from the 21 m-deep sandflat (*n* = 4) and the 30 m-deep canyon axis (*n* = 3). In this experiment (24) samples would be used: (1) sample per corral, (2) corral treatments per pair, (4) pairs of treatments per habitat, (3) habitats. The factors habitat and alga-treatment were tested using two-factor ANOVAs with unequal replication (only three pairs were sampled in the axis). These were followed by planned, single degrees of freedom, orthogonal contrasts because macrofauna were expected to be more abundant at the axis station than at the other two comparisons

(Day and Quinn 1989). Non-parametric, two factor ANOVAs were used when variances were heterogeneous. In appropriate cases, missing data were estimated using the protocol of Shearer (1973, *in* Zar 1984; p. 216).

Distribution study of swarming crustaceans - *Orchomene pacifica,* a swarming gammarid amphipod, was found to colonize patches of *Enteromorpha* spp. during sampling in the spring of 1989, indicating seasonal and habitat orientation (Chapter 1). However, because statistical tests in the current study did not show that crustaceans were oriented to seasons or habitats (*see* results), a distribution study was initiated to clarify and elucidate crustacean distribution and sources around Monterey Canyon head. Seasonal, habitat, and depth distributions of swarming-crustaceans were investigated using non-baited emergence trap sampling. These emergence traps were upside-down plastic waste cans, with upside-down funnels affixed within, placed .5 m above the bottom with their 350 cm^2 circular openings facing downward (Fig. 7). Triplicate arrays of these traps were placed in the main axis at depths of 30 m, 100 m, 300 m, and 500 m, the nearby sandflat at 21 m, and one trap was placed at 21 m in each of three separate hanging channels. This sampling took place in the fall of 1990 and in the spring of 1991. Each deployment spanned 48 hours. Shallow traps were deployed by divers. Deep sampling was accomplished by lowering trap arrays from the Moss Landing Marine Laboratories research vessels, *Point Sur* and *Ed Ricketts.* In these cases steel beams supported traps above each corner of buoyed triangular steel plates (Fig. 7).

RESULTS

Drift algae

Drift algae patches of different sizes and species composition accumulated in the shallow canyon axis. In the survey of 21 June 90, a total of 12 algae-patches covered 43% of the line under the transect tape. Patch lengths ranged from 0.1 to 3.6 m (x = 1.8 m ± 0.6 standard error). Six patches of mixed algae covered 29% of the line (x = 2.4 m ± 0.9 S.E.). Of these, five contained *M. pyrifera*, five contained *Enteromorpha* spp., one contained *Ulva* spp, and one contained other kelp forest algae. Four *Ulva* -only patches covered 7% of the line (x = 0.9 m ± 0.7 S.E.); one 3.6 m *Enteromorpha* spp. patch covered 7% of the line; and one 0.3 m *M. pyrifera* patch covered <1% of the line. This summer transect is presented as an example of spatial heterogeneity and to show the variety of algae types present at a given time.

Qualitative observations indicated that plant species composition and patch sizes varied with time in the shallow axis. *M. pyrifera* and other algae of the kelp forest assemblage appeared mostly during and after fall and winter storms, but often arrived throughout the year. These parcels varied from single blades to clumps up to 3 m in diameter. The arrival of *Enteromorpha* spp. peaked in April and May. This alga was at first more mobile, but by late May and early June, formed discrete and persistent patches in depressions. Most of the *Ulva* spp. arrived in the axis in July or August, often forming a continuous blanket more than a meter thick.

Stranded drift algae on the beach adjacent to the canyon head also varied with time and presumably provided an indicator of changes in alga composition in the shallow axis. There was considerable temporal variability in the type and abundance of drift algae along the strand-line of this beach. Highly significant differences in percent cover among dates were detected for both the *Enteromorpha* spp. and the laminarian algae (Kruskal-Wallis, $k = 16$,

$p < .001$). Along the strand-line, mean cover of *Enteromorpha* spp. ranged from 0.2% to 47.5% among sampling dates. It was most abundant during the 4 June 1990 sampling date, and its grand mean cover was 8.7% ± .94 standard error ($n = 160$ quadrat samples). Mean cover of laminarian algae (mostly *M. pyrifera, Nereocystis leutkeana* and *Egregia menziesii*) ranged from 0.5% to 27.5%, and the grand mean cover was 7.6% ± 1.17 S.E. ($n = 160$). These kelp forest algae were most abundant on 17 March 1990 and 4 August 1990 (late fall and winter were not sampled; these seasons are often the times of highest abundance). *Ulva* spp. was not tested because it was present only on a single date (29 July 1990; 1.9% ± 1.7 S.E.), but it is most abundant during the summer.

The natural patches of sunken drift-algae that were seasonally sampled for fauna consisted mainly of a mixture of kelp forest algae, but patch composition varied somewhat. The brown algae, *M. pyrifera, Cystoseira osmundacea,* and *Egregia menziesii,* made up the bulk of the biomass. They were mixed with a variety of foliose red algae including *Rhodymenia* spp., *Callophyllis* spp., *Prionitis* spp., and *Plocamium cartilagineum.* The green algae *Ulva* spp. and *Enteromorpha* spp., and the marine vascular plant *Phyllospadix* sp. were also present.

Degree of algal burial by sediment was not quantitatively assessed. However, some observations were persistently revealing. By the fall of each year layers of algae had become buried by sediment. Sediment fallout occurred all year round in the canyon head, but it seemed to be highest in the spring and fall. Crustaceans were generally found in the clean parts of the plants that protruded from the sediment, and polychaetes lived in the parts that were semi-incorporated into the sediment.

The dissolved oxygen concentration in the water 2-8 cm above the axis floor at 30 m depth was lowest in the late summer (4.5 mg/l; 19 September 90), when decomposing algae were most abundant, and highest in winter (8.2 mg/l; 16 January 91), when large storms occurred. fall and spring readings were intermediate at 7.3 mg/l on 28 October 90 and 7.4 mg/l on 29 April 91.

Community patterns

Seasonal variations in natural alga-patch fauna - Natural patches of drift algae in the canyon axis were utilized by different groups of benthic invertebrates throughout the year. From spring to fall of 1990, at depths of 24 to 30 m in the axis, crustaceans decreased while polychaetes increased in drift algae. This fall pattern of dense polychaetes and few crustaceans was then reversed by February sampling, after flushing (Fig. 8; *also see* Chapter 1). The spatial importance of sunken drift algae (inside vs. outside of patches) was addressed in Chapter 1.

Significant abundance differences among the four sampling dates were detected in three of the ten crustacean taxa that were tested: the gammarid amphipods *Atylus tridens, Aoroides columbiae,* and *Cancer gracilis* ($p < .05$, Kruskal-Wallis tests; $n = 3$ to 6). *A. tridens* and *C. gracilis* were most abundant in February of 1991. *A. columbiae* was most abundant in June. Significant differences among seasons were not detected in the other seven crustacean taxa, even though considerably fewer were present in October than in other months. However, the leptostracan *Nebalia pugettensis* was most abundant in October (58.1 ± 58.1 S.E. per 120 cm^2); its next most abundant date was in June (1.9 ± 1.9 S.E. per 120 cm^2). Small sample sizes and subsequent high variability for some of these species may have precluded detection of real differences among dates. The two most abundant crustaceans and the two most abundant polychaetes are included with total crustaceans and total polychaetes in Figure (6).

In contrast to the dominant crustacean pattern, significant differences among seasons were detected for all tested polychaete taxa. Total polychaetes were significantly more abundant in October 1990 than either May 1990 or February 1991 ($p < .05$, Games-Howell tests after Kruskal-Wallis tests; $n = 3$ to 6). They were also more abundant in October than in June; this was nearly significant ($.05 < p < .10$). *Capitella* spp. was most abundant in October. *Armandia brevis* and *Platynereis bicanaliculata* were most abundant in June 1990, but *P. bicanaliculata* was also abundant in the oxygen-stressed conditions of October 1990.

Spring algae experiment - Large numbers of crustaceans had colonized experimental patches of *Enteromorpha* spp. by the fifth day after emplacement of algae on the substratum. This did not occur in the *M. pyrifera*, empty corral, or no-corral treatments (Fig. 9). Total fauna was significantly more abundant in the *Enteromorpha* spp. treatment than in any of the other three treatments ($p < .05$, Tukey tests after randomized block, two-factor ANOVA; $n = 4$). This was probably because total numbers of crustaceans were significantly more abundant in the *Enteromorpha* spp. treatment than in either the empty-corral or the no-corral treatments (same tests); abundances of crustaceans in *M. pyrifera* were only slightly elevated over controls. Significant differences among treatments were not detected for total polychaetes.

Statistically significant differences in abundance among the four treatments were detected for most species. Most species were more abundant in the *Enteromorpha* spp. treatment than in the other treatments. They included the gammarid amphipods *Ischyrocerus pelagops*, *A. columbiae* (nearly significant: $p = .053$), *A. tridens*, *Pontogeneia* sp., and the polychaete *Nephtys cornuta* ($p < .05$, randomized block, two-factor ANOVAs, except for *I. pelagops*, and *Pontogeneia* sp. where Friedman's tests were used; $n = 4$).

Two gammarid amphipods, *A. columbiae* and *A. tridens,* colonized the *M. pyrifera* treatment in addition to the *Enteromorpha* spp. treatment, *A. columbiae* were more abundant in *M. pyrifera* than in empty-corral or no-corral treatments. The difference in *A. tridens* abundance between *Enteromorpha* spp. and *M. pyrifera* treatments was not significant, but this species was significantly more abundant in either algae treatment than in the empty or the no-corral treatments ($p < .05$, Tukey tests; $n = 4$).

