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ophiuroids on the continental slope off central California**

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San Jose State University, 1993

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BATHYMETRIC, SPATIAL AND LOCAL ZOOGEOGRAPHIC DISTRIBUTION
OF OPHIUROIDS ON THE CONTINENTAL SLOPE OFF CENTRAL CALIFORNIA

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

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

By
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May, 1993

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ABSTRACT

BATHYMETRIC, SPATIAL AND LOCAL ZOOGEOGRAPHIC DISTRIBUTION OF OPHIUROIDS ON THE CONTINENTAL SLOPE OFF CENTRAL CALIFORNIA

by Anne Cary Summers

Box cores were used to sample ophiuroids and surrounding sediments between 550-3,085 m southwest of the Farallon Islands, California. Otter and beam trawls were used to sample ophiuroids below 2,300 m at three sites along the central California coast between the Farallon Islands and Point Sur. A total of 17 ophiuroid species from six families was identified. Eighty percent of the individuals collected with box cores belonged to two species that were dominant between 1,000 and 2,000 m. The largest ophiuroid faunal break occurred at about 2,000 m and was associated with a rise in dissolved oxygen levels, and an increase in sediment organic content parameters. A comparison of box core and trawl data below 2,300 m showed that box cores undersampled the ophiuroid community on the continental slope. There was a change in species relative abundance patterns with latitude, with greatest differences occurring between sites that were farthest apart. Ophiuroids exhibited patchy spatial distribution patterns on both a small and large scale.

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INTRODUCTION

Although scientists have been exploring the deep-sea since the late 1860's (Tyler, 1980), little is known about this environment and the lifestyles of the creatures that inhabit it. Its inaccessibility and remoteness make it a difficult and expensive area to study, and past studies are few and far between, concentrating mostly on general descriptions of epibenthic megafaunal organisms.

The most abundant epibenthic megafaunal phylum in the deep-sea is the Echinodermata. Due to their large numbers, sedentary habits and relatively large size, more information exists on the echinoderms than any other group comprising the deep-sea fauna (Alton, 1972; Pawson, 1976; Haedrich et al., 1980; Gage et al., 1985; Sibuet, 1985). Early expeditions, such as the ALBATROSS and H.M.S. CHALLENGER, collected and described many echinoderm species from the deep-sea. Today many studies still focus on basic descriptions of species composition and distribution (e.g., Carey, 1990; Carey et al., 1990a; Carey et al., 1990b; Hecker, 1990; Kaufmann, Wakefield and Genin, 1989). Additional biological and ecological data are limited due to difficulties in sampling live animals.

The ophiuroids, or brittlestars, are the largest of the five extant classes of echinoderms consisting of over 1,900 species worldwide. They inhabit all areas of the world's oceans, exploiting both soft bottom and rocky substrates from the intertidal zone down to depths of over 8,000 m. In many areas of the deep-sea they numerically dominate the megafaunal catch, although the number of species decreases rapidly with depth (Tyler, 1980; Carey et al., 1990a; Gage and Tyler, 1991). Despite their abundance, ophiuroids are one of the least understood classes of echinoderms, and the impact such large numbers have on the deep-sea community has not been explored. One reason for this paucity of knowledge is that these animals present unique sampling problems. Their size range and lifestyle habits make them members of both the infauna and the epifauna. In addition they are fragile and hard to identify visually from camera sleds, remote vehicles or manned submersibles. It is therefore difficult to sample an entire ophiuroid assemblage with a single sampling method.

Most deep-sea benthic studies have focused on limited areas of the world's oceans. The Atlantic Ocean has received the most attention with recent research on ophiuroids concentrated in the Rockall Trough in the eastern North Atlantic (e.g., Gage and Tyler, 1981a,b, 1982; Gage et al., 1983, 1984; Pearson and Gage, 1984; Tyler, 1986),

and in various areas of the western North Atlantic (e.g., Schoener, 1967, 1968, 1969; Grassle et al., 1975; Haedrich et al., 1980; Haedrich and Maunder, 1985; Hecker, 1990). Deep-sea benthic studies in the Pacific Ocean are sparse, with research on ophiuroids consisting of only a few general faunal surveys conducted in the Northeastern Pacific. Only one published paper deals exclusively with deep-sea ophiuroids in the Pacific Ocean (Astrahantseff and Alton, 1965). Along the west coast of the United States, systematic deep-sea echinoderm studies are limited to areas off the northern Oregon coast (Astrahantseff and Alton, 1965; Alton, 1966, 1972; Pereyra and Alton, 1972; Carney and Carey, 1976, 1982; Carey, 1981, 1990; Carey et al., 1990a; Carey et al., 1990b) and the deep basins off southern California (Hartman and Barnard, 1958; Barham et al., 1967; Smith and Hamilton, 1983; Smith, 1985). The deep-sea benthic environment along the central California coast remains virtually unstudied in a qualitative or quantitative manner, with no published literature available.

This paper explores the bathymetric, spatial and local zoogeographic distribution of ophiuroids on the continental slope off central California. Changes in benthic species composition with increasing depth is a trend found so consistently throughout the world's oceans that it can be treated as a general phenomena (Carney et al., 1983). Echinoderm zonation in the deep-sea is particularly well documented (i.e., Astrahantseff and Alton, 1965; Alton, 1972; Carney and Carey, 1976; Haedrich et al., 1980; Gage et al., 1983, 1985; Carey, 1990). Although zoned with depth, deep-sea ophiuroids have been found to have rather broad depth distributions compared to other macrofauna (Tyler, 1980; Gage and Tyler, 1982 and 1991). This has been attributed in part to their predominantly lecithotrophic or planktotrophic mode of larval dispersal and to their relatively high fecundity (Schoener, 1972; Tyler, 1980; Gage and Tyler, 1982).

Additional factors controlling bathymetric distribution patterns of deep-sea ophiuroids remain obscure. Potential physical controls include the effects of hydrostatic pressure and temperature on physiological functions (Vinogradova, 1959; Madsen, 1961; Gage and Tyler, 1982; Carney et al., 1983; Billett, 1991), dissolved oxygen changes with depth (Thompson, 1983; Mullins et al., 1985; Vercoutere et al., 1987) and variations in sediment characteristics such as grain-size and organic content which supply both habitat and food (Sokolova, 1959, 1972; Tyler, 1980; Carey, 1981; Sibuet, 1985). Potential biological controls include predation and competition (Gage and Tyler, 1982).

Although many deep-sea ophiuroids are known only from a single locality, some show wide geographic distributions. A number of species, such as Asteronyx loveni and

Ophiomusium lymani, exhibit cosmopolitan distributions suggesting an absence of deep water horizontal barriers between oceans (Tyler, 1980; Gage, 1982; Fujita and Ohta, 1988). Bathymetric zones are generally much more distinct at lower latitudes (Pielou, 1979). At high latitudes, zones are compressed together so that ophiuroids of the order Euryale, characteristic of bathyal and abyssal depths at lower latitudes, often occur in shallow water in the polar regions (Tyler, 1980). This phenomenon, known as equatorial submergence, is believed to be determined by variations in water temperature as water temperatures on the continental shelf of polar regions are similar to those at abyssal depths at lower latitudes (Madsen, 1961).

The specific objectives of this study were as follows: (1) To describe the bathymetric distribution of ophiuroids between 550-3,085 m off the Farallon Islands, as sampled with box cores; (2) To describe the spatial distribution patterns of ophiuroids on the continental slope off central California; (3) To investigate whether ophiuroid species bathymetric distributions were associated with changes in dissolved oxygen, sediment grain size, and/or sediment organic content; (4) To determine if the observed distribution and abundance patterns of ophiuroids below 2,300 m changed when sampled with trawls as opposed to box cores; (5) To compare the relative abundance of ophiuroid species below 2,300 m among the Farallon Slope, Pioneer Canyon and Monterey Canyon study sites, as sampled with trawls.

MATERIALS AND METHODS

Background

The data for this project were collected as part of several studies designed for the U.S. Navy and the U.S. Environmental Protection Agency to assess the suitability of potential dredged material disposal sites on the continental slope off central California, in the vicinity of the Farallon Islands. These studies included biological, sedimentary, chemical and physical examinations of this deep-sea environment and resulted in five broad-based reports (SAIC, 1991; Blake et al., 1992; Hecker Environmental Consulting, 1992; Nybakken et al., 1992ab; SAIC, 1992). I had the opportunity to be a part of several of the research cruises undertaken for the U.S. Navy and U.S. EPA, and was able to use some of the data to examine more closely the ophiuroid assemblages in these areas. This paper will discuss the distribution of ophiuroids within the constraints of these sampling programs, as well as the appropriateness of several sampling methods as they relate to

ophiuroids in particular.

Box cores, trawls and camera sleds are commonly used to sample the deep-sea benthos, and their general advantages and disadvantages have been well documented in other studies (e.g., Hessler and Jumars, 1974; Uzmann et al., 1977; Butler et al., 1991). These three methods were used to sample the ophiuroid assemblage on the continental slope in the vicinity of the Farallon Islands, California. This study presents data collected with box cores and trawls. Camera sled results are presented in Hecker Environmental Consulting (1992).

Study Location

The majority of sampling took place in the vicinity of the Farallon Islands, California, located approximately 40 nautical miles west-southwest of San Francisco Bay, in water depths ranging from 500 m to over 3,000 m. Samples were collected in the vicinity of three study areas designated by EPA as potential dredged material disposal sites, known as Areas 3, 4 and 5 (Figure 1). Areas 3 and 4 are located on the upper and middle continental slope in and around Pioneer Canyon in water depths ranging from about 500 m to 1,925 m. Area 5 is located on the lower continental slope west of the Farallon Islands in water depths exceeding 2,000 m, and is dominated by a large sloping trough or valley with a gradient of about 3° (SAIC, 1991). For the purposes of this study, all samples taken in Areas 3, 4 and 5 will be referred to as Farallon Slope sites.

In addition to the Farallon Slope sites, two additional sites farther down the California coast were sampled. These were an area southwest of Pioneer Canyon located about 56 km south of Farallon Slope Area 5 and approximately 53 nm west of Point Año Nuevo, and an area on the fan of Monterey Submarine Canyon located about 145 km south of Farallon Slope Area 5 and approximately 48 nm southwest of Moss Landing off the Big Sur coast. The area southwest of Pioneer Canyon will be referred to as the Pioneer Canyon site, and the area on the Monterey Fan will be referred to as the Monterey Canyon site (Figure 2).

Box Core Sampling

Box core sampling took place with either a 0.25-m² Hessler-Sandia box core (Figure 3) or a smaller 0.16-m² BX-640 box core. The box core stations were located along transects in the vicinity of Areas 3, 4 and 5 at the Farallon Slope site, and one sample was taken at each station.

Sixty-eight successful box cores were collected on three different cruises during the summers of 1990 and 1991 between 550 m and 3,085 m. Box cores were deemed successful when adequate penetration of the sediment had taken place, and the surface layer of the sediment remained intact upon retrieval.

Sampling took place in Area 5 in August of 1990 from aboard the R/V Farnella and July of 1991 from the R/V Wecoma. Twenty-seven box cores were collected from Area 5 between 2,045 m and 3,085 m, and at one station at 1,263 m. Sampling took place in Areas 3 and 4 in September of 1991 from aboard the R/V Point Sur. Forty-one box cores were collected from Areas 3 and 4 between 550 m and 3,060 m. During each of these three cruises, samples were collected 24 hours a day (Table 1). A Mann-Whitney U test showed no significant difference in ophiuroid species composition or abundance within the same depth range (500 m) between the three areas sampled ($p > 0.05$), so for the purposes of this study, all box core samples were combined.

