PERGAMON

Deep-Sea Research II 47 (2000) 1107–1137

DEEP-SEA RESEARCH
PART II

Brittle star distribution patterns and population densities on the continental slope off central California (Echinodermata: Ophiuroidea)

Anne C. Summers[a,*], James Nybakken[b]

[a]*2112 Ione St., Sacramento, CA 95864, USA*
[b]*Moss Landing Marine Laboratories, P.O. Box 450, Moss Landing, California 95039, USA*

Received 2 May 1997; received in revised form 11 May 1998; accepted 24 July 1998

Abstract

The ophiuroid communities on the continental slope off central California were examined using box cores and trawls. Box cores were taken between 550 and 3085 m at sites southwest of the Farallon Islands, and otter and beam trawls were used below 2300 m at three sites between the Farallon Islands and Point Sur. Eighteen ophiuroid species from six families were identified. Eighty percent of the individuals collected with box cores belonged to two species, *Ophiura leptoctenia* and *Ophiacantha normani*, which were dominant between 1000 and 2000 m. The largest ophiuroid faunal break occurred at around 2000 m and was associated with elevated dissolved oxygen levels, decreasing sediment grain size, and increasing sediment organic content. A comparison of box-core and trawl data from below 2300 m showed that box cores undersampled the ophiuroid community on the continental slope, missing almost 50% of the species collected by trawls within the same area, whereas trawls underestimated ophiuroid densities, reporting on average 243 times fewer ophiuroids per m^2 than did box cores. There was a change in species relative abundance patterns between sampling locations. Ophiuroids exhibited patchy spatial distribution patterns on both a small scale of around 0.1 m^2 and a large scale on the order of 100–1000 s of square meters. © 2000 Elsevier Science Ltd. All rights reserved.

1. Introduction

Ophiuroids inhabit all areas of the world's oceans, exploiting both soft bottom and rocky substrates from the intertidal zone down to depths of over 8000 m. Although

---

[*] Corresponding author. Fax: 001-916-486-0803;.

PII: S0967-0645(99)00138-1

ophiuroid species diversity decreases rapidly with depth, in many areas of the deep sea they numerically dominate the megafauna (defined by Grassle et al., 1975 as those organisms large enough to be readily visible in photographs, typically $\geqslant 1$ cm; Tyler, 1980; Smith and Hamilton, 1983; Carey et al., 1990a,b; Gage and Tyler, 1991). Because of their abundance, feeding behavior, and high activity levels, ophiuroids are thought to significantly impact the energetics and ecology of bathyl soft-bottom communities through the utilization, processing and redistribution of organic matter at the sea floor (Smith and Hamilton, 1983), increasing bioturbation rates (Wheatcroft, 1991; Kaufmann and Smith, 1997), and as major links in local food chains (Warner, 1982).

Ophiuroids present unique sampling problems that make assessing their distribution and abundance in the deep sea a challenge. Their size range and lifestyle habits make them members of both the infauna and the epifauna, they are fragile, and they are 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. Precise dispersion patterns are hard to discern for the same reasons, and because they may vary considerably even for a single species on various spatial and temporal scales, and in response to density (Grassle et al., 1975; Warner, 1982; Smith and Hamilton, 1983; Lauerman et al., 1996).

Deep-sea benthic studies of ophiuroids in the Pacific Ocean are relatively sparse and have been confined to limited geographical areas. A few general faunal surveys exist from the Northeastern Pacific (Carey, 1990; Carey et al., 1990a,b). Along the west coast of the United States, published data are limited mostly to areas off the northern Oregon coast (Astrahantseff and Alton, 1965; Alton, 1972; Pereyra and Alton, 1972) and the deep basins off southern California (Hartman and Barnard, 1958; Barham et al., 1967; Smith and Hamilton, 1983; Smith, 1985; Wheatcroft, 1991; Hendler, 1996). No published literature exists for deep-sea ophiuroid assemblages off the northern portion of the central California coast.

The data and specimens for this project were collected as part of several studies designed for the US Navy and the US 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. A combination of box cores, trawls, and camera sleds was used to sample the benthic community. Two more southerly locations along the central California Coast, the Pioneer Canyon and the Monterey Canyon, were also sampled for comparative purposes (SAIC, 1991; Blake et al., 1992; Hecker Environmental Consulting, 1992; Nybakken et al., 1992a,b; SAIC, 1992). The distribution of ophiuroids is examined in this paper within the constraints of these other sampling programs, using data from the box core and trawl operations.

The objectives of this study were to examine the distribution and population density of ophiuroids on the continental slope off central California. The benthic sampling effort was most intensive in the vicinity of the Farallon Islands and allowed examination of the bathymetric and spatial distribution of ophiuroids in this area between 550 m and 3085 m. It also allowed for a comparison of species distributions with changes in dissolved oxygen, sediment grain size, and sediment organic content. Trawling efforts at the Farallon Slope, Pioneer Canyon and Monterey Canyon sites allowed for comparisons of ophiuroid species relative abundances below 2300 m among these three geographic locations. The data used in this study were influenced by sampling equipment and design. As a result, sampling methods were examined for ophiuroids by comparing data from box core and trawl operations where the two overlapped in depth at the Farallon Islands.

2. Materials and methods

2.1. Study site description

The majority of samples were collected near the Farallon Islands, California, approximately 70 km west–southwest of San Francisco Bay in the vicinity of three study areas designated by EPA as potential dredged material disposal sites (Areas 3–5; Fig. 1). Areas 3 and 4 both are located on the upper and middle continental slope in and around Pioneer Canyon at depths ranging from about 500 to 3000 m. Area 5 is located on the lower continental slope west of the Farallon Islands at depths exceeding 2000 m, and is dominated by a large sloping trough or valley with a gradient of about 3° (SAIC, 1991).

Two more southerly locations along the central California coast also were sampled, the Pioneer and Monterey Canyons. The Pioneer Canyon site is located southwest of Pioneer Canyon about 56 km south of Farallon Slope Area 5 at depths of between 3090 and 3300 m, and the Monterey Canyon site is located on the fan of Monterey Submarine Canyon about 145 km south of Farallon Slope Area 5 at depths of between 2300 and 3300 m (Fig. 1).

2.2. Box core sampling

Box core stations were located along transects in the vicinity of Areas 3–5, and one sample was taken at each station. Sixty-eight successful box cores were collected on three cruises during the summers of 1990 and 1991 between 550 and 3085 m. Nineteen box cores were taken near Area 3 between 604 and 2005 m, 23 near Area 4 between 550 and 3060 m, and 26 near Area 5 between 2045 and 3085 m (see Summers, 1993 for details concerning station data). Box cores were deemed successful when penetration of the sediment had taken place to a depth of at least 10 cm and the surface layer of sediment remained intact upon retrieval showing no signs of being disturbed on ascent. Mann–Whitney U tests showed no significant difference in ophiuroid species composition or abundance for comparable depth ranges between Areas 3 and 4 ($p > 0.05$) and Areas 4 and 5 ($p > 0.05$), so box core data from all three areas were combined for analysis and will be referred to as Farallon Slope sites. Because Area 3 did not overlap in depth with Area 5, it was not possible to directly test for significance between all three areas simultaneously.