The polychaete *P. bicanaliculata* was present, but not abundant, in the 18 m-deep channels where the spring experiment took place. They were more abundant in *Enteromorpha* spp. corrals than in the other two corral-treatments, but they were most abundant in no-corral samples. *Capitella* spp., which was found in very high numbers in naturally occurring patches of *Enteromorpha* spp. at the 24 m-deep axis station a year before (Chapter 1), did not colonize any day-5 treatment in this spring experiment.

Total crustacean abundance had decreased in algal corrals by day-19, while total polychaete abundance had increased (Fig. 9, Table 3). Amphipods, and the polychaete *N. cornuta,* had declined in algal corrals while another polychaete, *A. brevis,* had increased in all treatments, excluding the no-corral treatment. Also, *Capitella* spp. had increased in the *M. pyrifera* treatment from zero at day-5 to a mean of 28 (± 26.7 S.E.) at day-19, but no such *Capitella* spp. increase occurred in the *Enteromorpha* spp. treatment. Like *Capitella* spp., the leptostracan *Nebalia pugettensis* increased in the *M. pyrifera* treatment from zero at day-5 to 4 (± 4 S.E.) at day-19.

The assemblage of macrofauna that quickly colonized the *Enteromorpha* spp. treatments in the 21 m-deep channels was notably similar to the assemblage in naturally occurring algae in the 30 m-deep axis (Fig. 10). However, the assemblage found in naturally occurring patches of *Enteromorpha* spp. one year earlier (19 April 1989) was not similar; it was primarily polychaetes (Chapter 1, Figs. 3 and 4). In fact, total polychaetes were an order of magnitude more abundant (2618.7 ± 427.7 S.E.) than total crustaceans (233.3 ± 54.1 S.E.).

Treatments were reduced to *Enteromorpha* spp. and empty corrals, and randomized block analyses were discontinued for all experiments after the spring. The *M. pyrifera* treatment was discarded because the spring experiment already demonstrated that fauna have different responses to different algae. The no-corral treatment was discarded because no cage effect was detected at day-5, although the day-19 data indicated some cage effect for polychaetes (Fig. 9). This indication of cage effect was expressed only in the polychaete *A. brevis*. Randomized block ANOVAs were deemed unnecessary for future analyses because the p-value for variability among channels (blocks) was never less than .05 in any of the 24 cases; the four channels, in which treatments were blocked, were determined to be good replicates.

Alga experiments at four times during the year - Repetition of the algae experiment in June and September of 1990 and February of 1991 led to large numbers of crustaceans again rapidly colonizing newly arrived patches of *Enteromorpha* spp. (Fig. 11). This did not occur in the empty-corral treatments at any time. The number of algae-colonizing crustaceans per core (total crustaceans) in the channels was similar among May (197.5 ± 69.3 S.E.), June (272.5 ± 88.1), September (252.5 ± 221.3), and February (228.8 ± 88.8). There were no significant differences among months detected for total crustaceans, but they were significantly more abundant in *Enteromorpha* spp. than in empty corrals ($p < .05$, two-factor ANOVA; $n = 4$). The most abundant crustacean colonists in descending order were: the gammarid amphipods *Orchomene pacifica, I. pelagops, A. tridens, A. columbiae, Pontogeneia* sp., a species of *Stenothoidae,* and the caridean decapod *Heptocarpus cristatus*.

Most crustacean species were present *Enteromorpha* spp. during all seasons, but rare in September. *A. tridens,* for example, was absent in September, and *H. cristatus* was absent in September and February. Total crustaceans were, nonetheless, abundant in *Enteromorpha* spp. treatments in September because the most abundant amphipod, *O. pacifica,* was present in September and absent in May. Significant differences among seasons were not detected for any crustacean species, but every crustacean species that was tested (*O. pacifica, A. tridens, A. columbiae,* and *Pontogeneia* sp.) was significantly more abundant in *Enteromorpha* spp. than in empty corrals ($p < .05$, two-factor ANOVAs, and non-parametric, two-factor ANOVAs for *O. pacifica* and *A. tridens;* $n = 4$; Table 4). This same pattern held for *I. pelagops* and *Stenothoidae,* but was not statistically significant.

Polychaetes had the opposite pattern. Most polychaete species exhibited considerable seasonal change in abundance and responded very little to experimental patches of algae. In six out of the seven polychaete species tested there was no significant difference detected between the *Enteromorpha* spp. treatment and the empty corrals (Table 4). But significant difference in abundance among dates was detected for total polychaetes, nemerteans, and the polychaete species, *A. brevis, N. cornuta, L. luti,* and *M. sacculata* ($p < .05$, two-factor ANOVAs, except for total polychaetes and *M. sacculata* for which non-parametric, two-factor ANOVAs were used; $n = 4$). Also, differences among dates were nearly significant ($p = .065$) for numbers of *Capitella* spp.

Polychaete species abundances varied among seasons. Total polychaetes, *A. brevis*, and *Capitella* spp. were most abundant in September. *A. brevis* was significantly more abundant in the *Enteromorpha* spp. treatment in September than any of the other months ($p < .05$, Tukey tests). *N. cornuta* was significantly more abundant in the May *Enteromorpha* spp. treatment than the September or February *Enteromorpha* spp. treatment. *P. pygmaea* was present all year round, but it was most abundant in May. In the *Enteromorpha* spp.

treatment *M. sacculata* was significantly more abundant in June than in any of the other months ($p < .05$, Games-Howell tests). Nemerteans were also most abundant in June. *L. luti* was most abundant in February.

Like the crustaceans, large numbers of opportunistic polychaetes, *Capitella* spp., *A. brevis* and *P. bicanaliculata,* quickly (< 5 days) colonized *Enteromorpha* spp. (Fig. 11). This was an exception to the polychaete pattern, in which there was little difference between *Enteromorpha* spp. and no corrals, and happened only in September. By day-19 of the fall experiment there were 1,840.8 ± 500.9 S.E. *Capitella* spp. per core, and the density of total fauna was as high as 416, 667 individuals per m^2. The exception to the polychaete pattern was *P. bicanaliculata;* like the crustaceans, it was present throughout the year and was much more abundant in *Enteromorpha* spp. treatments than in empty-corrals (Table 4).

There were more macrofauna species in *Enteromorpha* spp. than in empty corrals. The grand means from all seasons were 24.9 species in *Enteromorpha* spp. compared with 20.1 species in empty corrals ($n = 16$ per date). This difference probably underestimates real differences, as *Enteromorpha* spp. cores were smaller than empty-corral cores in June and February.

Comparison of 5 and 19 day treatments in the spring and the fall - Rapid initial spring colonization of *Enteromorpha* spp. treatments (day-5) tapered off by day-19, whereas in the fall, initial colonization by some species took longer than five days; three polychaetes and three crustaceans were still increasing in numbers by day-19 (Table 3). The three most abundant colonists of the fall *Enteromorpha* spp. treatment *(Capitella* spp., *O. pacifica,* and *A. brevis)* are the same species that colonized naturally occurring patches of *Enteromorpha* spp. in the 24 m-deep axis station in 1988-1989, where they reached their highest abundances on 19 April 1989 (Chapter 1).

Crustaceans were more abundant in *Enteromorpha* spp. treatments than in empty corrals, and their abundances were often quite different between five and 19 days (Fig. 9, Fig. 11, and Table 3). *O. pacifica, A. columbiae, I. pelagops, A. tridens*, and *Pontogeneia* sp. were much more abundant in the *Enteromorpha* spp. treatments than in empty corrals, but these differences were statistically significant only for total crustaceans and *A. columbiae* ($p < .05$, two-factor repeated measures ANOVAs; $n = 4$). *A. tridens* was abundant in the spring and *O. pacifica* was abundant in the fall (Table 3). The two morphologically similar species *A. columbiae* and *I. pelagops* inhabited the algae simultaneously during both seasons.

Polychaetes again showed a pattern that was opposite to that of the crustaceans, but there was a considerable difference between the spring and the fall with respect to their colonization of *Enteromorpha* spp. In the spring, polychaetes were more abundant by 19 than 5 days, and there were no differences in abundances between *Enteromorpha* spp. treatments and empty corrals. In the fall not only were polychaetes more abundant by 19 days, as in the spring, but they were also more abundant in *Enteromorpha* spp. treatments than in empty corrals. The latter is a pattern similar to that of the crustaceans. However, due to fall interaction between corral treatment and sampling date, the only statistical pattern was that several polychaetes were significantly more abundant after 19 days than after 5 and no significant differences between alga treatments were detected; this is opposite the crustacean pattern. In the spring *A. brevis*, nemerteans, and *Capitella* spp. were significantly more abundant after 19 days than after 5 ($p < .05$, two-factor repeated measures ANOVAs; $n = 4$), although *Capitella* spp. totalled only eleven individuals. No significant differences were detected between *Enteromorpha* spp. treatments and empty corrals for any of the nine polychaete species that were tested in the spring. *P. pygmaea* was significantly more abundant after 5 days than after 19. In the fall total fauna, *A. brevis,* and *Phyllodoce* sp. were significantly more abundant after 19 days than after 5.

In the fall, when polychaetes colonized *Enteromorpha* spp., there were significantly more species in *Enteromorpha* spp. than in empty corrals, but this was not the case in the spring, when polychaetes did not colonize ($p < .05$, two-factor repeated measures ANOVAs; $n = 4$).