Both box core samplers were internally partitioned into aluminum subcores, each with a surface area of 0.01 m^2 . The 0.25-m^2 Hessler-Sandia box core was divided into 25 subcores and the 0.16-m^2 BX-640 box core into 16 subcores (Figure 4). Ten adjacent subcores within each box core were sampled for infauna by sieving the top 10 cm of mud through a 0.3 mm screen. These 10 subcores together made up a surface area of 0.1 m^2 which was the effective "quadrat size" for box core samples in this study.

After sieving, samples were preserved in 10% buffered formalin for 2-3 days, then transferred to 70% ethanol. All adult brittlestars were identified to species and enumerated. Brittlestars were counted as adults if they had developed the characteristic skeletal features necessary for identification to species. Although the minimum size of adults varied among species, juveniles generally had disc diameters of less than 0.5 mm. Unidentifiable juveniles were also enumerated, but further analyses were done with identifiable adults only.

To see whether there were any naturally occurring faunal breaks in ophiuroid species composition or abundance with depth, dendograms were created using Bray-Curtis cluster analysis and group average sorting without standardization. Both normal and inverse classification were done. For normal classification, stations were grouped using ophiuroid species composition and abundance as attributes. For inverse classification, ophiuroid species were grouped using their presence or absence at stations as attributes (Boesch, 1977). Species that were only collected in one box core were not included in inverse classification.

To examine the general abundance pattern of ophiuroids with depth, abundance of individuals of all species per 0.1 m² was compared over the depth range sampled using a scatter plot. This was also done for the two most abundant species collected. To more closely examine the distributions of the less abundant ophiuroid species, box core samples were divided into six, 500 m depth zones between 500 and 3,500 m, and the mean and variance of individuals of each species within each depth zone were compared. This was necessary because there was no replication of box cores per station. Small scale dispersion patterns were examined using both the variance to mean ratio of ophiuroid species within each of the 500 m depth zones, and Morisita's Index of Dispersion (Id) which was calculated for the six most abundant species over the depth ranges that they occurred (Krebs, 1989).

Because both cluster analysis and scatter plots showed a general faunal break at around 2,000 m, the relative abundances of ophiuroid species between 1,000-2,000 m and between 2,000-3,000 m were compared with histograms. There were 30 box cores above 2,000 m and 33 below.

Sediment samples for sediment grain size and organic content determination were collected from each of the 68 box cores, in subcores adjacent to the ten sampled for biology (Figure 4). These sediment samples were refrigerated at 4°C until analysis. Processing of sediment samples was handled by Science Applications International Corporation in Woods Hole, MA. (see SAIC, 1991; Blake et al., 1992; SAIC, 1992 for more information).

Water for dissolved oxygen determination was collected at various box core stations over the sampling period with a 10-bottle rosette sampler equipped with 10-l Niskin bottles. These Niskin bottles were tripped at various depths between the surface and 3,200 m. Water samples were analyzed for dissolved oxygen on board ship using the Winkler titration technique.

To see whether ophiuroid species distribution and abundance patterns with depth were associated with sediment characteristics or dissolved oxygen, scatter plots and relative abundance histograms of ophiuroid abundance per 0.1 m² with depth were compared with dissolved oxygen, sediment grain size and sediment organic content scatter plots between 400 and 3,200 m. Depth, sediment grain size and organic content parameters were compared with a correlation matrix after examining scatter plots of these parameters with depth to confirm linearity.

Trawl Sampling

Trawl samples were collected using either an otter trawl or a beam trawl. The otter trawl was a standard commercial otter trawl with a 40 foot foot-rope and fished with weighted aluminum doors. It had a stretch mesh opening of 3 cm with an inside bag liner of 1.5 cm stretch mesh. The beam trawl had a beam length of 2.1 m and a bag length of 6.7 m. The outside mesh was made from #60 nylon seine twine of 3 cm stretch mesh treated with a black net preservative. The inside bag liner was 1.5 cm stretch mesh. Trawls were taken in the vicinity of Area 5 on the Farallon Slope, and at the Pioneer Canyon and Monterey Canyon sites. A total of 33 trawls was taken, 29 of which successfully brought back samples. Two of these 29 were otter trawls, and 27 were beam trawls. Otter and beam trawls were combined in analyses, even though they may have fished differently, because the mesh sizes for both nets were comparable.

Trawl samples were collected on two different cruises in the summer of 1991 and the spring of 1992 between 2,300 m and 3,300 m. Sampling took place in Farallones Area 5 in July of 1991 from aboard the R/V Wecoma and in February of 1992 from the R/V Point Sur. Seventeen trawls were taken from Farallones Area 5 between 2,300 m and 3,075 m, 13 in July of 1991 and four in February of 1992. Ophiuroid samples from these two sampling periods showed an 83% similarity (sum of minimums, Sanders, 1960) so for the purposes of this study were combined.

Sampling took place at the Pioneer Canyon site in February of 1992 and at the Monterey Canyon site in March of 1992 from aboard the R/V Point Sur. Four trawls were taken at the Pioneer Canyon site between 3,090 m and 3,300 m, and eight trawls were taken at the Monterey Canyon site between 2,620 m and 3,270 m. During each of these cruises, samples were collected 24 hours a day (Tables 2 and 3).

The time and position of the ship were recorded when each trawl first engaged the bottom and began fishing, and when it first left the bottom to begin its ascent. All positions were taken using the ship's Global Positioning System (GPS). Upon retrieval of each trawl, ophiuroids were separated from the trawl catch and preserved in 10% buffered formalin. After 5-7 days they were transferred to 70% ethanol. All individuals were identified to species and enumerated.

Because the area sampled per trawl varied, ranging from 1,867 m² to 19,793 m², all trawl samples were converted to number of individuals per 100 m². To determine the total area sampled per trawl, the great circle distance in nautical miles between latitude and longitude readings taken when the trawl first engaged and first left the bottom was

calculated using a computer program (Moss Landing Marine Laboratories VAX). This distance in nautical miles was then converted to area covered in units of 100 m².

Because it was suspected that box cores were undersampling the ophiuroid assemblage on the continental slope, box core results below 2,300 m were compared with trawl data collected within the same depth range and area off the Farallon Islands. To examine the adequacy of sampling of the two methods, cumulative species curves were compared by plotting mean cumulative species plus or minus standard deviation for ten random combinations of samples (Pielou, 1966; Hurtubia, 1973). The cumulative species curves for box cores were determined separately between 1,000-2,000 m and between 2,000-3,000 m.

To examine whether trawls sampled differently from box cores, the relative abundances of ophiuroid species below 2,300 m were compared with histograms between Farallones trawls and Farallones box cores. In addition, the percent similarity (sum of minimums, Sanders, 1960) between these two distributions was calculated.

To determine whether ophiuroid species composition and abundance patterns changed with latitude along the California coast, trawl samples below 2,300 m were compared among the Farallon Slope, Pioneer Canyon and Monterey Canyon sites. To check for any naturally occurring faunal breaks in ophiuroid species composition or abundance with either depth or sampling location, dendograms were created using Bray-Curtis cluster analysis, group average sorting and standardization on totals. Both normal and inverse classification were used. To examine adequacy of sampling, cumulative species curves were compared between the three areas. In addition, the relative abundances patterns of ophiuroid species were compared with histograms, and percent similarity (sum of minimums, Sanders, 1960) was calculated. Large scale dispersion patterns were examined by comparing the variance to mean ratio of ophiuroid species collected with trawls within each sampling location (Krebs, 1989).

RESULTS

Box Core Data

Four hundred and thirty-seven adult ophiuroids were collected and identified from box cores, and these were distributed among five families, 10 genera and 12 species (Table 4). One hundred and forty-eight juvenile ophiuroids were collected from box cores that had not yet developed the characteristic skeletal features necessary to be positively

identified. Twenty of the 68 box cores, or 29%, contained no adult ophiuroids indicating patchy spatial distribution at 0.1 m² level. Juvenile ophiuroids were collected in six of the 20 box cores that did not contain adults.

Normal classification using Bray-Curtis cluster analysis showed a general faunal break between about 1,700 and 2,200 m with a similarity between box cores taken above and below this depth range of only 3% (Figure 5). Inverse classification showed a very slight grouping of Ophiura leptoctenia and Ophiophthalmus normani (48% similarity). The rest of the species all showed similarities of less than 30%. Species most abundant above about 2,000 m grouped separately from those most abundant below about 2,000 m, with a similarity of only 4% between them (Figure 6).

There were no adult ophiuroids collected between 500-985 m. Overall abundance was greatest between 1,000-2,000 m with a peak at around 1,500 m, declined between 2,200-2,700 m and appeared to increase slightly below 2,700 m (Figure 7).

The ophiuroid assemblage on continental slope off central California was heavily dominated by two species which together comprised 80% of the individuals collected. These were Ophiura leptoctenia which made up 50% and Ophiophthalmus normani which made up 30%. These two species were most abundant between 1,000-2,000 m with a peak at around 1,500 m, and were almost entirely responsible for the large peak in ophiuroid abundance within this depth range (Figure 8). Ophiura leptoctenia occurred in greatest numbers at depths shallower than 2,205 m, but was found sporadically down to 2,945 m. Ophiophthalmus normani was not found at depths greater than 2,065 m.

The other ten ophiuroid species collected with box cores were rare and scattered in comparison. Of the 12 species collected, four were found in only one box core each and three of these four were represented by only one individual. Due to their low abundances and patchy distribution, it was much more difficult to gain a clear picture of the bathymetric distributions of these ten species. While they did show some changing patterns of mean abundance between the six, 500 m depth zones, it was difficult to say whether these patterns were real, or purely an artifact of low sample size relative to abundance (Table 5).

The six most abundant ophiuroid species collected with box cores tended to show high variance to mean ratios within most of the six, 500 m depth zones suggesting patchy spatial distributions at the 0.1 m² level (Table 5). This was confirmed by Morisita's Index of Dispersion which was highly significant for all six species tested (usually $p < 0.001$) indicating these ophiuroids were not distributed randomly. Examination of the data

revealed their distributions to be patchy rather than even (Table 6).

The relative abundance pattern of ophiuroid species changed below 2,000 m as Ophiura leptoctenia and Ophiophthalmus normani decreased in abundance (Figure 9). Between 995-1,990 m, 89% of the individuals belonged to these two species with O. leptoctenia contributing 58% and O. normani contributing 31%. The other nine species found within this depth range contributed less than 3% each. Between 2,005-3,085 m Amphiura carchara and Amphiura diomedea were relatively most abundant, but at 26% and 22% respectively, they accounted for less than 50% of the individuals. With the exception of Dougaloplus gastracantha which accounted for only 2%, the other six species present below 2,000 m contributed between 7% and 12% of the individuals each so that individuals were spread more evenly among species below 2,000 m.

The general pattern of dissolved oxygen with depth was similar at all stations sampled, and showed consistency over both space and time (Figure 10). While surface waters had high oxygen values of around 8 mg/l, between about 500 and 1,000 m oxygen levels fell below 0.7 mg/l creating an oxygen minimum zone (OMZ). Below about 1,000 m oxygen levels increased again rising above 2.8 mg/l at depths greater than 2,000 m. Tyson and Pearson (1991) have defined dissolved oxygen levels of 2.8 mg/l to denote the boundary between oxic and dysoxic conditions. Where oxygen levels rose above 2.8 mg/l, the environment changed from dysoxic to oxic.