Box core samples were taken with a 0.25-m^2 Hessler-Sandia box core or a 0.16-m^2 BX-640 box core; both samplers were internally partitioned into aluminum subcores, each with a surface area of 0.01 m^2. 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

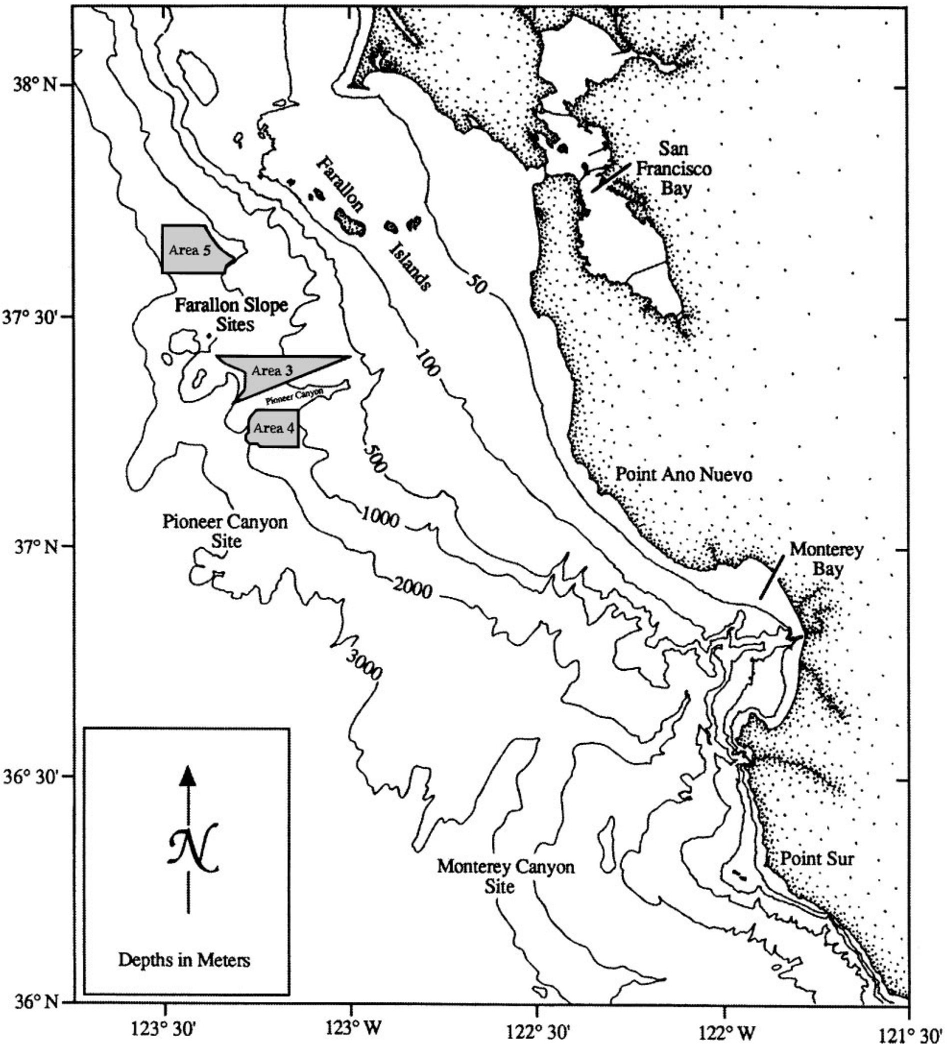

Fig. 1. Map of the Farallon Slope, Pioneer Canyon and Monterey Canyon study sites off the coast of central California. The Farallon slope site includes Areas 3–5 designated by EPA as potential dredged material disposal sites. Box core sampling took place in the vicinity of Areas 3–5. Trawl sampling took place in the vicinity of Area 5 at the Farallon Slope, and at the Pioneer Canyon and Monterey Canyon sites.

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.

Biological samples were preserved in 10% buffered formalin for 2–3 d, then transferred to 70% ethanol. All adult brittle stars were identified to species and enumerated. Brittle stars 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. All ophiuroid samples have been deposited at the Natural History Museum of Los Angeles County (LACM).

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

Dissolved oxygen values were determined at various box core stations using a 10-bottle rosette sampler equipped with 10-l Niskin bottles. Samples collected at depths between the surface and 3200 m were analyzed for dissolved oxygen on board ship using the Winkler titration technique.

2.3. Trawl sampling

Trawl samples were collected at Farallon Slope Area 5 and at the Pioneer and Monterey Canyon study sites on two cruises, in the summer of 1991 and the spring of 1992, between 2300 and 3300 m. Seventeen trawls were taken from the Farallon Slope site between 2300 and 3075 m, 13 in July of 1991 and four in February of 1992. Ophiuroid samples from these two sampling periods showed an 83% similarity in relative abundance (sum of minimums, Sanders, 1960) and so for the purposes of this study were combined. Four trawls were taken at the Pioneer Canyon site between 3090 and 3300 m in February of 1992, and eight at the Monterey Canyon site between 2620 and 3270 m in March of 1992.

Most trawl samples were collected with a beam trawl having a beam length of 2.1 m and a bag length of 6.7 m. Several trawls also were collected with a standard commercial otter trawl with a 12-m rope and weighted aluminum doors. Both trawls had a stretch mesh opening of 3 cm and an inside bag liner of 1.5 cm stretch mesh. Data from beam and otter trawls were combined in analyses because the mesh sizes for both nets were the same.

In order to try and maintain the trawl on the bottom during sampling, one or two deep water glass floats were attached to the towing cable about 5–7 m ahead of the beam, and a benthos pinger attached 70 m ahead of the beam. The trawl engaged the bottom when the pinger trace on the Precision Depth Recorder (PDR) was 25 m off the bottom trace, and the ratio of line out to bottom depth was usually in the range of 1.4–1.5 to 1. The time and position of the ship when the trawl first engaged and first left the bottom were recorded with the ship's global positioning system (GPS).

A total of 29 successful trawls were taken at the three sites and of these, 27 were beam trawls and two were otter trawls. Upon retrieval of each trawl, ophiuroids were separated from the trawl catch and preserved in 10% buffered formalin for 5–7 d, then transferred to 70% ethanol. All individuals were identified to species and enumerated. These ophiuroid samples also have been deposited at the LACM.