Alga experiment in different habitats - Large numbers of crustaceans colonized 5-day *Enteromorpha* spp. treatments in June 1990 at a 30 m-deep axis station, a 21 m-deep sandflat station, and the 21 m-deep channels (Fig. 11 and 12, Table 3). Most crustacean species colonized algae at all three stations. The gammarid amphipods *A. tridens, A. columbiae,* and *I. pelagops* were significantly more abundant in the *Enteromorpha* spp. treatment than in the empty corrals ($p < .05$, two-factor ANOVAs; $n = 4$) and *O. pacifica, Pontogeneia* sp. and *Parajassa* sp. were also more abundant in *Enteromorpha* spp. No significant differences among habitats were found for any other crustacean (Table 5; note the significant interaction).

This pattern persisted in spite of the fact that most of these crustacean colonists were an order of magnitude more abundant in the 30 m-deep axis *Enteromorpha* spp. treatments than at the 21 m-deep sandflat station or channels (variance was high, with significant interaction in two cases). Density of macrofauna in *Enteromorpha* spp. at the axis station was as high as 418,133 per m^2. The three numerically dominant species in this experiment, *A. tridens*, *O. pacifica* and *A. columbiae,* were much more abundant at the axis station than at the other two (Table 3). *O. pacifica* was most abundant in the axis, but it did not colonize sandflat treatments. Not all species, however, were most abundant in the axis. *I. pelagops* was 2.4 times more abundant in the channels or at the sandflat station than in the axis. *Parajassa* sp. was present in the channels (17.5 ± 7.8 S.E.) but was not present at the axis or sandflat. In general, however, crustaceans were significantly more abundant in *Enteromorpha* spp. treatments than empty corrals and they were not significantly different among habitats.

Polychaetes once again exhibited a pattern that was opposite to that of the crustaceans. Different polychaete species had significantly different abundances among habitats. Significant differences in abundances were detected among the three experimental habitat-stations for *A. brevis, P. pygmaea, M. californiensis, L. luti, P. bicanaliculata*, and nemerteans ($p < .05$, two-factor ANOVAs; $n = 4$; Table 5). However, during this 5-day-only habitat experiment, the only polychaete that was significantly more abundant in *Enteromorpha* spp. than in empty corrals was *P. bicanaliculata.* It was also the only polychaete that was found to be significantly more abundant at the axis station than at the sandflat station or the channels, in this experiment ($p < .05$, orthogonal tests).

A. brevis was significantly more abundant in the channels than at the sandflat station ($p < .05$, orthogonal tests). Nemerteans were also most abundant in the channels. Nemerteans in the *Enteromorpha* spp. treatment were significantly more abundant in the channels than at the axis station. But, in the empty corral treatment nemerteans were significantly more abundant at the sandflat station than at the axis station.

P. pygmaea, M. californiensis and *L. luti* were most abundant in the sandflat treatments. *P. pygmaea* in the *Enteromorpha* spp. treatment were significantly more abundant at the sandflat station than at the axis station. In the empty-corral treatment they were significantly more abundant at the sandflat station than the axis station or in the channels. *M. californiensis* had the latter pattern in both corral treatments. In the empty-corral treatment *L. luti* were significantly more abundant at the sandflat station than at the axis station.

The exception to the general polychaete pattern was the phytal polychaete *P. bicanaliculata*. Like the crustaceans, significant differences were detected not only among habitats, but also, between the *Enteromorpha* spp. treatment and the empty corrals ($p < .05$, two-factor ANOVA; $n = 4$; Table 5).

Distribution study of swarming crustaceans - The emergence trap sampling program indicated that swarming crustaceans are abundant in the shallow axis of Monterey Canyon (Table 6). They are not so abundant in other habitats or deeper in the canyon axis. The lysianassid amphipod *O. pacifica* was present in the axis in both the fall of 1990 and the spring of 1991. *O. pacifica* was captured in the channels in the spring (30.3 ± 17.1 S.E.), but it was rare at the sandflat station (.7 ± .7 S.E.). It was not present in the channels or at the sandflat station in the fall. *A. tridens* was abundant during the spring but sparse during the fall. This was also revealed by the experiments. *A. tridens* was captured in the channels in the spring (2.3 ± 2.3 S.E.), but it was not captured at the sandflat station, in spite of its abundance in the axis.

Swarming crustaceans were not abundant in the shallow axis during the fall. Although only one sample was recovered from the 30 m-deep axis in the fall, abundances were low for all groups except, perhaps, mysids (Table 6). This sample is thought to be reasonably representative for the sake of qualitative comparisons.

There may be some habitat and depth partitioning among swarming crustaceans. *I. pelagops,* the sandflat and channel colonist of the experiments, was captured only at the sandflat station in the spring (.3 ± .3 S.E.). Another gammarid amphipod, *Stylipes* sp., was present in the spring only at 300 m and 500 m in the axis. In the fall it occurred only at 100, 300, and 500 m in the axis (Table 6).

DISCUSSION

Sampling, field experiments, and observational studies show that sunken drift-algae is a significant influence on the abundance and distribution of benthic macrofauna in the shallow axis of Monterey Canyon. Distinct patches of various types of algae accumulate in the shallow axis of the canyon, where they were observed to slowly become incorporated into the sediment (*also see* Chapter 1). Moreover, different algae arrive during particular seasons. In the shallow axis of Monterey Canyon there is a changing mosaic of algae that function like disturbances. Others have also found it useful to discuss sunken drift algae as disturbances (Grassle and Morse-Porteus 1987, Smith and Brumsuckle 1989; *see* Sousa 1984 *for a relevant review of natural disturbances*).

Benthic algae are an important resource for both crustaceans and polychaetes, yet differences in the morphology and life-history of these two groups lead to different patterns of drift-algae utilization (Bedford and Moore 1984, Thrush 1986, Hacker and Steneck 1990, this study). Abundances of crustaceans and polychaetes were usually inverse in this study. Crustaceans are generally more motile than polychaetes (as adults). Hence, they can more rapidly exploit ephemeral resources such as patches of drift-algae. The first indication that crustaceans profusely colonized drift-algae came when large numbers of the lysianasid amphipod *O. pacifica* were found in *Enteromorpha* -samples from 19 April 1989 (Chapter 1). Other species in this widespread genus are known to be voracious and abundant scavengers on the sea floor (Slattery and Oliver 1986). Polychaetes are generally more oriented towards habitat, and although many larval forms are mobile and highly selective (Oliver 1979), they generally cannot exploit ephemeral resources as rapidly as crustaceans. Species that were consistently exceptions to their own groups (crustaceans and polychaetes), like the crustacean *Nebalia pugettensis* and the polychaete *Platynereis* *bicanaliculata,* may be using cross-over niches that cannot be fully used by species in the other group and are not used by other species in their own group.

Seasonal shift of macrofauna in natural algae-patches

The initial hypothesis of this study was accepted; macrofauna from naturally occurring patches of drift-algae varied among four seasonal sampling dates. The most conspicuous pattern that emerged from this axis sampling program was a numerical shift from crustaceans in the spring to polychaetes in the fall (Fig. 8). One explanation for this pattern is that highly motile crustaceans can more rapidly exploit the axis habitat after possible flushing events (*see* Chapter 1). Later experimental results indicate that differences in mobility may be important on smaller time scales, but this probably cannot explain the seasonal patterns observed in natural patches of algae in the axis. Four alternative explanations are as reasonable, and probably combine with flushing to influence community structure: variations in algal type, sediment characteristics, O_2 concentrations, and degree of algal burial by sediment. These are presented in order of decreasing evidence.

If there are algal preferences, then seasonal variations in algae may explain the crustacean to polychaete numerical shift. In fact, seasonal variations in algal composition were indicated during the later portions of this study; experiments detected significant differences in macrofaunal colonization between types of algae during the spring experiment (Fig. 9; discussed later). However, the natural patches sampled had similar algal composition among seasons; variations in algal composition probably did not fully account for the seasonal variation in faunal abundances. Nonetheless, subtle differences in algal composition may have influenced faunal composition to some extent.

Variations in sediment characteristics may influence the distribution of benthic macrofauna (Rhoads and Young 1970, Johnson 1971). It is possible that the seasonal shift from crustaceans to polychaetes is a reflection of a shift in sediment characteristics in the axis. Percent sand and mean grain size were low in a sample taken on 28 October 1990 (Table 1) near the fall faunal samples taken two days later, in which there were large numbers of deposit feeding polychaetes (Fig 8). However, these sediment parameters were also low in a sample from the following spring (Table 1), indicating that sediment characteristics are not the major structuring mechanism of the macrofaunal community. Changes in sediment characteristics in these few samples were useful for determining the existence and timing of axis flushing (*see* Chapter 1), but may not be a reliable predictor of faunal assemblage in this system.

The crustacean to polychaete shift from winter to fall may reflect depressed fall dissolved oxygen (DO) concentrations in the axis. Crustaceans were most abundant when DO was highest in the winter sample (8.2 mg/l). Polychaetes were most abundant in the when the DO concentration was lowest in the late summer/fall (4.5 mg/l). However, these measurements are of limited usefulness because samples were unreplicated, and because daily DO variations in the head of Monterey Canyon may be as much as half that of yearly variations (Broenkow and Mckain 1972). Nevertheless, DO concentrations were found to be lowest in the late summer when divers often could taste and smell hydrogen sulfide in the water above the axis sediment.