There were no adult ophiuroids found within the OMZ (Figure 11). At the deeper edge of the OMZ, around 1,000-1,200 m, there was a large increase in ophiuroid abundance, primarily due to large numbers of Ophiura leptoctenia and Ophiophthalmus normani. The largest change in ophiuroid species composition and abundance patterns was found at about 2,000 m where dissolved oxygen rose above 2.8 mg/l and the environment changed from dysoxic to oxic (Figure 9 and 11).

Numerous sediment parameters were correlated with each other as well as with depth (Table 7). These correlations, coupled with the low numbers of individuals collected for all but the two most abundant ophiuroid species, limited analyses to qualitative comparisons among ophiuroid species distributions and sediment parameters.

Sediment grain size tended to decrease with increasing water depth. In particular percent clay, which was the smallest grain size measured, increased with increasing water depth (Figure 12). Percent clay showed greatest increases below 2,000 m where dissolved oxygen changed from dysoxic to oxic, and where the largest change in ophiuroid species composition and relative abundance patterns were found.

Organic content parameters also showed increases with increasing water depth. Percent carbon and percent nitrogen, which were highly positively correlated with each other (0.999), steadily increased with increasing water depth. They showed positive correlations with depth of 0.861 and 0.862 respectively. Percent carbonate was more loosely correlated with depth (0.664) (Figure 13 and Table 7). Percent carbon and percent nitrogen were both positively correlated with percent clay (0.626 each).

Percent organic carbon (and thus percent nitrogen) also appeared to increase at about 2,000 m where dissolved oxygen changed from dysoxic to oxic and where the largest change in ophiuroid species composition and relative abundance patterns were found. The pattern with percent carbonate was not as clear, but increases did occur at depths greater than 2,000 m.

Farallon Slope Trawls vs. Box Cores

Two thousand five hundred and eighty-nine adult ophiuroids were collected and identified from the 17 Farallon Slope trawls and these were distributed among five families, eight genera and 11 species (Table 8). Trawls sampled a much larger area of the sea floor at the Farallon Slope than did box cores, covering an average of 5,411 m² per trawl for a total area sampled of 72,208 m² (Tables 2 and 3). Each box core sampled a 0.1 m² area for a total area sampled of 2.7 m².

Cumulative species curves showed that the Farallon Slope study area had been adequately sampled with trawls below 2,300 m. It had also been adequately sampled with box cores both above and below 2,000 m. Adequacy of sampling is indicated in these cumulative species curves when the rate of increase with addition of samples changes and the curve begins to level off. The number of samples at which the curve begins to level off is considered the minimum number of samples necessary to adequately characterize the ophiuroid assemblage in the area (Pielou, 1966; Hurtubia, 1973). The standard deviation around the mean indicates the amount of variability in number of species collected among samples.

As can be seen from the cumulative species curves for box cores at the Farallon Slope (Figure 14), it took about 20 to 21 box cores to adequately sample the ophiuroid assemblage between 1,000-2,000 m, and about 10 to 11 box cores to adequately sample this assemblage between 2,000-3,000 m. The somewhat erratic variation in the standard deviation around the mean with increasing number of samples in these two curves, especially within the shallower depth range, indicates wide variation in the number of

species collected among box cores. As can be seen from the cumulative species curve for Farallon Slope trawls (Figure 15), it took only about six or seven trawls to adequately sample the ophiuroid assemblage within this depth range and area. Here the standard deviation steadily decreased with increasing number of samples indicating there was less variation in the number of species collected among trawls.

Relative abundance histograms comparing trawl and box core data collected at the Farallon Slope below 2,300 m show that box cores completely missed almost 50% of the ophiuroid species collected by trawls, and many of those missed were abundant in trawls (Figure 16). Ophiocten hastatum, for instance, was the third most abundant species collected in trawls and Ophiomusium glabrum the fifth. Neither species was ever collected in box cores. Several species, such as Amphiura diomedea and Amphiura otteri, were collected relatively more in box cores than trawls. The most notable similarity in ophiuroid distribution patterns between trawl and box core collections was that Amphiura carchara was the most abundant species. Percent similarity between these two distributions was 60%.

Farallon Slope vs. Pioneer Canyon vs. Monterey Canyon Trawls

Six thousand one hundred and ninety adult ophiuroids were collected and identified from the 29 trawls taken at the Farallon Slope, Pioneer Canyon and Monterey Canyon sites. These were divided among the three sites as follows: From the 17 Farallon Slope trawls there were 2,589 individuals from five families, eight genera and eleven species. From the four Pioneer Canyon trawls there were 441 individuals from four families, five genera and seven species. From the eight Monterey Canyon trawls there were 3,160 individuals from five families, seven genera and nine species (Table 9).

Normal classification using Bray-Curtis cluster analysis showed grouping of trawls by depth as well as a slight grouping of trawls by area (Figure 17). There did not appear to be any major faunal differences among seasons, as trawls collected at the Farallon Slope in July of 1991 and February of 1992 were found within the same clusters.

Trawls taken within the 2,300 to 2,700 m depth range grouped separately from trawls taken deeper than 2,700 m, suggesting an ophiuroid faunal break at around 2,700 m. Although there were only four trawls taken shallower than 2,700 m, three of these four showed a 72% similarity to each other, and only a 9% similarity to the deeper trawls. Among the trawls taken deeper than 2,700 m, Monterey trawls tended to group together (greater than 58% similarity), and Farallon and Pioneer trawls tended to group together

(greater than 58% similarity). Monterey trawls were only 48% similar to Farallon and Pioneer trawls indicating some ophiuroid faunal differences between the Monterey Canyon site and the Farallon Slope and Pioneer Canyon sites.

Inverse classification showed a slight tendency for some ophiuroid species to be found together more often (Figure 18). For instance, there was a 53% similarity between Amphilepis platytata and Amphiura carchara and a 40% similarity between Amphiura diomedea, Ophiolimna bairdi and Ophiocten hastatum. Five of the remaining seven species showed a similarity to these two groups of less than 6%.

Cumulative species curves showed that while the Farallon Slope and Monterey Canyon sites were adequately sampled, not enough samples were taken at the Pioneer Canyon site to tell whether or not it had been adequately sampled (Figure 19). The Farallon Slope cumulative species curve leveled off after about six or seven trawls, indicating that six to seven trawls were adequate to sample the ophiuroid assemblage there. The Monterey Canyon cumulative species curve leveled off after only three or four trawls, indicating that half as many trawls were needed to adequately sample the ophiuroid assemblage at the Monterey Canyon site as opposed to the Farallon Slope site. The Pioneer Canyon cumulative species curve had not yet leveled off after four trawls so it is not known whether four trawls were adequate to sample the ophiuroid assemblage at this location.

Percent similarity generally decreased with increasing distance between sampling areas, indicating a change in ophiuroid species composition and abundance with latitude along the California coast (Table 10). The exception was the Pioneer Canyon site which was slightly less similar to the Monterey Canyon site (a distance of 88 km) than the Farallon Slope site was (a distance of 145 km). Trawls taken at the Farallon Slope and Pioneer Canyon sites, which were separated by 56 km, showed an 82% similarity. Trawls taken at the Farallon Slope and Monterey Canyon sites, which were separated by 145 km, showed only a 58% similarity. Trawls taken at the Pioneer Canyon and Monterey Canyon sites, a distance of 88 km, showed a 50% similarity. Farallon box cores were slightly more similar to Farallon trawls (60%) than to either Pioneer (55%) or Monterey trawls (56%), but these results indicate that box core samples were not very similar to trawl samples regardless of location.

Percent similarity results also did not show obvious seasonal differences in ophiuroid species composition or abundance over the course of this study. Pioneer Canyon trawls taken in February of 1992 were slightly more similar to Farallon Slope

trawls taken in July of 1991 (82%) than to Farallon trawls taken in February of 1992 (77%). Farallon trawls taken in July of 1991 and February of 1992 showed an 83% similarity to each other (Table 10).

A comparison of relative abundances of ophiuroid species among the three areas trawled reflected the percent similarity results, with the Monterey Canyon site showing different patterns than either the Farallon Slope or Pioneer Canyon sites (Figure 20). At the Farallon Slope and Pioneer Canyon sites, Amphiura carchara and Amphilepis platytata were relatively most abundant, together comprising 76% and 91% of the total number of individuals respectively. At the Farallon Slope A. carchara contributed 50% and A. platytata contributed 26%, whereas at Pioneer Canyon A. carchara accounted for 58% and A. platytata accounted for 33%. The rest of the species present in these two locations contributed less than 6% each.

At the Monterey Canyon site, Amphilepis platytata and Ophiolimna bairdi were relatively most abundant, but together accounted for only 52% of the total number of individuals. Amphilepis platytata accounted for 31% and O. bairdi accounted for 21%. Amphiura carchara, the most abundant species at the other two locations, ranked third in Monterey with 13%. Three additional species were also relatively more abundant in Monterey. These were Ophiocten hastatum at 11%, Amphiura diomedae at 11% and Amphiura otteri at 10%. Individuals were spread more evenly among species at the Monterey Canyon site, whereas the Farallon Slope and Pioneer Canyon sites were more heavily dominated by just a few.

Several species were not collected from all three of the trawl study sites (Table 9). Ophiacantha cf. pacifica was not found at the Farallon Slope, Ophiacantha eurypoma was not found at Pioneer or Monterey canyons and Ophiura bathybia was not found at Monterey Canyon. All three of these species, however, were rare and may have been present at all locations but missed due to their low numbers. This may be especially true for Pioneer Canyon which may not have been adequately sampled.

Ophiura leptoctenia was not collected at the Pioneer or Monterey canyon sites. This species was found to be most abundant with box cores between 1,000-2,200 m, however, and whereas the Farallones trawls sampled as shallow as 2,300 m, the Pioneer and Monterey trawls were all deeper than 2,600 m.

The variance to mean ratios of ophiuroid species abundances within each of the three trawl sampling locations tended to be fairly high for the more abundant species. This indicated some patchiness in the ophiuroid assemblage on the continental slope on

the scale of hundreds or even thousands of square meters (Table 11).

DISCUSSION

Comparison of Sampling Methods

A combination of lifestyle habits and morphological characteristics make ophiuroids a difficult taxon to adequately sample in the deep-sea. Members of the families Amphiuridae and Amphilepididae live semiburied in the sediment with only the tips of their arms sticking out to gather detrital food, and are effectively members of the infaunal community. Species belonging to the families Ophiuridae and Ophiacanthidae tend to be mobile epifaunal animals that crawl around on the seafloor searching for food, or perch on sessile epifauna or rocky outcrops with their arms outstretched into the water column (Gage and Tyler, 1991; Gordon Hendler, pers. comm.). Members of the family Asteronychidae such as Asteronyx loveni live almost exclusively above the sea floor with several arms wrapped around a gorgonian or pennatulid. From their perch about 20 to 35 cm above the sediment surface they catch small pelagic organisms with their free arms (Fujita and Ohta, 1988). In addition to a variation in lifestyle habits, ophiuroid species range in size from disk diameters of only a few centimeters to those over 40 cm. As their name suggests, all brittlestars have fragile morphologies, although robustness varies among species. It is rare to collect a deep-sea ophiuroid with all its arms intact, and many arrive on board in a mass of broken arms and torn discs.