2.4. Data analysis

Cluster analysis and scatter plots were used to examine general distribution patterns of ophiuroids with depth. Dendograms were created using Bray–Curtis cluster analysis and group average sorting and both normal and inverse classification were done. For normal classification, stations were grouped using ophiuroid species composition and abundance as attributes, and for inverse classification ophiuroid species were grouped using their presence or absence at stations as attributes. Box-core cluster analysis was done without standardization, and trawl cluster analysis was done with standardization on totals (Boesch, 1977). Species that were only collected in one box core were not included in inverse classification.

Because the area sampled per trawl ranged from 1867 to 19793 m^2, all trawl sample data were converted to number of individuals per 100 m^2. The total area sampled per trawl was determined by calculating the great circle distance in nautical miles between GPS latitude and longitude readings taken when the trawl first engaged and first left the bottom using a computer program, and then converting these data to area covered in units of 100 m^2.

To examine adequacy of sampling, cumulative species curves were compared by plotting mean cumulative number of species plus or minus standard deviation for ten random combinations of samples, and then looking for the number of samples it took to reach stabilization of the curve (Pielou, 1966; Hurtubia, 1973). Relative abundance patterns of ophiuroid species were compared between sampling methods within the same depth range and area, at different depths within the same area, and among areas. Percent similarity (sum of minimums, Sanders, 1960) also was calculated.

Because replicate box cores were not taken at a given station, box cores were grouped by depth for further analysis into six, 500-m depth zones between 500 and 3500 m. The mean and variance of individual ophiuroid species within each depth zone were then compared. 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) for the six most abundant ophiuroid species. 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).

3. Results

3.1. Box core data

The 437 adult ophiuroids collected from box cores were distributed among five families, 10 genera and 12 species (Table 1). In addition, 148 unidentifiable juveniles were collected. Twenty of the 68 box cores (29%) contained no adult ophiuroids, indicating patchy spatial distribution at the 0.1 m^2 level. Juvenile ophiuroids were collected in six of the 20 box cores that did not contain adults.

Table 1
Depth ranges in meters of all ophiuroid species collected with box cores and trawls between 550 and 3300 m at the Farallon Slope, Pioneer Canyon and Monterey Canyon sites. Reported depth ranges are from Clark (1911), D'yakonov (1954), Hendler (1996), Koehler (1914), Lauerman et al. (1996), Maluf (1988), and this study

	Farallon slope box cores 550–3085 m	Farallon slope trawls 2300–3075 m	Pioneer canyon trawls 3090–3300 m	Monterey canyon trawls 2620–3270 m	Reported depth range (in m)
Family asteronychidae					
Asteronyx loveni Müller & Troschel, 1842	—	2300–3075	—	2620–2900	152–3260
Family amphilepididae					
Amphilepis platytata H. L. Clark, 1911	2755–3060	2690–3075	3090–3300	2620–2900	2620–3607
Family amphiuridae					
Amphioplus sp. 2	1263	—	—	—	1263
Amphiurac archara H.L. Clark, 1911	1480–3085	2300–3075	3090–3300	2620–2900	110–4100
Amphiura diomedeae Lütken and Mortensen, 1899	1010–3085	2690–3075	3175–3180	2620–2900	71–3180
Amphiura otteri Ljungman, 1871	1880–2835	2690–3075	3150–3280	2620–2900	320–3280
Dougaloplus gastracantha (Lütken and Mortensen, 1899)	1427–2045	—	—	—	820–2045
Family ophiacanthidae					
Ophiacantha eurypoma H. L. Clark, 1911	—	2850–3000	—	—	1041–3000
Ophiacantha nr. *macrarthra* H. L. Clark, 1911	1263	—	—	—	1068–1263
Ophiacantha cf. *pacifica* Lütken and Mortensen, 1899	—	—	3090–3300	2620–2900	362–3300
Ophiolimna bairdi (Lyman, 1883)	1025–2955	2690–3075	—	2630–2900	578–3075
Ophiacantha normani Lyman, 1879	995–2065	—	—	—	51–2605
Family ophiuridae					
Amphiophiura hadra (Clark, 1911)	1263	—	—	—	1263–1603
Ophiocten hastatum Lyman, 1878	—	2300–3015	3090–3300	2620–2900	824–4700
Ophiosphalma glabrum (Lütken and Mortensen, 1899)	—	2300–2760	—	2620–2900	878–5203
Ophiura bathybia H. L. Clark, 1911	—	2690–3015	3090–3300	—	2690–4425
Ophiura leptoctenia H. L. Clark, 1911	1010–2945	2808–2930	—	—	122–3239
Family ophiurinae					
sp.1	1789	—	—	—	1789

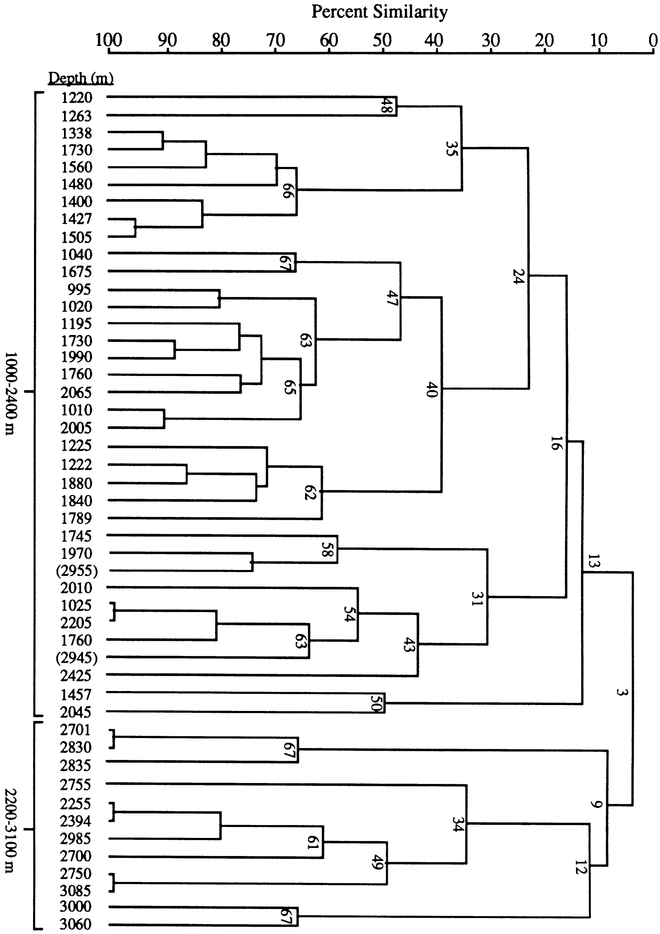

Fig. 2. Dendogram showing similarity of species relative abundances among individual box core stations (normal classification) from Farallon Slope Areas 3–5. Clustering is with Bray–Curtis and group average sorting, without standardization. Depth ranges for the two general clusters are shown to the left. Parentheses denote box core samples that did not fall within the depth range of their cluster.