Capitella spp. and *P. bicanaliculata* were the only abundant polychaetes in natural patches in late summer samples (Fig. 8). These genera are known to be tolerant of low levels of oxygen (Muus 1967, Reish 1971, Grassle and Grassle 1974, Pearson and Rosenberg 1978, Bedford and Moore 1984). *Capitella* spp., in particular, can tolerate low DO levels which are often associated with organic enrichment. Reish (1971) found a reduction to only five species of polychaetes in southern California harbors when DO concentrations were below 4.0 mg/l. In fact, *Capitella* spp. settled on plates when DO concentrations were below 0.1 mg/l. Henriksson (1969) found that in addition to *Capitella* spp. a nereid polychaete, *Nereis diversicolor,* was also extremely resistant to low oxygen. This literature suggests that these polychaetes would probably thrive in conditions that occur in the fall in the shallow axis of Monterey Canyon. Muus (1967) found that a phytal crustacean assemblage was more sensitive to low DO concentrations than a cohabitating polychaete assemblage, and indeed crustacean densities were lowest in the fall in the Monterey Canyon axis. Beukema (1991) found that the proportion of polychaetes increased relative to crustaceans during a period of eutrophication, when low DO levels caused local mass mortalities on a tidal-flat in the Dutch Wadden Sea. Although DO fluctuations were not rigorously tracked during this study, I include it as a likely factor in the model for faunal change in the axis of Monterey Canyon.

The exception to the seasonal crustacean pattern in Monterey Canyon was the leptostracan *N. pugettensis*. It was most abundant in the October samples during the season that intense methane percolation was observed. This may be the most abundant crustacean species inhabiting the sunken vegetation in Scripps Canyon (Vetter, personal communication), a known site of profuse methane percolation (Shepard 1949, Chamberlain 1964, Dill 1964, Shepard and Dill 1966).

Algae experiments

Amphipods always rapidly colonized newly arrived patches of *Enteromorpha* spp., but did not colonize *M. pyrifera* in the one experiment using this algae (Figs. 9, 11, and 12; Tables 4 and 5). This could be due to differences in algal architecture and utilizable energy between these algae. *Enteromorpha* spp. consists of masses of fine filamentous, one-cellthick, tubes. This configuration provides ideal habitat or food for animals of small body size such as amphipods, but corticated macrophytes, like *M. pyrifera*, are predicted to be suboptimal habitat or food for such animals (Hacker and Steneck 1990). Larger animals, however, may prefer macrophytes.

New patches placed in corrals were colonized more rapidly by swarming crustaceans than by polychaetes. Crustaceans are highly mobile and colonize algae by swimming as adults. This mobility was confirmed by emergence-trap sampling. Polychaetes, on the other hand, colonize by crawling, larval recruitment, or direct larval development (Grassle and Grassle 1974), and this is probably why they lagged behind the crustaceans. Larval recruitment into algae and direct larval development there by *Capitella* spp. was revealed on various occasions in this study by recent post-larval size distributions and tube-brooding respectively (*see* Muus 1967, Grassle and Grassle 1974, and Watling 1975).

In the seasonal experiment significant differences for crustaceans were detected among algae treatments, but not among seasons (Table 4). The perpetual presence and high mobility of crustaceans presumably allowed them to find algae during any season. Even if the dispersal stage of these animals is limited to the young they might still arrive all year if their reproduction is not strictly seasonal. In fact, *O. pacifica,* is from the deeper continental slope where reproductive seasonality would be expected to be less distinct.

The opposite pattern occurred in polychaetes; significant differences among seasons were detected, but differences among alga treatment were not. This may be because polychaetes are more dependent upon sediment characteristics that are likely to change seasonally, they are less mobile than crustaceans, and there is a strong seasonality to their larval availability in the water column (Oliver 1979). The exception, the polychaete *P. bicanaliculata,* was significantly more abundant in *Enteromorpha* spp., and it exhibited no seasonal pattern. This polychaete is relatively mobile and might even be considered epifaunal, ecologically similar to crustaceans.

Analysis of the crustacean pattern of non-seasonality may only be valid in comparison to polychaete patterns; they do in fact have some seasonal trend. The distribution study of swarming crustaceans also hints that there may be some seasonality in crustacean populations (Table 6). The statistical patterns from the experiments are nonetheless useful for the sake of comparison (crustaceans vs. polychaetes; Tables 4 and 5); but should be interpreted in light of small sample sizes ($n = 4$).

Polychaetes colonized experimental treatments after the crustaceans did so in the fall. Large numbers of *Capitella* spp. colonized experimental patches of *Enteromorpha* spp. by day-19; this did not happen in the spring (Table 3). Evidence suggests that in this setting *Capitella* larvae are abundant in the water column only during the late summer and early fall, and that they only settle into fine silt or mud in sheltered habitats (Oliver 1979). This evidence reinforces the above experimental findings that *Capitella* spp. only colonized algae during the fall. Enrichment conditions, which promote *Capitella* spp. recruitment, may be stronger during fall in the canyon head and similar habitats. Oliver's (1979) data also indicate that *Capitella* spp. larvae can be present during other seasons, albeit at low numbers. At these times, they could better exploit rare resources by direct larval development (Grassle and Grassle 1974).

In fact, the initial algae-macrofauna data contradict the fall-only *Capitella* spp. colonization in the seasonal experiment. In the spring of 1989 large numbers of *Capitella* spp. were found in natural *Enteromorpha* spp. patches (Fig. 4). These patches were semi-incorporated into the sediment, and probably had been there for longer than 19 days. In this case, high larval availability in the water column may not have been necessary; direct larval development was indicated by abundant broods of juveniles found in adult tubes. When the

19 April 89 sampling took place there had been no substantial wave or wind event for more than three weeks (Fig. 3). This may help to explain why persistent *Enteromorpha* spp. patches could have high *Capitella* spp. density in the spring, and why the experimental *Enteromorpha* spp. treatments were not colonized by *Capitella* spp. larvae recruits in the spring like they were in the fall. However, the natural algae patches that were sampled seasonally may also have been there for longer than 19 days but harbored comparatively few polychaetes in the spring like the experiments. Still, these were kelp forest algae and not semi-incorporated *Enteromorpha* spp. The spring experiment revealed that fauna respond differently to these alga types.

Some cage effect was apparent in *A. brevis*, the only species apparently oriented to the habitat changes created by the corral structure; it was more abundant in the empty corrals than in the no-corral samples. Similarly, Hulberg and Oliver (1980) found that this species colonized wire-mesh cages in large numbers, apparently as the result of sedimentary habitat modifications. Cage effect (ie. corral vs. no-corral) was not tested in other seasons, but it was controlled for by the continued use of empty corrals (ie. empty-corrals vs. *Entero* - corrals). Not only *Capitella* spp., but also large numbers of *A. brevis* colonized the day-19 fall *Enteromorpha* spp. treatments (562 ± 128 s.e; Table 3), and were less abundant in empty-corral treatments (281.5 ± 96.1 s.e.; *compare to* Table 3 and Figs. 9 and 11). This is surprising not only because of the spring cage-effect on this species, but also because the 19 April 89 sampling revealed that *A. brevis* had no preference for the *Enteromorpha* spp. patches (Fig. 5). One hypothesis for this fall colonization of *Enteromorpha* spp. by *A. brevis* is that the algae itself may have influenced the sedimentary regime in the fall. *Capitella* spp. density in the day-19 fall empty-corrals was a mere 36.5 (± 21.4 s.e.). This fall colonization of *Enteromorpha* spp. treatments by polychaetes was the reason that there were more species in *Enteromorpha* spp. treatments than in empty corrals in the fall, but not in the spring.

In the habitat experiment, crustaceans and polychaetes again had opposite numerical patterns because of differences in life-habits (Figs. 11 and 12; Table 5). Crustaceans were more abundant in *Enteromorpha* spp. treatments, but no differences were detected among habitats. Polychaetes were found to be significantly more abundant in particular habitats, but no differences between alga treatments were detected. These clear pattern differences reflect the greater mobility of adult crustaceans than polychaetes of any life-stage. Crustaceans in *Enteromorpha* spp. were an order of magnitude more abundant in the axis than either the channels or the sandflat. This is probably because sunken drift-algae normally accumulates in the axis, but rarely in the other two habitats.

Both crustaceans and polychaetes had exceptions in the habitat experiment. *I. pelagops* was the only phytal amphipod that was oriented to the channels and the sandflat station rather than the axis station. There are clearly less algal resources on the sandflat and presumably fewer niches there. It seems that this single amphipod exploits the scarce algae on the sandflat while several species exploit the abundant algae in the axis. Small pieces of stray algae are sometimes observed drifting along the sandflat bottom, and on rare occasions patches of *Enteromorpha* spp. were seen in ray-pits. While *I. pelagops* was an exception to crustacean patterns, the phytal polychaete *P. bicanaliculata* is a partial exception to the polychaete pattern (*see* Tables 4 and 5). It is significantly more abundant in *Enteromorpha* spp. treatments than in empty corrals. This is probably due to its high mobility and its algae-oriented life-habits. Again, this exception was only partial, for significant differences among habitats were detected in *P. bicanaliculata,* like the other polychaetes. Not surprisingly, it was most abundant at the axis station.

Oliver and Slattery (1981) found that community resilience (rebound after introduced disturbances) at a sandflat station near Monterey Canyon and one in Antarctica was negatively correlated with habitat complexity. A similar pattern was revealed in the present study. The sandflat had more species (Table 2) and the most limited colonization of algal patches. Conversely, the axis station had the fewest species and clearly the largest number of individuals that reacted to disturbances. If abundance of colonizers is a measure of community resilience, then this correlation survives herein, for accumulations of drift-algae contribute to the habitat complexity of Monterey Canyon's axis, yet the sandflat is conspicuously featureless.

Mosaics and ecosystem-level interactions

The frequent arrival of parcels of drift-algae created a temporal and spatial mosaic of disturbances during this study. The Loma Prieta earthquake created a spatial mosaic at the head of the Monterey Canyon, and axis-flushing perhaps represents part of a large-scale mosaic of mass wasting on the continental margin (Chapter 1). All are part of Monterey Canyon's overall disturbance regime that influences the abundance and distribution of benthic organisms there.