A comparison of box core and trawl samples collected below 2,300 m at the Farallon Slope study site highlights some of the unique sampling problems presented by deep-sea ophiuroids. While it took only 10 to 11 box cores to adequately sample the ophiuroid assemblage between 2,000 and 3,000 m on the continental slope off central California (Figure 14), box cores missed almost 50% of the ophiuroid species collected by trawls within this same depth range and area (Figure 16). Box cores are primarily designed to sample small infaunal organisms. Because of this there is a bias associated with sampling animals with box cores that are as large and patchy as ophiuroids. Box cores therefore adequately sampled only those ophiuroid species they were likely to collect which were smaller, less patchy or more abundant species. Box cores also sampled a very small portion of the sea floor compared to trawls. It appears that the 0.1 m² area sampled for infauna from box cores was smaller than the average patch size for these ophiuroid species. This led to wide variation among samples in both number of

species collected and number of individuals. In contrast, it took only six to seven trawls to adequately sample almost twice the number of ophiuroid species in this same ophiuroid assemblage (Figure 15). Because trawls sampled a much larger area than box cores, covering an average at the Farallon Slope of 5,411 m² per trawl as opposed to 0.1 m² per box core, it took much less time and effort to adequately sample the ophiuroid assemblage on the continental slope with trawls. In addition, there was less variation among trawl samples in the number of ophiuroid species collected suggesting that the large area sampled by trawls was greater than small scale patch size.

Despite the bias associated with box core sampling, box cores are a useful tool for sampling ophiuroids. Some of the advantages of box cores over trawls are that they are able to sample a discrete area and depth of the sea floor, and bring all ophiuroids they encounter to the surface in a relatively undisturbed manner. This makes it possible to examine small scale patchiness of ophiuroids, as well as measure density of animals per unit area. Trawls on the other hand, may bounce along the sea floor often covering depth ranges of 100 m or more, and lose undetermined numbers of ophiuroids through the net mesh. It is therefore not possible to examine small scale patchiness with trawls because they combine all patches they encounter into one sample. Nor is it possible to determine accurate densities per unit area. Unlike trawls, box cores also allow for collection of data on associated sediment characteristics along with ophiuroids, which give insight into the physical environment these animals inhabit.

A comparison of the relative abundances of ophiuroid species between box cores and trawls showed that box cores missed almost 50% of the species collected by trawls within the same depth range, and many of those were very abundant in trawls (Figure 16). The disparity in sampling area between box cores and trawls can explain why many of these species were missed by box cores. A maximum of 1,268 individual ophiuroids divided among nine species were collected in a single trawl in this study whereas the maximum collected in a single box core was only 49 individuals divided among three species. Because box cores sampled such a small area, they were more likely to miss patchy or rare species.

Some of the differences in relative abundance patterns between box cores and trawls can also be attributed to size and morphological variations among species. Ophiomusium glabrum was the largest ophiuroid found in this study with a disc diameter of up to 40 mm and was collected in trawls but not box cores. The 0.1 m² box core very rarely collected large animals of any species because there are fewer per unit area and

they are thus more likely to be missed by such a small box core. Amphiura otteri was collected relatively more in box cores than trawls. It is a very fragile species and was therefore preserved better in box cores. Trawls mangled these delicate animals and a disproportionate number were probably lost through the net mesh. Asteronyx loveni was collected in trawls but not box cores probably because it is almost always found above the sediment surface attached to seaweeds. Trawls would tend to catch animals living above the sea floor, whereas box cores would not. Box cores and trawls each had limitations so that neither were sufficient to completely sample the entire ophiuroid assemblage on the continental slope. Because of this, some combination of both may be best.

Ophiuroid distribution patterns from camera sled data were not analyzed for this study because it was usually impossible to identify individual species from photographs, and many species were not visible. While camera sled data have contributed valuable in situ information regarding spatial distribution patterns and inter- and intraspecific interactions for many large epifaunal invertebrates, the variations in lifestyle habits and morphological characteristics of ophiuroids mentioned earlier limit the usefulness of camera sled data for this taxon. Despite these limitations, photographic techniques currently offer the only insight into ophiuroid in situ interactions.

Bathymetric Distribution

As expected, ophiuroids collected on the continental slope off central California showed changes in species distribution and abundance patterns with increasing depth (Figures 5 and 7, and Table 5). Ophiuroids collected with box cores between 550 and 3,085 m showed two general faunal breaks, one at about 1,000 m and another at about 2,000 m. Ophiuroids collected with trawls between 2,300 and 3,300 m showed a general faunal break at about 2,700 m (Figure 17). The faunal break detected with trawls must be interpreted with caution because very few of the 29 trawls were taken between 2,300 and 2,700 m, and unlike box cores which sampled a discrete depth, trawls in this study sampled depth ranges of between 5 m and 325 m (mean of 107 m) per trawl (Tables 2 and 3). Although there does appear to be some sort of a faunal break occurring here, its precise location remains unclear due to the overlapping depths sampled by trawls.

Zones of rapid faunal change separated by zones of relative faunal homogeneity have been reported in other areas of the world's oceans (Astrahantseff and Alton, 1965; Haedrich et al., 1980; Percy et al., 1982; Gage et al., 1985; Carey, 1990; Hecker, 1990).

The exact number and location of faunal breaks vary between oceans depending on local topographic variation and the animal group being examined. This has led to numerous schemes to subdivide the ocean vertically into bathymetric zones, each with its own terminology (reviews in Menzies et al., 1973 and Carney et al., 1983). Although generalizations are difficult, faunal breaks often correspond with the boundaries between the continental shelf, slope, rise and abyssal plane. Because of these disparities, no further attempt will be made to correlate ophiuroid distribution on the continental slope off central California with distribution schemes found in other studies from around the world. It seems more appropriate to look for local rather than global causes to zonation.

Only two ophiuroid species were collected in high enough numbers with box cores to adequately discern their distribution patterns with depth. These two species were Ophiura leptoctenia and Ophiophthalmus normani (Figure 8). The other ten species collected did show some changing patterns of mean abundance with depth (Table 5), but because they were rare and scattered in their distributions it was impossible to tell if the observed patterns were real, or merely an artifact of low sample size relative to abundance. For this reason, no detailed analysis of the bathymetric distribution patterns of these ten ophiuroid species will be made, and analysis will focus instead on the possible causes of zonation. Finding a few abundant species and many rare ones within a taxonomic group is typical of many benthic studies (Grassle et al., 1975; Boesch, 1977).

While the results of this study indicate that ophiuroids on the continental slope off central California show changing patterns of zonation with depth, the causes of this zonation are not as clear. Biological controls such as predation and intra- and interspecific competition most likely play a role in regulating the distributions of deep-sea ophiuroids, as has been found in shallow water (Austin and Hadfield, 1980; Sides, 1984; Oliver et al., 1985; Sides and Woodley, 1985). Presently, however, no adequate means for examining these interactions among species under natural conditions in the deep-sea have been devised (Gage and Tyler, 1982). There is some evidence that predation may be high. Smith (1985) found that at least three predators were drawn to high concentrations of the ophiuroid Ophiophthalmus normani, which were attracted to bait in water depths of 1,300 m in Santa Catalina Basin. These predators were the rockfish Sebastes altivelis, the asteroid Nearchaster aciculosus and the crab Paralomis multispina. Smith concluded that all three preyed on O. normani because O. normani showed avoidance behavior in the presence of the starfish and crab, and was found in high numbers in the rockfish gut. Off the coast of central Oregon between 46 and 4,260 m, ophiuroids were found in the gut

contents of 13 of the 29 asteroid species examined, and were the dominant food items for many (Carey, 1972). Ten of these asteroid species were collected between 500 and 3,000 m, the depth range of this study.

There are numerous physical parameters that change with depth that could potentially influence the distribution of ophiuroids on the continental slope off central California. Of these, three were examined in this study: dissolved oxygen, sediment grain size and sediment organic content.

Off the coast of central California is a well developed seasonal upwelling system that leads to high planktonic productivity in surface waters. As this photodetritus sinks to the ocean floor it creates an oxygen minimum zone (OMZ) centered around 800 m and a changing pattern of dissolved oxygen with depth (Figure 10; Thompson, 1983). This pattern is remarkably consistent over time (Vercoutere et al., 1987). Numerous studies on the continental shelf and slope have found that dissolved oxygen concentrations can strongly influence the distribution of macro- and microfauna, and thus their effects on bottom sediment characteristics such as sediment grain size and organic content (Thompson, 1983; Mullins et al., 1985; Vercoutere et al., 1987). While the core of the OMZ tends to be faunally depauperate, the edges or boundaries are usually highly productive areas of increased biological activity and organic enrichment (Thompson, 1983; Mullins et al., 1985; Vercoutere et al., 1987; Rhoads et al., 1991).

In this study, the OMZ fell between about 500 and 1,000 m where oxygen levels dropped below 0.7 mg/l, and although only five box cores were taken within this depth range, no adult ophiuroids were found here (Figure 11). This is consistent with Thompson (1983) who found that the core of the OMZ off Big Sur in central California was devoid of ophiuroids. Two box cores within the OMZ did contain juvenile ophiuroids. Juvenile organisms are often relatively more tolerant of low oxygen because of their lower respiratory demands and more favorable surface area to volume ratios (Tyson and Pearson, 1991). It may be that these juvenile ophiuroids represent non-viable settlement in an area unfavorable to adults as was found by Gage and Tyler (1981a) for ophiuroids in the Rockall Trough.

At the lower edge of the OMZ, there was a large increase in ophiuroid abundance (Figure 11). These findings are also consistent with Thompson (1983) who reported that ophiuroids were most abundant at the lower edge of the OMZ. It is possible that the two species primarily responsible for this increase, Ophiura leptoctenia and Ophiophthalmus normani, are exhibiting what is referred to as OMZ "edge effects" (Mullins et al., 1985).

At the lower edge of the OMZ, in addition to higher oxygen levels, nutrient concentrations are increased and there is a larger food supply in the form of bacteria (Thompson, 1983; Mullins et al., 1985; Vercoutere et al., 1987).

When dissolved oxygen levels fall below 2.8 mg/l, the environment changes from oxic to dysoxic (Tyson and Pearson, 1991). The term "dysoxic" is generally used to indicate that range of oxygen values associated with the dysaerobic biofacies, and is defined by Tyson and Pearson (1991) to be oxygen values between 2.8 and 0.3 mg/l. When the partial pressure of dissolved oxygen falls below about 2.8 mg/l it becomes a first-order ecological factor affecting the distribution of marine benthos (Tyson and Pearson, 1991). In this study, dissolved oxygen levels rose above 2.8 mg/l below about 2,000 m, and the environment changed from dysoxic to oxic (Figure 10). Two thousand meters was also where the largest change in ophiuroid species composition and relative abundance patterns were found (Figure 9). It may be that ophiuroids living on the continental slope off central California respond differentially to the partial pressure of dissolved oxygen, and that species dominant below 2,000 m are more oxygen sensitive and do better in oxic conditions.

The two other physical parameters measured in this study also changed with depth. While sediment grain size decreased with increasing water depth (Figure 12), organic content increased (Figures 13). These results are in agreement with Vercoutere et al. (1987) from the continental slope northwest of Point Sur, CA. They report that the most conspicuous feature in the distribution of total organic carbon (TOC) in surface sediments is its increase with both increasing water depth and increasing clay content. They also report that the TOC content of surface sediments surprisingly mimics the distribution curve for dissolved oxygen versus water depth.

In this study, both percent clay and percent organic carbon qualitatively appeared to show greatest increases at around 2,000 m where the environment changed from dysoxic to oxic and the largest change in relative ophiuroid species abundance patterns occurred. While ophiuroid species may be responding differentially to the partial pressure of dissolved oxygen, they may also be responding to increases in the amount of available food in the form of organically enriched sediment.