Normal classification using Bray–Curtis cluster analysis suggested a general faunal break at around 2000 to 2200 m (Fig. 2). Box cores collected above 2000 m showed a similarity of only 3% to those collected below this depth. Inverse classification showed a very slight grouping of *Ophiura leptoctenia* and *Ophiacantha normani* (48% similarity; Fig. 3). The three species most abundant above about 2000 m grouped separately from the five species most abundant below 2000 m, with only 4% similarity between these two groups.

Adult ophiuroids were not collected between 500 and 985 m, although only five box cores were taken in this depth range. Overall abundance was greatest between 1000

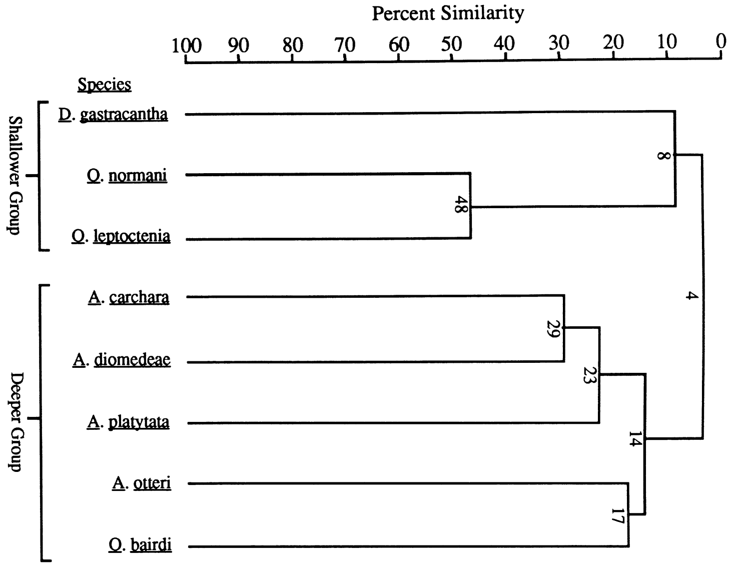

Fig. 3. Dendogram showing similarity of relative abundances among ophiuroid species (inverse classification) collected with box cores at Farallon Slope Areas 3–5. Clustering is with Bray–Curtis and group average sorting, without standardization. Species that occurred in only one box core were not included. The "Shallower Group" includes species most abundant above 2000 m, and the "Deeper Group" those most abundant below 2000 m.

and 2000 m with a peak at around 1500 m, declined between 2200 and 2700 m, and appeared to increase slightly below 2700 m (Fig. 4).

Two species composed 80% of the individuals collected with box cores: 50% were *Ophiura leptoctenia* and 30% were *Ophiacantha normani.* These were almost entirely responsible for the large peak in ophiuroid abundance between 1000 and 2000 m (Table 2). *Ophiura leptoctenia* was found sporadically down to 2945 m, but *O. normani* was not found below 2065 m. The other ten ophiuroid species were considerably less common with four found in only one box core each, and three of these four represented by only one individual. These ten species varied in abundance among depth zones without a clear relationship between population density and depth (Table 2).

The relative abundance pattern of ophiuroid species changed below about 2000 m as *Ophiura leptoctenia* and *Ophiacantha normani* decreased in abundance (Fig. 5). Between 995 and 1990 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 2005 and 3085 m, *Amphiura carchara* and *Amphiura diomedeae* were most abundant, but at 26 and 22% respectively they accounted for less than 50% of the individuals. With the exception of *Dougaloplus gastracantha* (2%), the other six species present below 2000 m each comprised between 7 and 12%. It took 20 to 21 box cores to sample

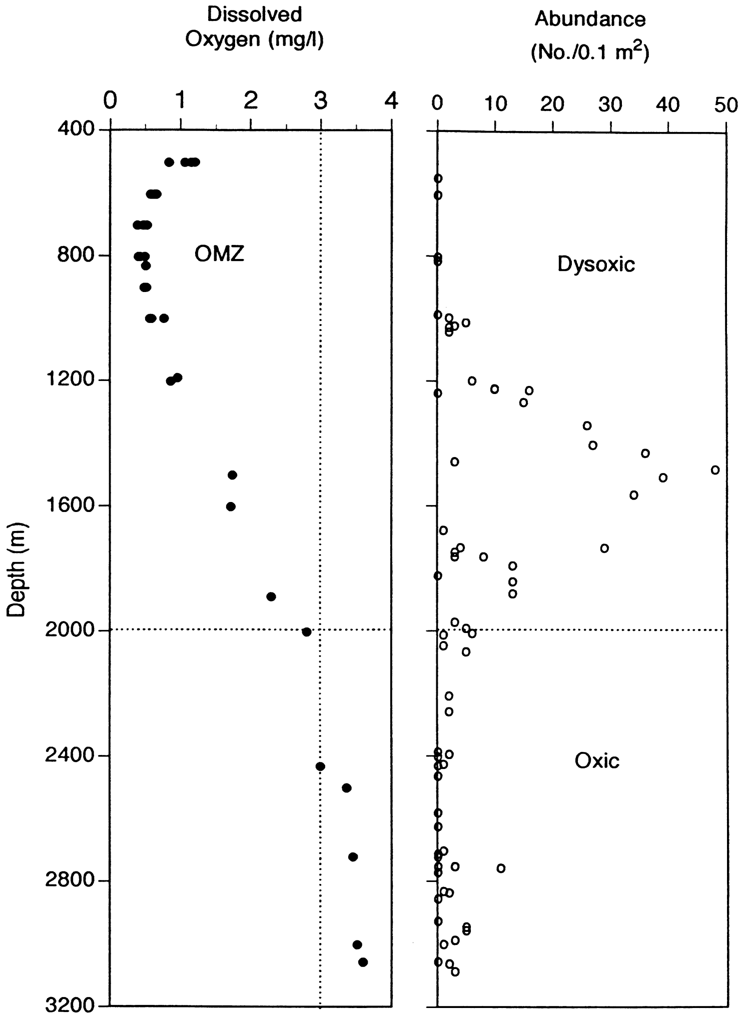

Fig. 4. Comparison of the composite profile of dissolved oxygen with the overall abundance pattern of ophiuroids per 0.1 m^2 ($n = 68$ box cores) between 550 and 3085 m off the Farallon Islands. Oxic = dissolved oxygen levels greater than 2.8 mg/l, dysoxic = dissolved oxygen levels between 2.8 and 0.3 mg/l and the OMZ (oxygen minimum zone) = dissolved oxygen levels below 0.7 mg/l (Tyson and Pearson, 1991). The dotted line at 2000 m denotes the change from dysoxic to oxic conditions.

adequately the ophiuroid assemblage between 1000 and 2000 m, but only half that number (10–11) to adequately sample the assemblage between 2000 and 3000 m (Fig. 6).