Many benthic megafauna were observed in association with sunken drift-algae in the canyon axis. The asteroid *Pycnopodia helianthoides* was regularly observed with its stomach everted on the stipes of *M. pyrifera.* The suspension feeding anemone *Metridium senile* used the stipes of *M. pyrifera* for attachment. Fishes seasonally associated with algae included young of the year *Sebastes* spp., *Scorpanichthys marmoratus*, and *Ophiodon elongatus* and the adult embiotocids *Damalichthys vacca* and *Cymatogaster aggregata.* The large deep-sea demersal shark *Echinorhinus cookei* aggregated in the shallow canyon-head during the spring and summer. These were mostly observed along an upper wall but they were also seen in the axis. Swarms of squid, *Loligo opalescens*, and masses of their egg cases were observed attached to drift-algae in the axis during winter and spring. Large aggregations of juvenile *Cancer gracilis* were observed around the shallow head.

Some megafauna used the corral structures as refuges. *Cancer gracilis* used the protection of the corrals for molting. During the same period a sea otter, *Enhydra lutris*, had been observed feeding in the vicinity, and most of the corral lids were caved inwards. Some small fishes also hid among these structures. Although some of the above fauna were present in the canyon head during crucial reproductive stages, it is possible that they were all finding food or refuge there.

Crustaceans in the canyon axis may be eaten by the abundant fish fauna observed with patches of sunken drift-algae. Not only were crustaceans abundant in emergence traps from the axis but large numbers of *Orchomene pacifica* have also been captured with Hagfishes in 1,000 m-deep traps in the canyon axis (Johnson in prep.) and observed in *M. pyrifera*-baited traps used for capturing megafauna in the 150 m-deep canyon head (Roddy in prep.). This species is the primary food source for the Persimmon Eelpout, *Eucryophycus californica*. Kliever (1976) found that *O. pacifica* was the most abundant and voluminous prey item for these fish. The phytal polychaete *P. bicanaliculata* was also present in their gut contents. If other drift-algae-inhabiting fish species, such as those in the shallow canyon axis, have similar food preferences, and algal drift is abundant, then the algae-macrofauna link in the axis of Monterey Canyon may be quite important to the locally abundant fish, bird, and mammal populations. Furthermore, fish may be an important check on populations of herbivorous amphipods. Tegner and Dayton (1987) observed that El Nino-related reductions in Embiotocid fish predators caused an outbreak of herbivorous amphipods that denuded a portion of the Point Loma kelp forest and postponed its recovery. The forest recovered after the fish eventually increased and released the kelp from heavy grazing pressure by eating the amphipods. This anecdote suggests that phytal amphipods can be an influential and explosive component of subtidal algal ecosystems, but some data indicate that their actual role is not so easily predictable. For example, phytal amphipods have been shown to slow the decomposition of sunken drift-algae by cropping microbes (Bedford and Moore 1984).

Macrofaunal responses to mosaics created by the continuous arrival of patches of drift algae are comparable to the creation of tree-gaps in forests (Collins et al. 1985, Runkle 1985, Veblen 1985, Frelich and Lorimer 1991), or to small scale biogenic disturbances on prairies, which create new space for opportunistic plant species (Loucks et al. 1985). Even more analogous to faunal patterns herein are the responses of insects to terrestrial disturbances, such as mosaics of plant litter accumulations (Schowalter 1985). The recent shift in emphasis from equilibrium theories of community structure to non-equilibrium theories, such as disturbance and mosaic phenomena, is especially appropriate for dynamic environments like forests and grasslands (Wiens 1976, Whittaker and Levin 1977, Connell 1978, Sousa 1984, Pickett and White 1985, Shugart and Seagle 1985), and perhaps the head of Monterey Canyon.

CONCLUSIONS

The shallow head of the Monterey Canyon is a dynamic, highly disturbed environment where benthic macrofauna respond to accumulations of drift-algae, large-scale axis-flushing, and earthquake-induced slumping. In this chapter, sunken drift-algae were shown to influence the spatial and temporal distribution of benthic macrofauna in the shallow head of Monterey Canyon. The long term habitat modification and stresses brought on by decomposing algae, as well as the specific physical and chemical effects of flushing and other oceanographic processes, appear to be of central importance to the organisms that live in this system, but fully addressing these was beyond the scope of this study. In particular, a well designed and rigorous oxygen sampling program is needed to complement thorough faunal sampling.

SUMMARY

1. Naturally occurring patches of sunken drift *Enteromorpha* spp. were a significant influence on the distribution of some, but not all, macrofaunal species.
2. Naturally occurring patches of sunken drift-algae were inhabited by motile crustaceans in the spring and by large numbers of low-oxygen tolerant, enrichment-opportunist polychaetes in the fall.
3. A manipulative field experiment revealed that a suite of motile amphipods rapidly colonized (< 5 days) newly arrived patches of *Enteromorpha* spp., but not *M. pyrifera,* in separate hanging channels, at the end of a 15 m deep bench. However, two amphipods, *A. tridens* and *A. columbiae,* colonized *M. pyrifera* in low numbers.
4. When these experiments were repeated in different seasons and in different habitats it was revealed that amphipods rapidly colonized *Enteromorpha* spp. patches and polychaetes colonized more slowly or not at all. Amphipods were present during all seasons and in all habitats, but polychaetes were present only during particular seasons and in particular habitats. These abundance differences between crustaceans and polychaetes probably reflect differences in morphology, physiology, and life-history. These may include differences in O_2 tolerances and a higher mobility in the swarming amphipods than in polychaetes.
5. Numerical trends from algae-patch sampling, alga experiments, and a crustacean distribution study indicate crustacean seasonality and habitat orientation. Although the number of experimental replicates ($n = 4$) provided adequate resolution to detect

differences between crustacean and polychaete patterns, sample size may have been too low to detect seasonal and habitat differences.

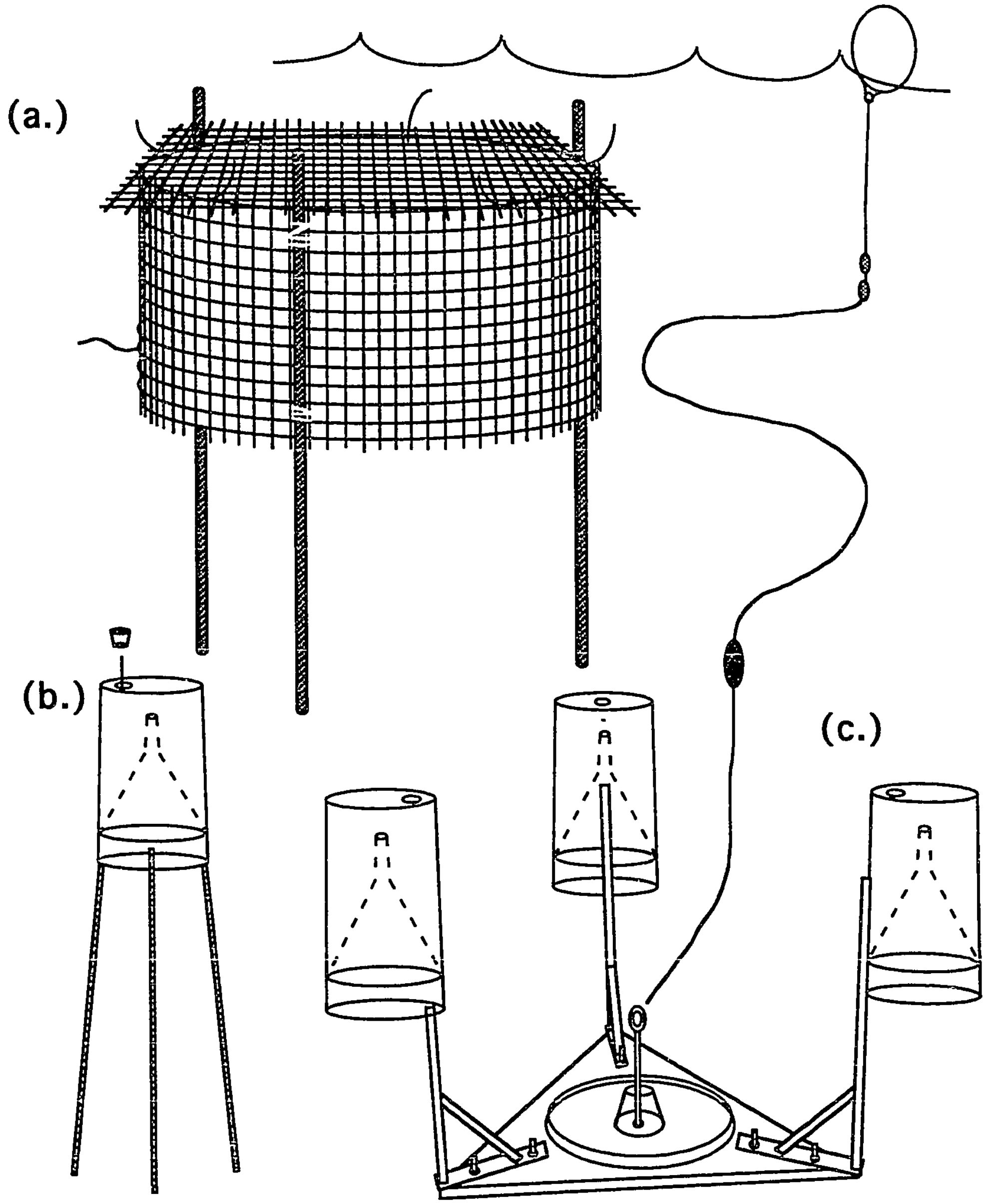

Fig. 7. Special sampling devices developed or modified for this study: (a) algal corral, (b) emergence trap, (c) triple emergence-trap array (the Triple Slattery Swarmer Sampler).