Most deep-sea ophiuroids appear to be omnivorous, feeding on detritus in the sediment or small epi- or infaunal organisms (Tyler, 1980; Pearson and Gage, 1984; Gage and Tyler, 1991). The diets of most of the ophiuroid species collected in this study, however, have never been examined. In their study of the diets of six deep-sea brittle

stars in the Rockall Trough, Pearson and Gage (1984) attributed slight dissimilarities in diet between species to differences in lifestyle. The more motile epifaunal species of the family Ophiuridae showed the greatest variety in food items.

The two ophiuroid species dominant between 1,000 and 2,000 m in this study, Ophiura leptoctenia and Ophiophthalmus normani, are most likely mobile scavengers. Ophiophthalmus normani was observed to congregate in huge numbers around a baited time-lapse camera in the Santa Catalina Basin, and was occasionally seen capturing small pelagic fish and medusae with its arms (Smith and Hamilton, 1983; Smith, 1985). While no direct feeding observations of O. leptoctenia exist, it is a member of the family Ophiuridae which are active bottom-crawling species that 'row' over the sediment surface using their flexible arms to scavenge for food. It has been reported to feed on detritus and small animals including cumaceans (Tyler, 1980). Amphiura carchara and Amphiura diomedea, the two ophiuroid species dominant between 2,000 and 3,000 m, are both members of the family Amphiuridae. Species in this family usually live semiburied with only the ends of their long arms exposed to explore the sediment surface for detrital food (Gage and Tyler, 1991).

This changing pattern of dominance in ophiuroid species from mobile scavengers to deposit feeders with depth on the continental slope off the central California coast may reflect changes in food availability with depth. Off the coast of Oregon, Carey (1972) examined the diets of numerous asteroid species and found a general decrease in predation with depth. He concluded that food quality and supply is a regulator of faunal abundance and energy use in the deep-sea. In addition, as depth increases and prey density decreases, organisms will become less specialized feeders and will tend toward deposit-detrital and omnivorous feeding. This trend has also been suggested by others (Sokolova, 1959; Sibuet, 1985; Gage and Tyler, 1991). Where there is sufficient oxygen at the sea floor, sediment variation, especially as a food supply, probably plays an important role in ophiuroid distribution (Carney et al., 1983; Levin et al., 1991).

Spatial Distribution

The ophiuroid assemblage on the continental slope off central California exhibited a patchy spatial distribution on both a small scale of around 0.1 m² (box cores) and a large scale of hundreds or even thousands of square meters (trawls). Small scale patchiness was evident in the large percentage of box cores that contained no adult ophiuroids (29%), in the high variance to mean ratios of species abundances within most

500 m depth intervals (Table 5) and in the highly significant values of Morisita's Index of Dispersion for species collected with box cores (Table 6). Large scale patchiness was evident in the large variance to mean ratios of species abundances collected with trawls within each of the three sampling locations along the California coast (Table 11), and was also supported by camera sled observations (Hecker Environmental Consulting, 1992). Camera sled transects frequently traveled through areas 300 m long or more where ophiuroid abundances were visibly high, then equal distances where almost no ophiuroids were seen (Susan Craig and Lisa Weetman, pers. comm.). The camera sled data was of limited use, however, because it was usually impossible to tell ophiuroid species apart from photographs.

Spatial distribution patterns of deep-sea benthic megafauna have been found in other studies to vary from random to regular to aggregated depending upon the organism being examined, and the spatial scale being analyzed. Further variations in dispersion patterns may be found for a single organism at different depths, and at different population densities (Grassle et al., 1975; Jumars and Eckman, 1983; Carey et al., 1990b). Spatial distribution patterns of deep-sea ophiuroids are particularly difficult to discern due to their often cryptic lifestyle and relatively small size. Many species live buried or semiburied in the sediment, and those that are exposed are hard to identify visually with camera sleds or other photographic techniques commonly used to examine dispersion patterns among deep-sea organisms (Hecker Environmental Consulting, 1992).

An exception is the large cosmopolitan deep-sea ophiuroid Ophiomusium lymani. This animal is a surface deposit feeder and because of its large size generally shows up well in photographs and is not easily confused with other ophiuroid species. Grassle et al. (1975) did a thorough examination of the spatial distribution of O. lymani and found that at low densities it was weakly aggregated at all three spatial scales examined, but at high densities its distribution pattern changed. At high densities O. lymani showed a regular spacing pattern among individuals at the smallest scale examined, but as the scale increased this pattern became random. The patchiness of O. lymani at low densities was attributed to avoidance of disturbed areas on the sea floor. At high densities individuals were observed to actively space themselves so that the tips of their arms were not touching. As is evident from these results, the nature and causes of dispersion patterns may be complex even for a single species.

While this study did detect patchiness in the ophiuroid assemblage on the continental slope off central California at several spatial scales, it was not designed to

examine the finer details of spatial distribution. Potential causes therefore remain speculative. It has been reported by other authors that deep-sea echinoderms congregate in high nutrient areas, and consequently tend to exhibit highly patchy distribution patterns (Pawson, 1976; Billett, 1991). Nutrient availability may play a role in the aggregated distribution patterns of ophiuroids in this study. Deep-sea benthic habitats are far from homogeneous, and the continental slope off central California is no exception. Camera sled photographs taken in Area 5 at the Farallon Slope study site in conjunction with box core and trawl operations showed variations in benthic microtopography from undisturbed areas of relatively smooth featureless sediment to highly disturbed areas covered by mounds and depressions due to biological activity (Hecker Environmental Consulting, 1992). Large scale differences in bottom topography that influenced sediment deposition and accumulation were also present within the area sampled by box cores. Three depositional sites of low kinetic energy were identified that tended to occur at the base of a canyon or trough, and these were found to have higher concentrations of organic matter than the steeper sides or flanks (Blake et al., 1992; SAIC, 1992). Given these apparent small and large scale variations in topographic relief that regulate the distribution of sediment grain sizes and concentrations of organic matter, it seems likely that the spatial distribution of ophiuroids may also be influenced by nutrient availability.

Other factors that could potentially influence the spatial distribution pattern of deep-sea ophiuroids on the continental slope off central California that were not examined in this study include behavior patterns stemming from activities such as reproduction, predation and competition. A general observation from trawl and camera sled data collected at the Farallon Slope and Monterey Canyon sites was that brittlestars were either absent or present only in low numbers in areas where large herds of elasipodid holothurians were found. Out of the 29 trawl samples collected in this study, the only two without brittlestars were collected in Monterey Canyon and each contained close to 3,000 holothurians, the majority being Scotoplanes globosa, Peniagone cf. incerta and Elpidia cf. theeli (Nybakken et al., 1992a and b). Camera sled photographs confirmed these observations indicating that lack of brittlestars was not purely an artifact of trawl sampling (Susan Craig and Lisa Weetman, pers. comm.). Holothurians of the order Elasipodida are mobile surface deposit feeders that walk on modified ventrolateral tubefeet "legs" picking up soft surface sediments with their tentacles (Hansen, 1975). They are often found in large herds in or near canyon systems and have been reported in abundances as high as 500,000 individuals per hectare (Billett, 1991). While these

holothurians are attracted to nutrient rich areas that would seem to be favorable to ophiuroids, their sheer numbers may exclude ophiuroids by disturbance.

Alternately, ophiuroid dispersion patterns may reflect a dependence on sediment transport. Camera sled data showed that small white ophiuroids were often found in association with seapen beds (Order Pennatulacea) at the Farallon Slope site (Hecker Environmental Consulting, 1992). Seapens are filter feeders and would seem to prefer areas where organic matter was suspended in the water column by currents (Gary Williams, pers. comm.). While these ophiuroids were often found nestled at the base of seapens as if for protection, it may be they are attracted to these areas because of higher availability of suspended food. Gage and Tyler (1991) have postulated that large-bodied epifaunal deposit feeders such as elasipodid holothurians may become favored in areas where the flow regime is fairly quiet. If this is the case, an alternate explanation of why ophiuroids were not found with large elasipodid herds is that current speeds were too slow to suspend organic matter into the water column. What factors regulate the dispersion patterns of deep-sea ophiuroids will remain speculative until more information on the life history of individual species is gathered. As with bathymetric distribution, it is most likely that a number of different mechanisms interact to regulate the spatial distribution of different species of ophiuroids at different times.

Local Zoogeographic Distribution

Latitudinal changes in ophiuroid species composition and abundance patterns were observed on the continental slope below 2,300 m along the central California coast between the Farallon Slope and Monterey Canyon, with greatest changes occurring between sites that were farthest apart (Table 10). The closest sites, Farallon Slope and Pioneer Canyon, were most similar to each other (80%), and were both less similar to the Monterey Canyon site (60% and 50% respectively). The Farallon Slope site showed a slightly higher similarity to Monterey Canyon than did the Pioneer Canyon site which was 56 km closer. However, both the Farallon Slope and Monterey Canyon sites were adequately sampled, whereas it is not known whether this was true for the Pioneer Canyon site (Figure 19). If more trawls had been taken at Pioneer Canyon the similarity with Monterey Canyon may have increased. When the twenty most abundant species of all taxa collected in trawls was compared among the Farallon Slope, Pioneer and Monterey Canyon sites, similarity decreased regularly as distance between sites increased (Nybakken et al., 1992b).

Comparison of relative abundance patterns of ophiuroid species between the three geographic locations indicated that animals were spread more evenly among species at the Monterey Canyon site (Figure 20). Although many of the same species were found at all three locations, individuals were proportioned differently among species in Monterey. In addition, it took only half as many trawls to adequately sample the ophiuroid assemblage at the Monterey site as it did at the Farallones site, indicating a more homogeneous environment in Monterey (Figure 19).

These differences may be due to a number of factors including the degree of microhabitat heterogeneity and the amount of available nutrients. In all three areas, trawls were taken near the base of submarine canyons on flat areas of relatively low topographic relief. However, from qualitative examination of trawl catches and camera sled data it appeared that the three areas differed (Hecker Environmental Consulting, 1992; Susan Craig and Lisa Weetman, pers. comm.). Local topographic variation and difference in the depositional environment between sites may have influenced ophiuroid abundance patterns.

Camera sled photographs taken at both the Farallon Slope and Monterey Canyon sites in 1991 and 1988 respectively showed the benthic environment at the Farallones site to contain more variety in microtopography than the Monterey site. Whereas the Farallones site ranged from smooth sediment to rocky outcrops to areas covered by mounds and depressions, the Monterey site appeared to be a more uniform, sedimentary environment. The Farallones also seemed to contain more discrete faunal patches and areas of zonation, whereas animals seemed more evenly distributed in Monterey (Nybakken et al., 1992b; Susan Craig and Lisa Weetman, pers. comm.). The Monterey Submarine Canyon is one of the largest underwater canyons on the west coast of North America and is much larger and deeper than either the Pioneer Canyon or the canyon at the Farallon Slope site. At depths of around 3,000 m where trawl samples were collected, the Monterey Canyon opens onto the head of the Monterey Deep-Sea Fan (Greene, 1977; Allen, 1982). This deep-sea fan extends for many kilometers probably leading to greater homogeneity in bottom topography.