In most depth zones, the six most abundant ophiuroid species tended to show high variance-to-mean ratios suggesting patchy spatial distributions at the 0.1 m^2 level

Table 2

Mean abundance and variance per 0.1 m^2 of ophiuroid species collected with box cores at the Farallon Slope within each 500 m depth zone, listed in order of overall abundance

Depth zone (m) sample size	550–995 $n = 6$		1010–1480 $n = 15$		1505–1990 $n = 14$		2005–2462 $n = 12$		2580–2985 $n = 17$		3000–3085 $n = 4$		Total 550–3085 $n = 68$	
Species	x	s^2	x	s^2	x	s^2	x	s^2	x	s^2	x	s^2	x	s^2
Ophiura leptoctenia	0	0	9.00	119.57	6.00	102.77	0.33	0.24	0.12	0.24	0	0	3.31	59.59
Ophiacantha normani	0.33	0.67	3.93	38.50	4.07	14.99	0.58	1.90	0	0	0	0	1.84	14.88
Amphiura carchara	0	0	0.07	0.07	0.64	4.55	0	0	0.71	1.47	0.75	0.92	0.37	1.40
Ophiolimna bairdi	0	0	0.07	0.07	0.71	0.68	0.25	0.20	0.24	0.32	0	0	0.26	0.32
Amphiura diomedeae	0	0	0.20	0.17	0	0	0.42	0.63	0.41	0.51	0.25	0.25	0.24	0.30
Dougaloplus gastracantha	0	0	0.13	0.12	0.43	0.88	0.08	0.08	0	0	0	0	0.13	0.24
Ophiacantha nr. *macrarthra*	0	0	0.40	2.40	0	0	0	0	0	0	0	0	0.09	0.53
Amphiura otteri	0	0	0	0	0.07	0.07	0	0	0.24	0.19	0	0	0.07	0.07
Amphilepis platytata	0	0	0	0	0	0	0	0	0.18	0.53	0.50	0.33	0.07	0.16
Amphioplus sp. 2	0	0	0.07	0.07	0	0	0	0	0	0	0	0	0.01	0.01
Ophiurinae sp. 1	0	0	0	0	0.07	0.07	0	0	0	0	0	0	0.01	0.01
Amphiophiura hadra	0	0	0.07	0.07	0	0	0	0	0	0	0	0	0.01	0.01
Total	0.33	0.67	13.90	204.35	12.00	164.77	1.67	3.88	1.88	8.49	1.50	1.67	6.43	110.64
Unidentifiable juveniles	3.50	30.30	3.00	11.71	1.36	2.71	0.58	1.36	3.06	13.31	1.00	4.00	2.18	10.00

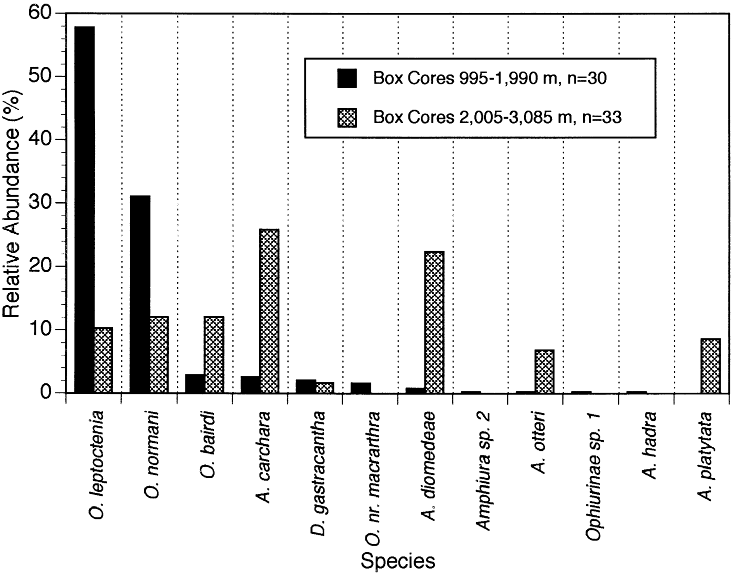

Fig. 5. Relative abundances of ophiuroid species collected with box cores above and below 2000 m at the Farallon Slope study site.

(Table 2). The total area sampled in each of these zones was very small, however, ranging from 0.4 to 1.7 m^2. Morisita's Index of Dispersion for these six species also indicated non-random distributions (Table 3). While it appears these ophiuroids may be exhibiting aggregated distributions on a small scale, the results are not definitive. Both the variance to mean ratio and Morisita's Index of Dispersion are affected by the size of the sampling unit (the 0.1 m^2 box core) relative to the scale of aggregation, and Morisita's Index also is dependent on sample size which was not equal among species ($n = 20$–62 box cores) (Andrew and Mapstone, 1987).

The general pattern of dissolved oxygen with depth showed consistency over both space and time. Surface waters had high oxygen values of around 8 mg/l, but between about 500 and 1000 m oxygen levels fell below 0.7 mg/l creating an oxygen minimum zone (OMZ). Oxygen levels rose above 2.8 mg/l at depths greater than 2000 m (Fig. 4).

No adult ophiuroids were found within the OMZ, although sample size in this area was small ($n = 5$). At the deeper edge of the OMZ, around 1000–1200 m, there was a large increase in ophiuroid abundance, primarily due to large numbers of *Ophiura leptoctenia* and *Ophiacantha normani*. The largest change in ophiuroid species composition and abundance patterns was found at about 2000 m where dissolved oxygen rose above 2.8 mg/l and the environment changed from dysoxic to oxic (Tyson and Pearson, 1991; Figs. 4 and 5).

Sediment grain size tended to decrease with increasing water depth as reflected by percent clay, whereas organic content tended to increas as reflected by percent carbon and nitrogen (Fig. 7). Percent clay showed the largest increase below about 2000 m,