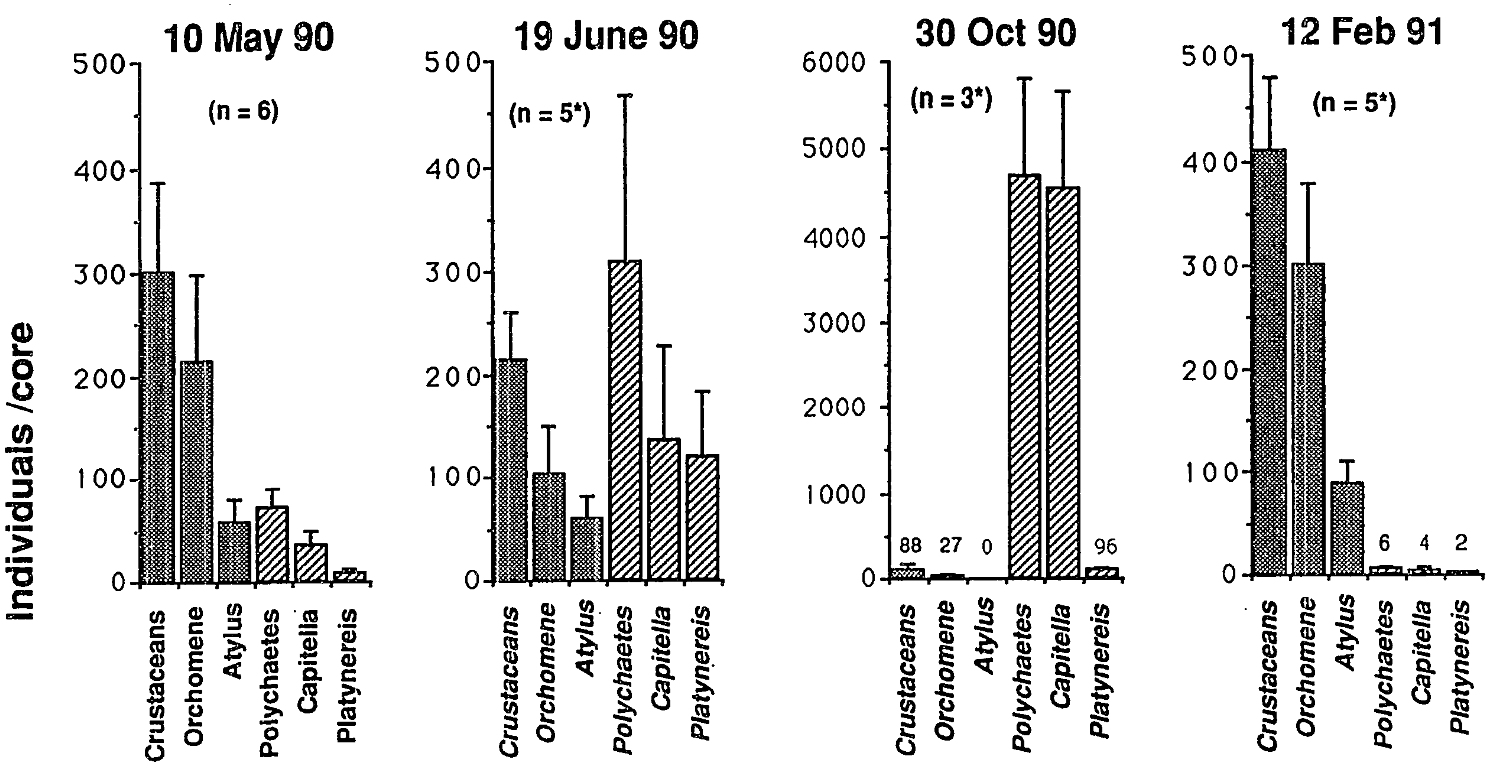

Fig. 8. Changes in numerically dominant crustaceans (grey bars) and polychaetes (cross-hatched bars) in naturally occurring patches of drift algae in the axis of Monterey Canyon. Mean number of individuals per 120 cm^2 core ± standard error (sample sizes in parentheses). Note the scale of 30 Oct 90. The latter data (*) were converted from a core area of 75 cm^2.

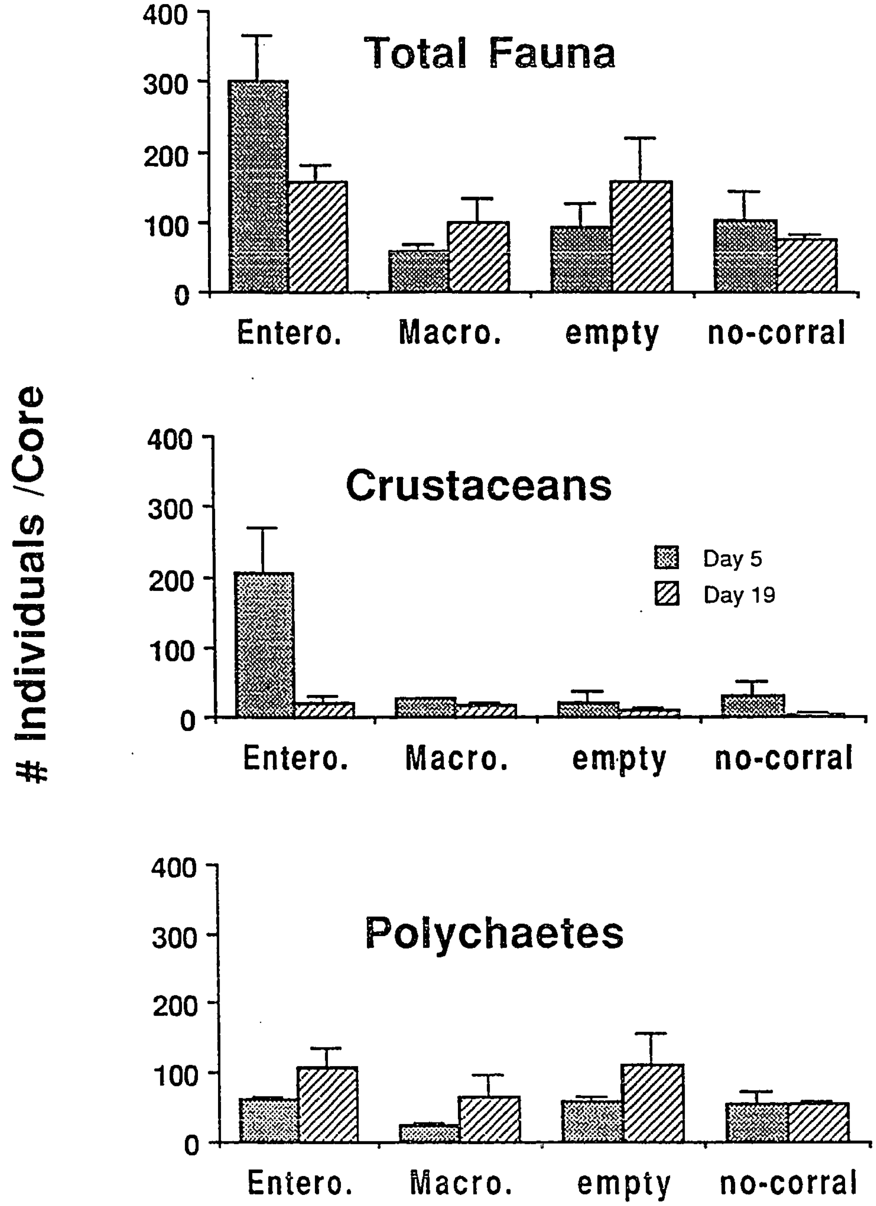

Fig. 9. Colonization of benthic animals into experimental patches of algae after five and 19 days (7 - 26 May 1990). Mean number of individuals per 120 cm^2 core ± standard error ($n = 4$ replicates per datum).

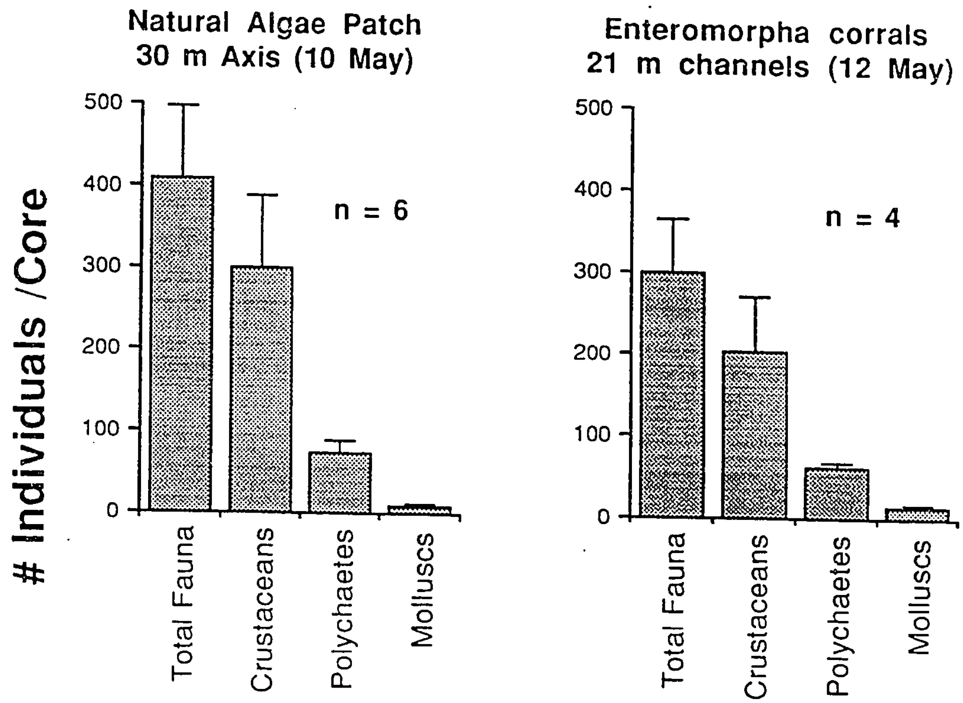

Fig. 10. Similarities of major taxonomic groups between macrofaunal assemblages in naturally occurring sunken drift algae at 30 m depth and those in experimental *Enteromorpha* spp. treatments in hanging channels at 21 m depth in early May 1989. Mean number of individuals per 120 cm^2 core ± standard error.