The huge size of the Monterey Canyon may also lead to greater sediment and organic accumulation from both down-canyon flow and settlement of photodetritus from planktonic blooms. Sediment and organic debris from all over Monterey Bay are funneled into the Monterey Submarine Canyon, and large scale turbidity flows are probably not uncommon. This nearshore supply of deep, cold canyon water may also lead to greater

intensities of upwelling. The area off Pt. Sur, near the Monterey Canyon site sampled in this study, is one of the major upwelling centers along the west coast of California (Breaker and Broenkow, 1989). This scenario of greater sediment and organic accumulation is supported by the higher numbers of holothurians found at Monterey Canyon, especially of the order *Elasipodida*. As mentioned earlier, these animals thrive in organic rich environments, and are believed to be opportunistic species adapted to live in unstable sedimentary environments (Billett, 1991).

Another general difference between the Farallon Slope and Monterey Canyon sites was that while large seapen beds were quite common in the Farallones (Hecker Environmental Consulting, 1992), seapens were sparse in Monterey Canyon and were never found in large beds (Nybakken et al., 1992b; Susan Craig and Lisa Weetman, pers. comm.). This disparity in seapen populations between the Monterey and Farallones sites gives further clues as to the nature of these deep-sea environments. Sessile, filter feeding seapens probably need areas of constant water circulation to thrive (Gary Williams, pers. comm.).

In summary, circumstantial evidence suggests that the Farallon Slope and Pioneer Canyon sites are areas of greater microtopographic variability and higher water motion, whereas the Monterey Canyon site appears to be more homogeneous and depositional in nature. The change in ophiuroid species relative abundance patterns between the two northern sites and Monterey Canyon most likely reflect these disparities.

While regional habitat characteristics affect ophiuroid distribution patterns, latitudinal gradations in physical parameters such as temperature, salinity and nutrient availability are also important (Pielou, 1979). Due to a general decrease in water temperature with increasing latitude, a given faunal zone occupies progressively shallower depths at higher latitudes. Given adequate dispersal of larvae in the water column, a species' geographic range is limited by its tolerance to such variables as temperature and pressure (Pielou, 1979).

Clark (1911) described two general ophiuroid faunistic groups for the North Pacific Ocean, the Oceanic and American. The Oceanic group is comprised of species that occur throughout the entire North Pacific from both the Asiatic and American coasts. These species generally have wide bathymetric and temperature ranges and were described by Clark (1911) as "a hardy and adaptable group, able to live and apparently prosper under very diverse conditions." The American group is comprised of species known to occur only off the west coast of North America from the Alaskan Peninsula

south to California. They tend to have more restricted bathymetric and temperature ranges. Of the 16 identifiable ophiuroid species collected in this study, nine fit into the Oceanic group, three fit into the American group, and the remaining four have not been encountered enough to determine their affinity (Table 12). Three of the nine species in the Oceanic group, Asteronyx loveni, Amphiura otteri and Ophiocten hastatum, are cosmopolitan in their distributions. Among the Oceanic species, all but one are reported to have bathymetric ranges of over 2,000 m (Table 12; Clark, 1911; Koehler, 1914; D'yakonov, 1954; Maluf, 1988).

It is reasonable that a majority of ophiuroid species collected between 550 and 3,085 m off the central California coast fit into the Oceanic faunistic group. This study took place in what is referred to as the Archibenthal Zone which is transitional between the Shelf and Abyssal Zones, and at most latitudes falls on the continental slope (Menzies et al., 1973; Pielou, 1979). The unique location of the continental slope between the continental shelf and abyssal plain greatly influences the nature of its sediments. The changeover from the terrigenous sediments of the continental shelf to the oceanic clays and pelagic oozes of the abyss occur here, leading to a wide range of sediment types. Ophiuroid species with wide bathymetric distributions on the continental slope are well suited to a variety of sedimentary environments, and it has been shown that the extent of a species' geographic range depends on its bathymetric depth range. The more eurybathic a species is, the greater its geographic range tends to be (Pielou, 1979). The proportion of geographically wide-ranging species has been found to be greatest among members of the Archibenthal Zone fauna, and data from this study support these findings (Vinogradova, 1959; Menzies et al., 1973; Pielou, 1979).

Although seasonality was poorly sampled in this study, temporal changes in ophiuroid species composition and abundance patterns on the continental slope off central California appeared negligible. Trawls collected at the Pioneer Canyon site in the spring of 1992 were more similar to trawls collected at the Farallon Slope site in the summer of 1991 (82%) than the spring of 1992 (77%) (Table 10). Seasonal variations in reproduction leading to changes in population size structure among ophiuroid species have been reported for deep-sea ophiuroids in the Atlantic (Schoener, 1968; Gage and Tyler, 1981a; Tyler, 1986). While such seasonality may exist on the continental slope off central California, these patterns would have been missed in this study. Trawl sampling took place during two seasons but did not retain small individuals. Box core sampling, which did retain small individuals, only took place during the summer. Seasonal

reproductive patterns in deep-sea ophiuroids have been suggested to be tied to seasonal changes in the downward flux of surface produced organic matter (Tyler, 1986). Given the seasonal upwelling pattern off the central California coast (Bolin and Abbott, 1963), reproductive seasonality in these deep-sea ophiuroids seems likely. In order to gain a better understanding of the nature and scale of temporal changes in deep-sea ophiuroid populations in the Northeastern Pacific, more intensive sampling is needed during different seasons within the same study location as well as seasonal sampling with box cores.

Summary

Physical and biological factors regulating the bathymetric, spatial and zoogeographic distribution of ophiuroids on the continental slope off central California remain speculative due to a lack of basic life-history information on individual species. Compounding this is the fact that the deep-sea environment worldwide, and off the central California coast in particular, is poorly understood. From circumstantial evidence, many of the factors regulating ophiuroid distribution appear to be similar both vertically and horizontally, and to act on various spatial scales. It seems likely that dissolved oxygen levels, food availability, predation, competition, and habitat heterogeneity are all significant and that the relative importance of these factors and the spatiotemporal scales on which they operate vary both bathymetrically and geographically. Differential tolerances and responses of individual ophiuroid species to these factors presumably regulate distributions. More research into the biology and life-history of North Pacific deep-sea ophiuroids is sorely needed and would be aided greatly by the development of more appropriate methods to sample these cryptic, fragile animals in their own environment.

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Table 1. Summary of 1990 and 1991 box core station information from the Farallon Slope study site.

STATION	DATE	DEPTH (m)	LATITUDE (N)	LONGITUDE (W)
S-19	13 Aug. 90	2,580	37°38.41'	123°24.36'
I-19	13 Aug. 90	2,835	37°38.38'	123°27.77'
E-19	14 Aug. 90	2,955	37°38.40'	123°29.21'
F-17	14 Aug. 90	2,945	37°38.96'	123°28.83'
K-15	14 Aug. 90	2,830	37°39.38'	123°27.23'
L-17	14 Aug. 90	2,855	37°38.94'	123°26.85'
Q-15	14 Aug. 90	2,752	37°39.53'	123°25.01'
E-7	15 Aug. 90	2,462	37°41.64'	123°29.16'
J-13	15 Aug. 90	2,770	37°40.01'	123°27.45'
N-13	15 Aug. 90	2,623	37°40.01'	123°26.06'
EPA-1	15 Aug. 90	1,263	37°23.94'	123°14.86'
B-1	18 July 91	2,255	37°39.64'	123°30.02'
B-2	19 July 91	2,701	37°40.36'	123°27.96'
B-3	20 July 91	2,385	37°40.06'	123°23.69'
B-4	20 July 91	3,055	37°38.46'	123°30.07'
B-5	20 July 91	2,925	37°38.94'	123°28.81'
B-6	21 July 91	2,720	37°38.78'	123°25.21'
B-7	21 July 91	2,430	37°38.12'	123°21.44'
B-8	24 July 91	2,985	37°38.58'	123°29.86'
B-9	24 July 91	2,710	37°37.59'	123°28.06'
B-10	24 July 91	2,400	37°37.84'	123°26.06'
B-12	22 July 91	2,700	37°34.28'	123°28.29'
B-14	22 July 91	3,000	37°32.94'	123°28.21'
B-15	23 July 91	2,750	37°32.37'	123°26.09'
B-19	23 July 91	2,425	37°31.39'	123°24.78'
B-20	24 July 91	3,085	37°37.65'	123°30.58'
B-22	25 July 91	2,045	37°31.75'	123°17.95'
3-1	Sept. 91	1,338	37°23.82'	123°15.55'
3-3	Sept. 91	800	37°27.25'	123°07.66'
3-4	Sept. 91	1,040	37°27.83'	123°11.60'
3-5	Sept. 91	1,195	37°27.39'	123°14.42'
3-6	Sept. 91	1,505	37°27.54'	123°16.99'
3-7	Sept. 91	1,675	37°27.44'	123°19.50'
3-8	Sept. 91	2,005	37°27.13'	123°23.02'
3-10	Sept. 91	985	37°26.00'	123°10.83'
3-11	Sept. 91	1,225	37°25.50'	123°15.02'
3-12	Sept. 91	1,745	37°25.03'	123°18.00'

Table 1. (Continued) Summary of 1990 and 1991 box core station information from the Farallon Slope study site.

STATION	DATE	DEPTH (m)	LATITUDE (N)	LONGITUDE (W)
3-13	Sept. 91	1,789	37°24.30'	123°20.02'
3-14	Sept. 91	1,880	37°23.51'	123°21.62'
3-15	Sept. 91	1,010	37°24.71'	123°12.16'
3-16	Sept. 91	1,220	37°23.20'	123°14.44'
3-17	Sept. 91	1,457	37°22.18'	123°16.76'
3-18	Sept. 91	1,990	37°22.31'	123°19.24'
3-19	Sept. 91	1,760	37°26.05'	123°19.99'
3-20	Sept. 91	604	37°25.04'	123°01.85'
4-2	Sept. 91	995	37°15.29'	123°07.13'
4-3	Sept. 91	1,222	37°15.13'	123°10.83'
4-4	Sept. 91	1,427	37°16.13'	123°14.18'
4-5	Sept. 91	1,820	37°13.54'	123°16.26'
4-6	Sept. 91	2,010	37°14.03'	123°16.84'
4-7	Sept. 91	1,020	37°13.47'	123°07.48'
4-8	Sept. 91	1,235	37°13.38'	123°10.46'
4-9	Sept. 91	1,560	37°13.85'	123°13.50'
4-10	Sept. 91	1,760	37°11.26'	123°15.26'
4-11	Sept. 91	1,970	37°10.14'	123°16.61'
4-12	Sept. 91	1,480	37°10.78'	123°09.87'
4-13	Sept. 91	1,730	37°10.34'	123°10.78'
4-14	Sept. 91	812	37°14.75'	123°05.82'
4-15	Sept. 91	1,730	37°12.42'	123°15.81'
C-1	Sept. 91	550	37°22.47'	123°55.67'
C-2	Sept. 91	1,025	37°20.81'	123°02.32'
C-3	Sept. 91	1,400	37°20.21'	123°08.84'
C-5	Sept. 91	2,065	37°17.00'	123°15.81'
C-7	Sept. 91	1,840	37°17.57'	123°13.50'
DS-1	Sept. 91	2,205	37°10.97'	123°19.09'
DS-2	Sept. 91	2,394	37°10.50'	123°20.52'
DS-3	Sept. 91	2,755	37°09.86'	123°22.71'
DS-4	Sept. 91	3,060	37°10.04'	123°24.95'

Table 2. Summary of 1991 trawl information from the Farallon Slope study site.