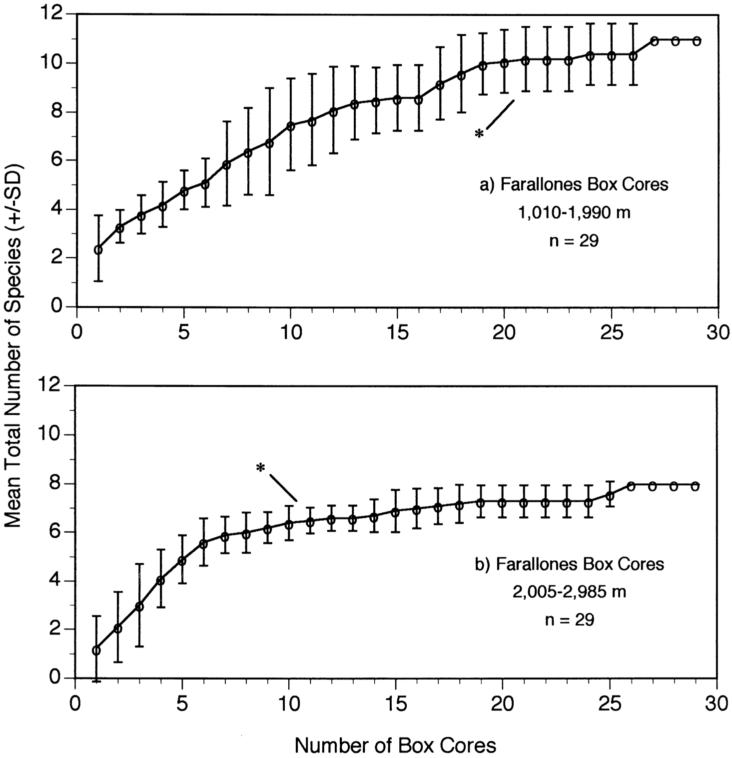

Fig. 6. Cumulative species curves for ophiuroids collected with box cores (a) between 1000 and 2000 m and (b) between 2000 and 3000 m. Each value is the mean cumulative number of species plus or minus the standard deviation for 10 random combinations of samples. The "*" indicates the number of samples necessary to reach stabilization of the curve.

Table 3
Results of unstandardized Morisita's index of dispersion (Id) for the six most abundant species collected with box cores. Values are for the number of box cores (*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 (Krebs, 1989)

Species	Depth range (m)	*n*	Id	X^2	Significance level
Ophiura leptoctenia	1010–2945	56	2.876	872.785	$p < 0.001$
Ophiacantha normani	995–2065	34	2.417	208.745	$p < 0.001$
Amphiura carchara	1480–3085	48	6.240	172.760	$p < 0.001$
Ophiolimna bairdi	1025–2955	55	1.438	61.444	$p < 0.25$
Amphiura diomedeae	1010–3085	62	2.067	77.000	$p < 0.10$
Dougaloplus gastracantha	1427–2045	20	2.222	28.778	$p < 0.10$

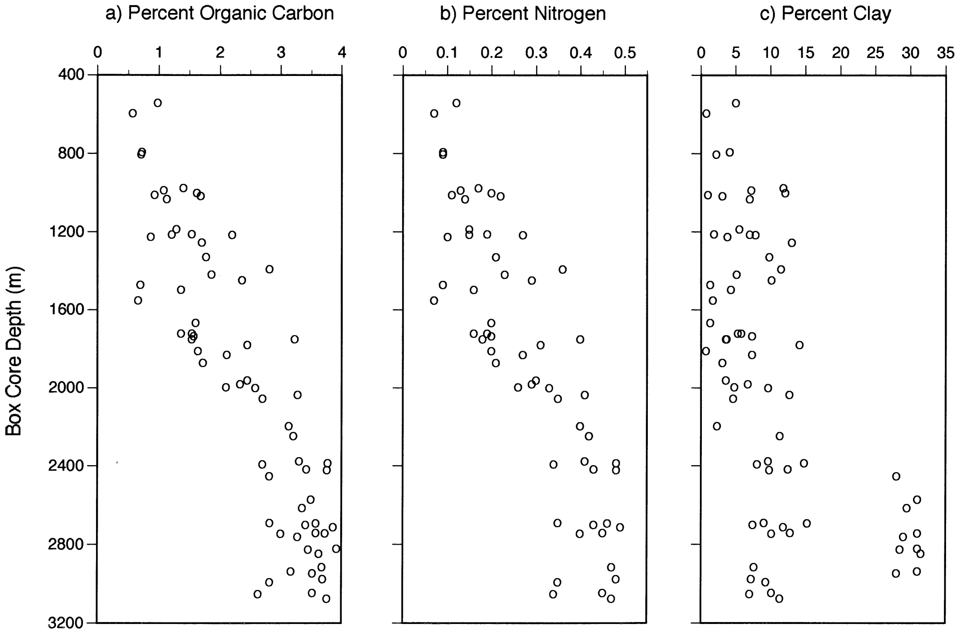

Fig. 7. Composite profiles for (a) percent organic carbon ($n = 68$ box cores), (b) percent nitrogen ($n = 57$ box cores) and (c) percent clay ($n = 68$ box cores) with depth between 550 and 3085 m off the Farallon Islands. Organic carbon and nitrogen values were sampled from the same subcores. Note scale differences on x-axis.

whereas percent carbon and percent nitrogen increased more steadily with increasing water depth. Percent carbon and percent nitrogen were highly positively correlated with each other (correlation matrix, 0.999), and with increasing water depth (0.861 and 0.862 respectively). Percent clay was positively correlated with both percent carbon and percent nitrogen (0.626).

3.2. *Trawl data*

The 29 trawls yielded 2589 adult ophiuroids from the 17 Farallon Slope trawls, 441 from the four Pioneer Canyon trawls, and 3160 from the eight Monterey Canyon trawls (Table 1). Cumulative species curves showed that while the Farallon Slope and Monterey Canyon sites were adequately sampled with 6–7 and 3–4 trawls, respectively, the Pioneer Canyon site was not adequately sampled (Fig. 8).

The most notable result of normal classification using Bray–Curtis cluster analysis was a grouping of trawls by depth regardless of area, with the exception of one anomalous trawl from the Monterey Canyon at 3260 m that contained large numbers of elasipodid holothurians almost exclusively (Fig. 9). Trawls taken within the 2300 to 2700 m depth range grouped separately from trawls taken deeper than 2700 m.

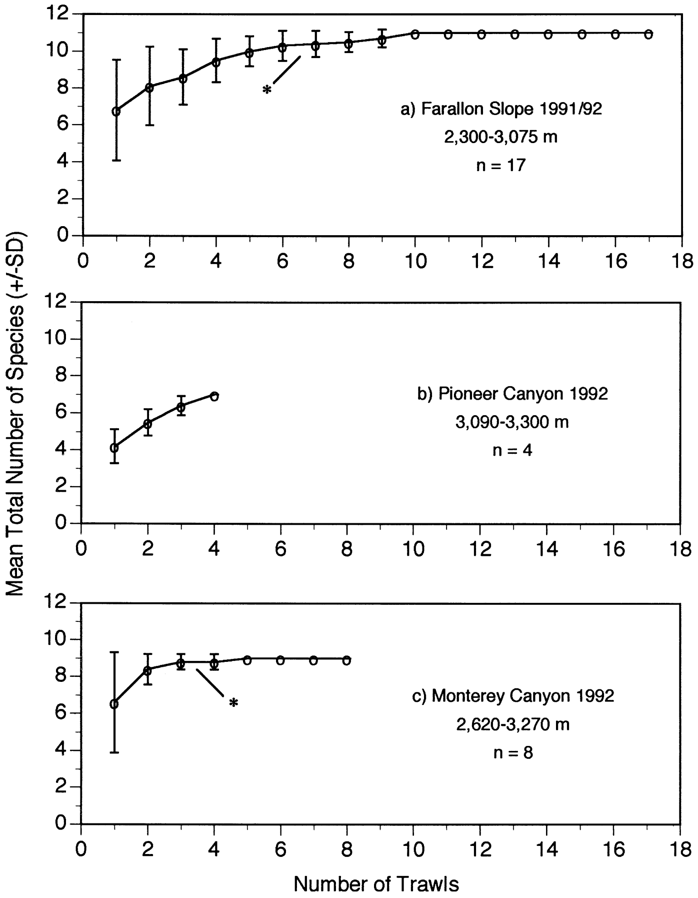

Fig. 8. Cumulative species curves for ophiuroids collected with trawls at the (a) Farallon Slope, (b) Pioneer Canyon, and (c) Monterey Canyon study sites. Each value is the mean cumulative number of species plus or minus the standard deviation for 10 random combinations of samples. The "*" indicates the number of samples necessary to reach stabilization of the curve.