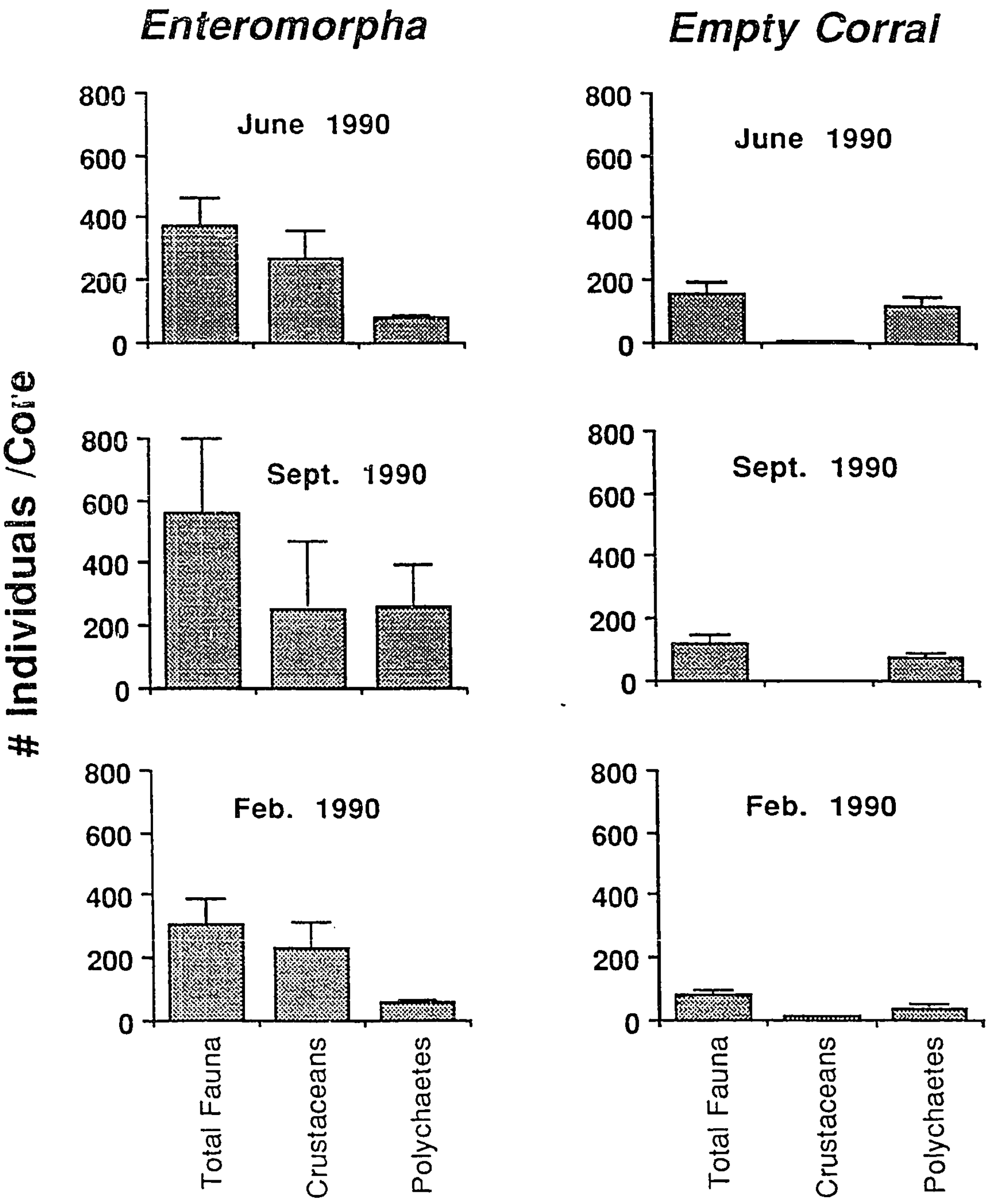

Fig. 11. Seasonal differences in the day-5 responses of benthic macrofauna to experimental patches of the alga *Enteromorpha* spp. in the 21m deep channels (see Fig. 7 for spring data). Mean number of individuals per 120 cm^2 core ± standard error ($n = 4$ replicates per datum).

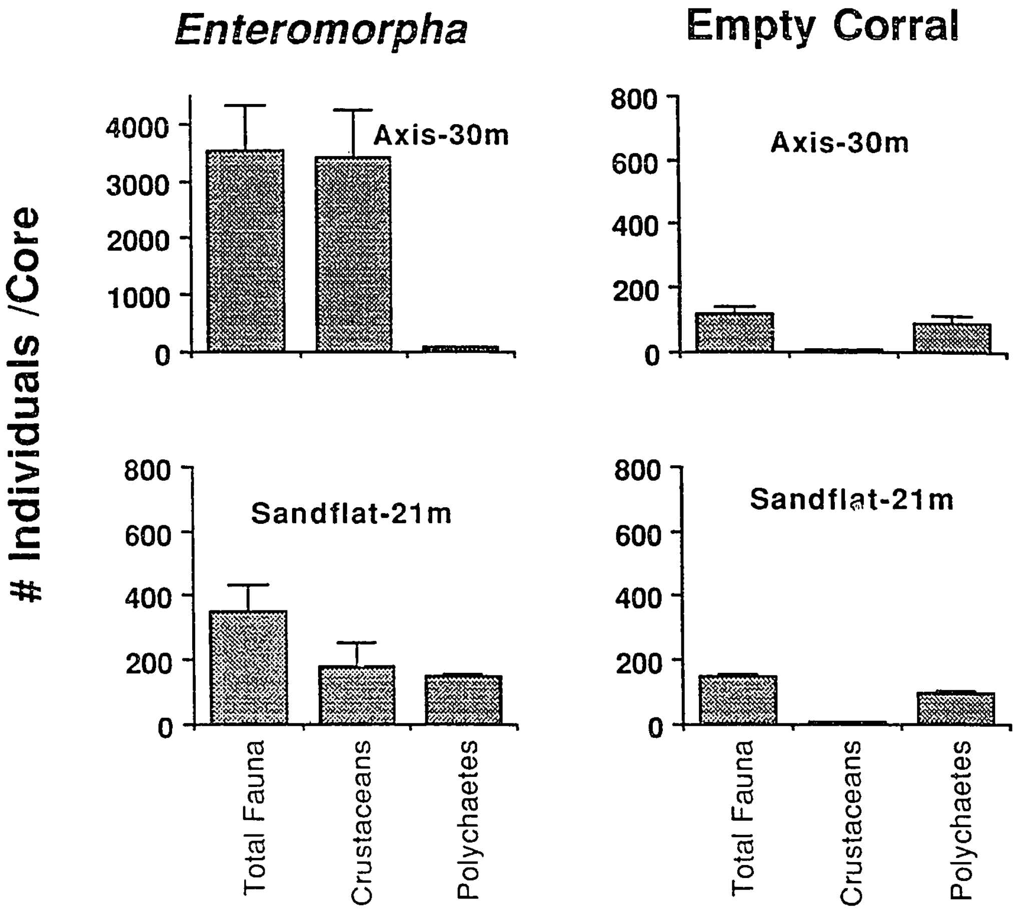

Fig. 12. Differences in the day-5 responses of benthic macrofauna to experimental patches of *Enteromorpha* spp. implaced in the 30 m-deep axis, and on the 21m sandflat (17 - 22 June 90). Compare colonization pattern at the same time in the 21m channels (see Fig. 8). Mean number of individuals per 120 cm^2 core ± standard error ($n = 4$ patches per datum). Note the scale of the 30 m axis, *Enteromorpha* spp. treatment.

Table 3. Differences in mean abundances of the eleven numerically dominant species in experimental patches of *Enteromorpha* spp. among four seasons, two short term sampling periods, and three habitats. Mean number of individuals per 120 cm^2 core ± standard error ($n = 4$ replicates per datum).