TRAWL #	TRAWL TYPE	DATE (1992)	DEPTH (m)	POSITION (on bottom)	POSITION (off bottom)	BOTTOM TIME (on-off)	TOTAL BOTTOM TIME (min.)	DIST-ANCE (nm)	AREA TOWED (m ²)
II-1	Beam	27 July	2,975-3,010	37°38.45' / 123°29.83'	37°38.53' / 123°29.23'	01:41-02:04	23	0.48	1,867
II-2	Beam	27 July	2,795-2,865	37°38.90' / 123°27.96'	37°39.56' / 123°27.00'	06:32-07:18	46	1.01	3,928
II-3	Beam	27 July	2,850-2,910	37°38.42' / 123°28.60'	37°39.14' / 123°27.52'	11:28-12:23	55	1.12	4,356
II-4	Beam	27 July	2,945-3,075	37°37.35' / 123°30.61'	37°37.55' / 123°29.63'	16:03-16:43	40	0.80	3,111
II-5	Beam	27 July	2,840-3,075	37°38.62' / 123°28.03'	37°39.05' / 123°27.18'	20:35-21:40	45	0.80	3,111
II-6	Otter	28 July	2,760-2,865	37°38.97' / 123°27.70'	37°39.61' / 123°26.59'	03:16-04:09	53	1.09	11,789
II-7	Otter	28 July	2,880-2,935	NO FISHING	—	—	—	—	—
II-8	Otter	28 July	2,760-2,875	37°37.58' / 123°29.27'	37°38.07' / 123°27.04'	15:45-16:50	65	1.83	19,793
II-9	Beam	28 July	2,775-2,840	37°39.05' / 123°27.36'	37°39.20' / 123°25.60'	21:20-22:41	81	1.40	5,445
II-10	Beam	29 July	2,605-2,760	37°39.20' / 123°25.38'	37°38.85' / 123°23.94'	03:00-03:53	53	1.19	4,628
II-11	Beam	29 July	2,470-2,570	37°38.86' / 123°23.67'	37°38.83' / 123°22.00'	07:44-08:40	56	1.32	5,134
II-12	Beam	29 July	2,300-2,375	37°38.40' / 123°21.53'	37°38.36' / 123°19.90'	12:20-13:10	83	1.29	5,017
II-13	Beam	29 July	2,895-2,900	RADIOACTIVE	—	—	—	—	—
II-14	Beam	30 July	2,690-3,015	37°34.99' / 123°30.07'	37°35.03' / 123°28.75'	01:13-02:05	52	1.05	4,084
II-15	Otter	30 July	2,790-?	NO FISHING	—	—	—	—	—
II-16	Beam	30 July	2,900-3,000	37°37.50' / 123°29.98'	37°37.79' / 123°29.03'	13:50-14:35	45	0.81	3,150

Table 3. Summary of 1992 trawl information from the Farallon Slope, Pioneer Canyon and Monterey Canyon study sites.

BEAM TRAWL #	STATION LOCATION	DATE (1992)	DEPTH (m)	POSITION (on bottom)	POSITION (off bottom)	BOTTOM TIME (on-off)	TOTAL BOTTOM TIME (min.)	DIST- ANCE (nm)	AREA TOWED (m ²)
F-1	Farallones	27 Feb.	2,850-2,990	37°39.47' / 123°30.19'	37°39.51' / 123°28.34'	20:40-21:33	53	1.47	5,717
F-2	Farallones	27 Feb.	2,850-3,100	NET RIPPED	—	—	—	—	—
F-3	Farallones	28 Feb.	2,890-2,970	37°38.05' / 123°29.62'	37°38.34' / 123°28.62'	07:03-07:40	37	0.84	3,267
F-4	Farallones	28 Feb.	2,900-3,000	37°39.24' / 123°30.79'	37°39.35' / 123°29.34'	10:53-11:43	50	1.15	4,473
F-5	Farallones	28 Feb.	2,850-2,950	37°39.07' / 123°29.79'	37°39.53' / 123°28.96'	15:57-16:32	35	0.80	3,111
P-1	Pioneer Canyon	28 Feb.	3,150-3,280	37°04.35' / 123°26.42'	37°04.75' / 123°25.89'	23:38-00:02	24	0.58	2,256
P-2	Pioneer Canyon	29 Feb.	3,190-3,200	37°05.36' / 123°24.91'	37°05.61' / 123°23.97'	03:54-04:33	39	0.79	3,072
P-3	Pioneer Canyon	29 Feb.	3,090-3,300	37°03.27' / 123°26.30'	37°03.97' / 123°25.26'	08:17-09:07	50	1.09	4,239
P-4	Pioneer Canyon	29 Feb.	3,175-3,180	37°04.44' / 123°24.40'	37°04.72' / 123°23.77'	11:57-12:35	38	0.58	2,256
M-1	Monterey	1 March	2,820-2,960	36°15.94' / 122°36.66'	36°16.71' / 122°36.41'	10:14-10:47	33	0.80	3,111
M-2	Monterey	1 March	2,650-2,680	36°16.57' / 122°35.61'	36°17.67' / 122°35.53'	13:39-14:25	46	1.10	4,278
M-3	Monterey	1 March	2,620-2,800	36°20.30' / 122°36.17'	36°19.19' / 122°35.85'	17:03-17:59	56	1.14	4,434
M-4	Monterey	1 March	2,630-2,790	36°18.39' / 122°36.44'	36°19.77' / 122°35.71'	20:25-21:29	64	1.50	5,834
M-5	Monterey	1 March	3,250-3,270	36°23.88' / 122°39.27'	36°24.98' / 122°38.60'	00:22-01:17	55	1.23	4,784
M-6	Monterey	2 March	3,150-3,200	36°25.71' / 122°37.69'	36°27.05' / 122°37.51'	04:05-05:11	66	1.35	5,250
M-7	Monterey	2 March	2,810-2,900	36°26.53' / 122°30.71'	36°27.72' / 122°30.81'	08:15-09:12	57	1.19	4,628
M-8	Monterey	2 March	2,800-2,900	36°26.61' / 122°30.73'	36°27.67' / 122°30.71'	11:49-12:48	59	1.06	4,123

Table 4. List of all ophiuroid species collected with box cores between 550-3,085 m from the Farallon Slope study site.

Family Amphilepididae
<u>Amphilepis platytata</u> Clark, 1911
Family Amphiuridae
<u>Amphioplus</u> sp. 2
<u>Amphiura carchara</u> Clark, 1911
<u>Amphiura diomedae</u> Lyman, 1882
<u>Amphiura otteri</u> Ljungman, 1871
<u>Dougaloplus gastracantha</u> (Lutken & Mortensen, 1899)
Family Ophiacanthidae
<u>Ophiacantha</u> nr. <u>macrarthra</u> Clark, 1911
<u>Ophiolimna bairdi</u> (Lyman, 1883)
<u>Ophiophthalmus normani</u> (Lyman, 1879)
Family Ophiuridae
<u>Amphiophiura hadra</u> (Clark, 1911)
<u>Ophiura leptoctenia</u> Clark, 1911
Family Ophiurinae
sp. 1

Table 5. Mean abundance and variance per 0.1 m² of ophiuroid species collected with box cores within each 500 m depth zone.

DEPTH ZONE (m) sample size SPECIES	550-995 n = 6 x s ²	1,010-1,480 n = 15 x s ²	1,505-1,990 n = 14 x s ²	2,005-2,462 n = 12 x s ²	2,580-2,985 n = 17 x s ²	3,000-3,085 n = 4 x s ²	TOTAL 550-3,085 n = 68 x s ²
<u>Ophiura leptoctenia</u>	0 0	9.00 119.68	6.00 102.82	0.33 0.24	0.12 0.24	0 0	3.31 3,550.97
<u>Ophiophthalmus normani</u>	0.33 0.67	3.93 38.44	4.07 14.98	0.58 1.90	0 0	0 0	1.84 221.41
<u>Amphiura carchara</u>	0 0	0.07 0.07	0.64 4.54	0 0	0.71 1.46	0.75 0.92	0.37 1.96
<u>Ophiolimna bairdi</u>	0 0	0.07 0.07	0.71 0.69	0.25 0.20	0.24 0.31	0 0	0.27 0.10
<u>Amphiura diomedea</u>	0 0	0.20 0.17	0 0	0.42 0.62	0.41 0.50	0.25 0.25	0.24 0.09
<u>Dougaloplus gastracantha</u>	0 0	0.13 0.12	0.43 0.88	0.08 0.08	0 0	0 0	0.13 0.06
<u>Ophiacantha nr. macrathra</u>	0 0	0.40 2.40	0 0	0 0	0 0	0 0	0.09 0.28
<u>Amphiura otteri</u>	0 0	0 0	0.07 0.07	0 0	0.24 0.19	0 0	0.07 <0.01
<u>Amphilepis platytata</u>	0 0	0 0	0 0	0 0	0.18 0.53	0.50 0.34	0.07 0.03
<u>Amphioplus sp. 2</u>	0 0	0.07 0.07	0 0	0 0	0 0	0 0	0.02 <0.01
<u>Ophiurinae sp. 1</u>	0 0	0 0	0.07 0.07	0 0	0 0	0 0	0.02 <0.01
<u>Amphiophiura hadra</u>	0 0	0.07 0.07	0 0	0 0	0 0	0 0	0.02 <0.01
TOTAL	0.33 0.67	13.90 204.49	12.00 164.87	1.67 3.88	1.88 8.47	1.50 1.66	6.43 12,241.21

Table 6. Results of Morisita's Index of Dispersion (Id) for the six most abundant species collected with box cores (Krebs, 1989). Values are for the number of samples (n) within the depth range that each species occurred in the box core portion of this study. Significance level indicates the probability that the observed dispersion pattern was random.

Species	Depth Range (m)	n	Id	χ^2	Significance Level
<u>Ophiura leptoctenia</u>	1,010-2,945	56	2.876	872.785	$p < 0.001$
<u>Ophiophthalmus normani</u>	995-2,065	34	2.417	208.745	$p < 0.001$
<u>Amphiura carchara</u>	1,480-3,085	48	6.240	172.760	$p < 0.001$
<u>Ophiolimna bairdi</u>	1,025-2,955	55	1.438	61.444	$p < 0.25$
<u>Amphiura diomedae</u>	1,010-3,085	62	2.067	77.000	$p < 0.10$
<u>Dougaloplus gastracantha</u>	1,427-2,045	20	2.222	28.778	$p < 0.10$

Table 7. Correlation matrix for sediment parameters collected with box cores, and box core depth.

	Depth in meters	% carbon	% nitrogen	% carbonate	% gravel	% sand	% silt
% carbon	0.861	1	---	---	---	---	---
% nitrogen	0.862	0.999	1	---	---	---	---
% carbonate	0.664	0.742	0.735	1	---	---	---
% gravel	0.479	0.503	0.509	0.689	1	---	---
% sand	-0.170	-0.377	-0.371	-0.257	-0.063	1	---
% silt	-0.061	0.058	0.051	0.041	-0.172	-0.858	1
% clay	0.438	0.626	0.626	0.415	0.372	-0.419	-0.105

Table 8. List of all ophiuroid species collected with otter and beam trawls between 2300-3075 m at Farallon Slope Area 5.