Although only four trawls were taken shallower than 2700 m, three showed a 72% similarity to each other and only a 9% similarity to the deeper trawls. There also was a slight tendency for Monterey trawls to group together between 2700 and 2900 m ($>$ 58% similarity as opposed to 48% similar to Farallones and Pioneer trawls). This may indicate some ophiuroid faunal differences between the Monterey Canyon site and the two northern sites. There did not appear to be any major faunal differences for ophiuroids among seasons, as trawls collected at the Farallon Slope in July and February were found within the same clusters.

Inverse classification revealed a tendency for some ophiuroid species to occur together (Fig. 10). For instance, there was a 53% similarity between *Amphilepis*

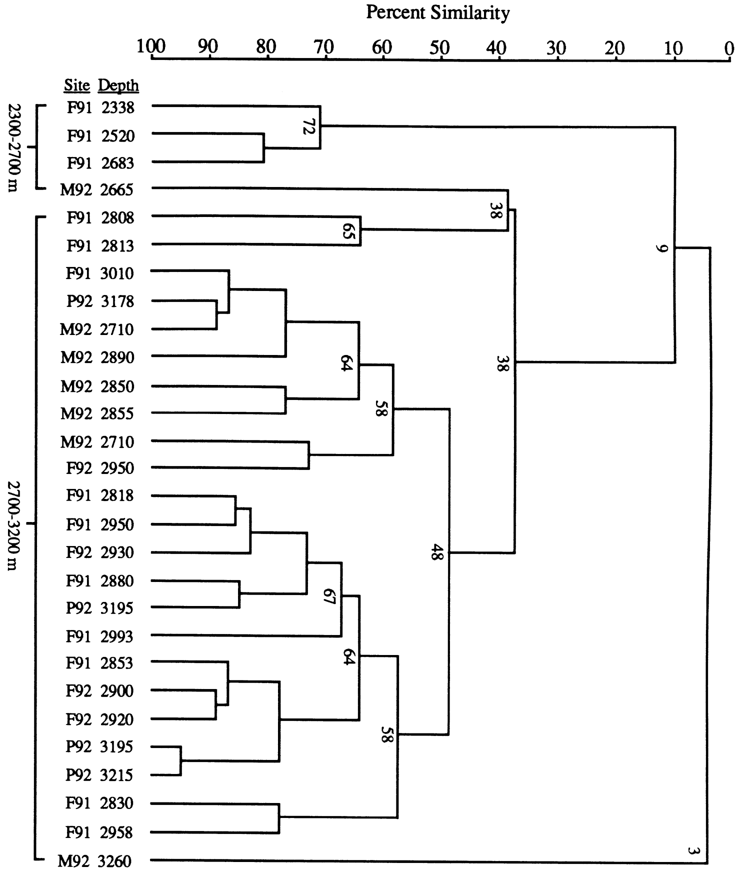

Fig. 9. Dendogram showing similarity of species relative abundances among individual trawls (normal classification) from the Farallon Slope, Pioneer Canyon and Monterey Canyon study sites. Clustering is with Bray–Curtis and group average sorting, with standardization on totals. Depths are in meters and 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.

platytata and *Amphiura carchara* and a 40% similarity between *Amphiura diomedeae*, *Ophiolimna bairdi* and *Ophiocten hastatum*. Five of the remaining seven species showed < 6% similarity to these two groups.

Trawl data were pooled over the depth range sampled within each of the three sampling locations for further comparison. This led to pooling of data over 775 m in depth at the Farallon Slope, 210 m at Pioneer Canyon, and 650 m at Monterey Canyon. This was done for the following reasons: Trawls covered depth ranges of between 5 m and 325 m each (mean of 107 m) and often were overlapping in depth so comparisons of discrete depths were impossible. While the inclusive depth range of all 29 trawls collected in this study was between 2300 and 3300 m, a majority of trawls at

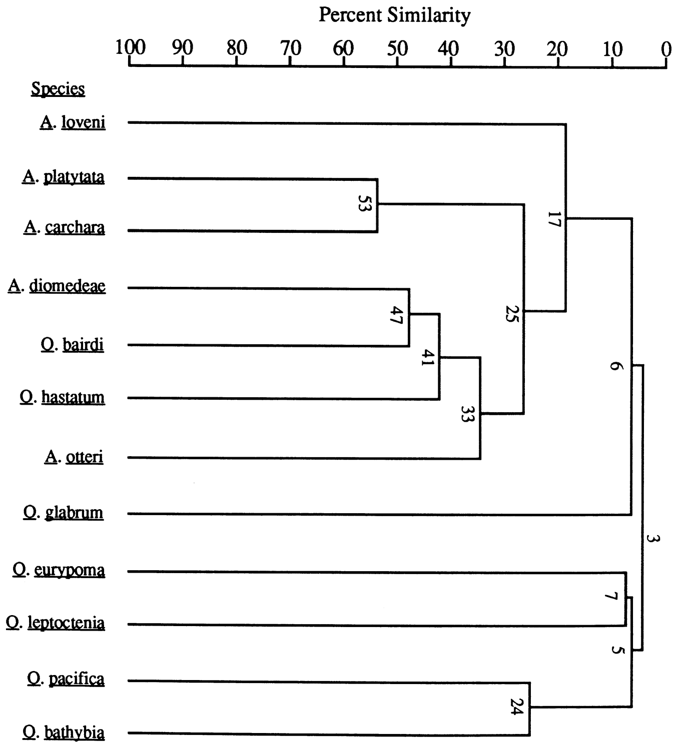

Fig. 10. Dendogram showing similarity of relative abundances among ophiuroid species (inverse classification) collected with trawls at the Farallon Slope, Pioneer Canyon and Monterey Canyon study sites. Clustering is with Bray–Curtis and group average sorting, with standardization on totals.

the Farallones (12 of 17) and Monterey (6 of 8) were taken between 2600 and 3000 m. When the relative abundances of ophiuroid species between 2600 and 3000 m were compared, the overall pattern was the same as between 2300 and 3300 m. Finally, the reported depth ranges of ophiuroid species collected with trawls were all at least 1000 m and for the most part encompassed the 2300–3300 m depth range sampled here (see Table 1). The Pioneer Canyon site was included in analysis even though it was not adequately sampled because nothing is known of this area, and the results are interpreted with caution.