	May '90		June '90			September '90		February '91
	Channels 21m		Channels	Axis 33m	Sandflat	Channels 21m		Channels 21m
	Day 5	Day 19	Day 5 *	Day 5 *	Day 5 *	Day 5	Day 19	Day 5 *
Crustaceans								
Orchomene pacifica	0 ± 0	1 ± 1	45 ± 45	339 ± 238	0 ± 0	233 ± 225	656 ± 489	63 ± 56
Ischyrocerus pelagops	71 ± 24	1 ± 1	83 ± 18	35 ± 28	85 ± 40	2 ± 1	14 ± 9	38 ± 19
Atylus tridens	31 ± 10	2 ± 2	13 ± 1	2723 ± 1040	20 ± 8	0 ± 0	0 ± 0	74 ± 36
Aoroides columbia	46 ± 24	13 ± 9	41 ± 22	206 ± 80	53 ± 31	6 ± 6	109 ± 38	11 ± 6
Pontogeneia sp.	27 ± 21	0 ± 0	21 ± 8	93 ± 18	6 ± 6	1 ± 1	1 ± 1	1 ± 1
Polychaetes								
Armandia brevis	7 ± 4	63 ± 22	21 ± 5	12 ± 9	0 ± 0	160 ± 82	562 ± 128	4 ± 1
Capitella spp.	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	59 ± 48	1841 ± 501	9 ± 7
Nephtys cornuta	36 ± 11	9 ± 2	11 ± 5	14 ± 5	16 ± 2	8 ± 5	4 ± 1	4 ± 4
Lumbrineris luti	3 ± 1	8 ± 2	5 ± 2	1 ± 1	9 ± 4	4 ± 2	2 ± 1	11 ± 5
Magelona sacculata	1 ± 0	0 ± 0	21 ± 4	9 ± 8	44 ± 13	0 ± 0	0 ± 0	0 ± 0
Platynereis bicanaliculata	2 ± 1	1 ± 0	4 ± 1	12 ± 4	5 ± 2	7 ± 3	34 ± 11	8 ± 3

* Data were converted from a core area of 24 cm^2 to 120 cm^2.

Table 4. Significant results of two-factor, model-one ANOVAs illustrating the difference between crustacean and polychaete species patterns with respect to Enteromorpha spp. corral treatments and date (season). Crustaceans and polychaetes are each in decending order of abundance. Nonparametric ANOVAs were used when transformations failed to alleviate heteroscedasticity. H is the Kruskal-Wallis statistic.

taxa	alga	date	a * b interaction
Total Fauna	F = 22.3, p = .0001		
Total Crustaceans	F = 32.05, p = .0001		
Orchomene pacifica	H = 8.00, p < .05		
Ischyrocerus pelagops	F = 58.45, p = .0001	F = 4.69, p = .0102	F = 5.36, p = .0057
Atylus tridens	H = 19.45, p < .05		
Aoroides columbiae	F = 21.17, p = .0001		
Pontogeneia sp.	H = 9.588, p < .05		
Stenothoidae sp.	F = 15.07, p = .0007	F = 5.74, p = .0042	F = 5.74, p = .0042
Heptacarpus cristatus	H = 8.51, p < .05	H = 8.56, p < .05	H = 8.56, p < .05
Total Polychaetes		H = 9.906, p < .05	
Armandia brevis		F = 14.15, p = .0001	
Capitella spp.		**F = 2.73, p = .066**	
Nephtys cornuta		F = 7.39, p = .0011	
Magelona sacculata		H = 18.56, p < .05	
Lumbrineris luti		F = 5.87, p = .0037	
Prionospio pygmaea			
Platynereis bicanaliculata	F = 29.14, p = .0001		
Nemertea		F = 3.21, p = .0409	

Table 5. Significant results of two-factor, model-one ANOVAs illustrating the difference between crustacean and polychaete species patterns with respect to Enteromorpha spp. treatments and habitats. Crustacean and polychaete species are each in descending order of abundance. Nonparametric ANOVA was used when transformations failed to alleviate heteroscedasticity. H is the Kruskal-Wallis statistic.

taxa	alga	habitat	a * b interaction
Total Fauna	F = 75.40, p = .0001	F = 27.98, p = .0001	F = 31.65, p = .0001
Total Crustaceans	F = 109.83, p = .0001	F = 31.56, p = .0001	F = 30.29, p = .0001
Atylus tridens	H = 16.36, p < .05		
Orchomene pacifica	H = 5.95, p < .05	H = 6.55, p < .05	H = 6.53, p < .05
Aoroides columbiae	F = 33.97, p = .0001		
Ischyrocerus pelagops	F = 14.24, p = .0017		
Pontogeneia sp.	F = 42.73, p = .0001	F = 10.11, p = .0014	F = 10.34, p = .0013
Amphiodia sp.	F = 19.46, p = .0001		
Total Polychaetes			
Magelona sacculata			
Armandia brevis		F = 8.26, p = .0034	
Nephtys cornuta			
Capitella spp.			
Prionospio pygmaea		F = 11.32. p = .0009	
Mediomastus sacculata		F = 15.06, p = .0002	
Lumbrineris luti		F = 4.02, p = .0386	
Platynereis bicanaliculata	F = 22.35, p = .0002	F = 4.89, p = .0220	
Nemertea		F = 4.62, p = .0261	

Table 6. Differences in mean abundances of swarming crustaceans captured in emergence traps in the Monterey Canyon axis. Mean number of individuals per trap ± standard error ($n = 3$ samples per datum).

	30 m	100 m	300 m	500 m
2 May '91				
Total Fauna	858 ± 76	86 ± 13	17 ± 6	8 ± 6
Orchomene pacifica	106 ± 3	31 ± 2	1 ± 1	4 ± 3
Atylus tridens	664 ± 73	0 ± 0	0 ± 0	0 ± 0
Stylipies sp.	0 ± 0	0 ± 0	2 ± 1	2 ± 2
mysids	11 ± 1	2 ± 2	8 ± 2	0 ± 0
calanoid copepods	48 ± 8	36 ± 7	5 ± 5	0 ± 0
16 November '90	*			
Total Fauna	22	396 ± 102	100 ± 12	64 ± 28
Orchomene pacifica	3	323 ± 101	19 ± 6	35 ± 14
Atylus tridens	0	2 ± 1	0 ± 0	0 ± 0
Stylipies sp.	0	41 ± 22	5 ± 2	26 ± 13
mysids	16	21 ± 8	6 ± 6	1 ± 0
calanoid copepods	3	23 ± 4	19 ± 0	1 ± 1

* Data are from a single sample on 20 September 1990.

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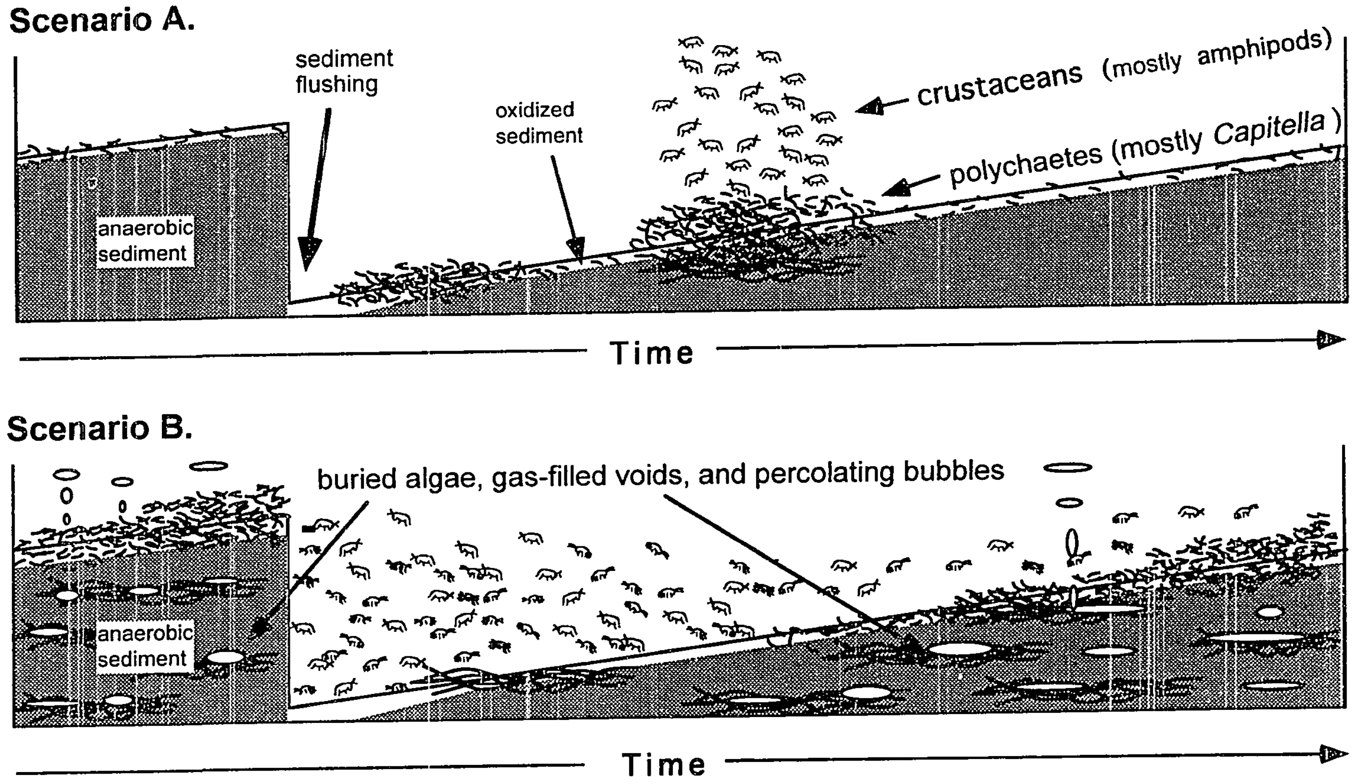
Appendix A

Cartoon Models of Physical and Biological Changes in the Axis of Monterey Canyon



Scenario A.

Scenario B.

Appendix A. These two cartoon models depict changes in polychaetes and crustaceans in the axis of Monterey Canyon. They were constructed with information from Chapter 1 (Scenario A) and Chapter 2 (Scenario B). The x-axis represents time from October of one year through September of the next (Chapter 1: 1988-1989; Chapter 2: 1989-1990 and 1990-1991). Abrupt deepenings represent presumed fall/winter axis flushing.