Family Asteronychidae
<u>Asteronyx loveni</u> Muller & Troschel, 1842
Family Amphilepididae
<u>Amphilepis platytata</u> Clark, 1911
Family Amphiuridae
<u>Amphiura carchara</u> Clark, 1911
<u>Amphiura diomedae</u> Lyman, 1882
<u>Amphiura otteri</u> Ljungman, 1871
Family Ophiacanthidae
<u>Ophiacantha eurypoma</u> Clark, 1911
<u>Ophiolimna bairdi</u> (Lyman, 1883)
Family Ophiuridae
<u>Ophiocten hastatum</u> Lyman, 1878
<u>Ophiomusium glabrum</u>
Lutken & Mortensen, 1899
<u>Ophiura bathybia</u> Clark, 1911
<u>Ophiura leptoctenia</u> Clark, 1911

Table 9. List of all ophiuroid species collected with trawls between 2,300-3,300 m at Farallon Slope, Pioneer Canyon and Monterey Canyon study sites.

	FARALLON SLOPE	PIONEER CANYON	MONTEREY CANYON
Family Asteronychidae <u>Asteronyx loveni</u> Muller & Troschel, 1842	x		x
Family Amphilepididae <u>Amphilepis platytata</u> Clark, 1911	x	x	x
Family Amphiuridae <u>Amphiura carchara</u> Clark, 1911 <u>Amphiura diomedea</u> Lyman, 1882 <u>Amphiura oteri</u> Ljungman, 1871	x x x	x x x	x x x
Family Ophiacanthidae <u>Ophiacantha euryopoma</u> Clark, 1911 <u>Ophiacantha</u> cf. <u>pacifica</u> Lutken & Mortensen, 1899 <u>Ophiolimna bairdi</u> (Lyman, 1883)	x x	x	x x
Family Ophiuridae <u>Ophiocten hastatum</u> Lyman, 1878 <u>Ophiomusium glabrum</u> Lutken & Mortensen, 1899 <u>Ophiura bathybia</u> Clark, 1911 <u>Ophiura leptoctenia</u> Clark, 1911	x x x x	x x	x x

Table 10. Percent similarity among trawl dates and locations, as well as box cores.
Calculated as sum of minimums (Sanders, 1960).

	Farallones 1992 Trawls	Farallones 1991/92 Trawls	Pioneer 1992 Trawls	Monterey 1992 Trawls	Farallones 1990/91 Box Cores
Farallones 1991 Trawls	82.53	93.38	82.37	58.00	57.93
Farallones 1992 Trawls		89.15	76.54	58.59	63.71
Farallones 1991/92 Trawls			80.16	59.33	60.12
Pioneer Trawls 1992				49.92	54.80
Monterey 1992 Trawls					55.47

Table 11. Mean abundance and variance per 100 m² for ophiuroid species collected with trawls at the Farallon Slope, Pioneer Canyon and Monterey Canyon study sites.

STUDY SITE SPECIES	Farallon Slope 1991/92		Pioneer Canyon 1992		Monterey Canyon 1992	
	x	s ²	x	s ²	x	s ²
<u>Amphiura carchara</u>	1.92	9.92	2.04	4.04	1.03	1.04
<u>Amphilepis platytata</u>	1.03	2.86	1.16	1.59	2.50	6.50
<u>Ophiocten hastatum</u>	0.22	0.09	0.02	<0.01	0.92	1.37
<u>Amphiura diomedae</u>	0.19	0.10	0.06	0.01	0.91	1.21
<u>Ophiomusium glabrum</u>	0.19	0.27	0	0	0.22	0.15
<u>Ophiolimna bairdi</u>	0.17	0.04	0	0	1.70	11.97
<u>Amphiura otteri</u>	0.07	0.01	0.16	0.08	0.85	1.30
<u>Asteronyx loveni</u>	0.04	<0.01	0	0	0.06	0.01
<u>Ophiacantha eurypoma</u>	0.04	<0.01	0	0	0	0
<u>Ophiura leptoctenia</u>	0.01	<0.01	0	0	0	0
<u>Ophiura bathybia</u>	0.004	<0.01	0.05	<0.01	0	0
<u>Ophiocten cf. pacificum</u>	0	0	0.02	<0.01	0.02	<0.01

Table 12. List of all ophiuroid species collected with box cores and trawls between 550-3,300 m at Farallon Slope, Pioneer Canyon and Monterey Canyon sites showing which faunistic group they fit into as described by Clark (1911), and their depth ranges. Depth range information is from Clark (1911), Maluf (1988) and this study, unless otherwise stated. # = Koehler (1914), * = D'yakonov (1954). Ophiuroids not identifiable to species were not included.

	FAUNISTIC GROUP	REPORTED DEPTH (m)	DEPTH RANGE (m)
Family Asteronychidae <u>Asteronyx loveni</u>	Oceanic (cosmopolitan)	152-3,260	3,108
Family Amphilepididae <u>Amphilepis platytata</u>	?	2,665-3,607	942
Family Amphiuridae <u>Amphiura carchara</u> <u>Amphiura diomedae</u> <u>Amphiura oteri</u> <u>Dougaloplus gastracantha</u>	Oceanic Oceanic Oceanic (cosmopolitan) Oceanic	110-3,611 44-3,178 320-3,215 # 820-2,045 *	3,501 3,134 2,895 1,225
Family Ophiacanthidae <u>Ophiacantha eurypoma</u> <u>Ophiacantha</u> nr. <u>macrarthra</u> <u>Ophiacantha</u> cf. <u>pacifica</u> <u>Ophiolimna bairdi</u> <u>Ophiophthalmus normani</u>	? ? ? Oceanic Oceanic	1,041-2,950 1,068-1,263 362-3,195 578-3,010 51-2,600	1,909 195 2,833 2,432 2,549
Family Ophiuridae <u>Amphiophiura hadra</u> <u>Ophiocten hastatum</u> <u>Ophiomusium glabrum</u> <u>Ophiura bathybia</u> <u>Ophiura leptocenia</u>	American Oceanic (cosmopolitan) American American ? Oceanic	1,263-1,603 824-4,700 878-5,203 2,853-4,425 27-3,239	340 3,876 4,325 1,572 3,212

Figure 1. Map of Farallon Slope study Areas 3, 4 and 5 designated by EPA as potential dredged material disposal sites. Sixty eight box cores were taken in the vicinity of these three study areas in 1990 and 1991 between 550-3,085 m.

Figure 2. Map of the Farallon Slope, Pioneer Canyon and Monterey Canyon study sites. Twenty-nine trawls were taken at these three locations off the central California coast in 1991 and 1992 between 2,300-3,300 m.

Figure 3. Diagram of the 0.25 m² Hessler-Sandia box core, adapted from SAIC (1991). a) Front view with spade in closed position, b) Side view with spade in cocked position.

a)

1	2 0.01 m ²	3	4	5
6 Biology	7 Biology	8 Biology	9 Biology	10 Biology
11 Biology	12 Biology	13 Biology	14 Biology	15 Biology
16 Carbonate	17 Grain-size	18 CHN	19	20
21	22	23	24	25

b)

1 0.01 m ²	2 CHN	3 Grain-size	4 Carbonate
5	6 Biology	7 Biology	8
9 Biology	10 Biology	11 Biology	12 Biology
13 Biology	14 Biology	15 Biology	16 Biology

Figure 4. Diagram of box core partitions showing subcores from which individual samples were taken. a) 0.25 m² Hessler-Sandia box core, b) 0.16 m² BX-640 box core.

Figure 5. Dendrogram showing similarity among individual box core stations (normal classification) from Farallon Slope Areas 3, 4 and 5. Clustering is with Bray-Curtis and group average sorting, without standardization. Depth ranges for the two general clusters are shown to the left. Parentheses denote box core samples that did not fall within the depth range of their cluster.

Figure 6. Dendrogram showing similarity among ophiuroid species (inverse classification) collected with box cores at Farallon Slope Areas 3, 4 and 5. Clustering is with Bray-Curtis and group average sorting, without standardization. Species that occurred in only one box core were not included.

Figure 7. Abundance per 0.1 m² of the total number of individual ophiuroids collected per box core, all species combined, over the depth range sampled. N = 68 box cores.

Figure 8. Abundance per 0.1 m² of the two most abundant ophiuroid species collected with box cores, *Ophiura leptoctenia* and *Ophiophthalmus normani*, over the depth range sampled. N = 68 box cores.

Figure 9. Comparison of the relative abundances of ophiuroid species collected with box cores above and below 2,000 m at the Farallon Slope study site. There were 30 box cores taken above 2,000 m, and 33 below.

Figure 10. Composite profile of dissolved oxygen concentrations in the water column between the surface and 3,200 m at the Farallon Slope study site. Data were collected at various box core stations in July and September of 1991. Oxic = dissolved oxygen levels greater than 2.8 mg/l, dysoxic = dissolved oxygen levels between 2.8 and 0.3 mg/l and the OMZ (oxygen minimum zone) = dissolved oxygen levels below 0.7 mg/l (Tyson and Pearson, 1991).

Figure 11. Comparison of the composite profile of dissolved oxygen with the overall abundance pattern of ophiuroids per 0.1m² (n = 68 box cores), between 550-3085 m. Oxic = dissolved oxygen levels greater than 2.8 mg/l, dysoxic = dissolved oxygen levels between 2.8 and 0.3 mg/l and the OMZ (oxygen minimum zone) = dissolved oxygen levels below 0.7 mg/l (Tyson and Pearson, 1991). The dotted line at 2,000 m denotes the change from dysoxic to oxic conditions.

Figure 12. Percent clay with depth. N = 68 box cores.

Figure 13. Sediment organic content parameters with depth. N = 68 box cores for percent organic carbon, n = 57 box cores for percent nitrogen, and n = 53 box cores for percent carbonate.

Figure 14. Comparison of the cumulative species curves for ophiuroids collected with box cores between 1,000-2,000 m and 2,000-3,000 m. There were 29 box cores taken within each depth range. Each value is the mean cumulative number of species plus or minus the standard deviation for 10 random combinations of samples. The "*" indicates the number of samples necessary to reach stabilization of the curve.

Figure 15. Cumulative species curve for ophiuroids collected with trawls at the Farallon Slope study site. There were 17 trawls collected in 1991/92 between 2,300-3,075 m. Each value is the mean cumulative number of species plus or minus the standard deviation for 10 random combinations of samples. The "*" indicates the number of samples necessary to reach stabilization of the curve.

Figure 16. Comparison of the relative abundances of ophiuroid species collected with box cores and trawls below 2,300 m at the Farallon Slope study site. There were 17 trawls taken in 1991/92 and 27 box cores taken in 1990/91.

Figure 17. Dendrogram showing similarity among individual trawls (normal classification) from the Farallon Slope, Pioneer Canyon and Monterey Canyon study sites. Clustering is with Bray-Curtis and group average sorting, with standardization on totals. Depths are in meters and show the median depth for each trawl. Depth ranges to the left denote general groupings of shallower and deeper trawls, even though not all clusters fit this pattern exactly.

Figure 18. Dendrogram showing similarity among ophiuroid species (inverse classification) collected with trawls at the Farallon Slope, Pioneer Canyon and Monterey Canyon study sites. Clustering is with Bray-Curtis and group average sorting, with standardization on totals.

Figure 19. Comparison of the cumulative species curves for ophiuroids collected with trawls among the Farallon Slope, Pioneer Canyon and Monterey Canyon study sites. There were 17 trawls taken at the Farallones in 1991/92, four at Pioneer in 1992 and eight at Monterey in 1992. Each value is the mean cumulative number of species plus or minus the standard deviation for 10 random combinations of samples. The "*" indicates the number of samples necessary to reach stabilization of the curve.

Figure 20. Comparison of the relative abundance of ophiuroid species collected with trawls among the Farallon Slope, Pioneer Canyon and Monterey Canyon study sites. There were 17 trawls taken at the Farallones in 1991/92, four at Pioneer in 1992 and eight at Monterey in 1992.