Percent similarity (sum of minimums, Sanders, 1960) of species relative abundances over the depth ranges sampled indicated a change in ophiuroid species composition and abundance between the two northern sites and the Monterey Canyon site. Percent similarity between trawls taken at the Farallon Slope and Pioneer Canyon sites ranged from 77 to 82%. Percent similarity between these two northern sites and the Monterey Canyon site ranged from 50 to 59%. Farallon box cores were slightly more similar to Farallon trawls (60%) than to either Pioneer (55%) or Monterey

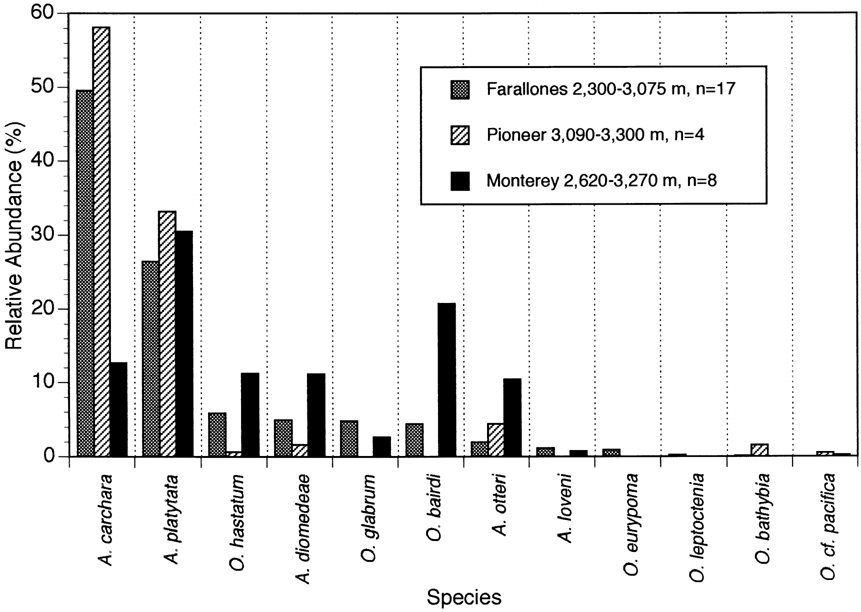

Fig. 11. Relative abundances of ophiuroid species collected with trawls at the Farallon Slope, Pioneer Canyon and Monterey Canyon study sites.

trawls (56%), but these results indicate that box core samples were not very similar to trawl samples regardless of location.

Although seasonality was not well sampled in this study, percent similarity did not show obvious seasonal differences in ophiuroid species composition or abundance. Pioneer Canyon trawls taken in February of 1992 were 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.

A comparison of relative abundances of ophiuroid species among the three areas trawled were consistent with percent similarity results, with the Monterey Canyon site showing different patterns than either the Farallon Slope or Pioneer Canyon sites (Fig. 11). At the Farallon Slope and Pioneer Canyon sites, *Amphiura carchara* and *Amphilepis platytata* were the most abundant species. At the Farallon Slope, *A. carchara* contributed 50% and *A. platytata* 26%, whereas at Pioneer Canyon *A. carchara* accounted for 58% and *A. platyata* for 33%. The rest of the species present in these two locations contributed less than 6% each to relative abundance. At the Monterey Canyon site, *Amphilepis platytata* and *Ophiolimna bairdi* were the most abundant species, but together accounted for only 52% of the total number of individuals. Next in abundance were Amphiura *carchara* with 13%, *Ophiocten hastatum* with 11%, *Amphiura diomedeae* with 11% and *Amphiura otteri* with 10%.

The Farallon Slope and Pioneer Canyon sites were more heavily dominated by just a few ophiuroid species, as compared to the Monterey Canyon site.

Several species were not collected from some or all of the trawl study sites (Table 1). *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. *Ophiura leptoctenia* was not collected at the Pioneer or Monterey canyon sites but was present at the Farallones. This species was found to be most abundant with box cores between 1000 and 2200 m, however, and whereas the Farallones trawls sampled as shallow as 2300 m, the Pioneer and Monterey trawls were all deeper than 2600 m. Alternately, the lack of *O. leptoctenia* at two of the trawl sites may be gear dependent as this species is small (disc diameters usually less than 8 mm; Hendler, 1996) and may have been disporportionately lost through the net. *Ophiosphalma glabrum* was not collected at the Pioneer Canyon site, and while this could have been due to insufficient sampling, this species was not found below 2900 m at the Farallones or Monterey sites, and Pioneer trawls were all deeper than 3000 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, indicating patchiness in species distribution on the continental slope on the scale of hundreds or even thousands of square meters (Table 4).

Table 4
Mean abundance and variance per 100 m^2 for ophiuroid species collected with trawls at the Farallon Slope, Pioneer Canyon and Monterey Canyon study sites. Listed in order of abundance at the Farallon Slope

Study site	Farallon slope 1991/92 2300–3075 m $n = 17$		Pioneer canyon 1992 3090–3300 m $n = 4$		Monterey canyon 1992 2620–3270 m $n = 8$	
Species	x	s^2	x	s^2	x	s^2
Amphiura carchara	1.92	9.93	2.04	4.04	1.03	1.04
Amphilepis platytata	1.03	2.87	1.16	1.60	2.50	6.48
Ophiocten hastatum	0.22	0.09	0.02	<0.01	0.92	1.36
Amphiura diomedeae	0.19	0.10	0.06	0.01	0.91	1.21
Ophiosphalma glabrum	0.19	0.27	0	0	0.22	0.15
Ophiolimna bairdi	0.17	0.04	0	0	1.70	11.98
Amphiura otteri	0.07	0.01	0.16	0.08	0.85	1.30
Asteronyx loveni	0.04	<0.01	0	0	0.06	0.01
Ophiacantha eurypoma	0.04	<0.01	0	0	0	0
Ophiura leptoctenia	0.01	<0.01	0	0	0	0
Ophiura bathybia	0.004	<0.01	0.05	<0.01	0	0
Ophiocten cf. *pacificum*	0	0	0.02	<0.01	0.02	<0.01
Total	3.88	28.00	3.50	5.53	8.20	69.13

3.3. Trawls vs. box cores

Trawls sampled a much larger area of the sea floor at the Farallon Slope than did box cores, covering an average of 5411 m^2 per trawl for a total area sampled of 72208 m^2. Each box core sampled a 0.1 m^2 area for a total area sampled of 6.8 m^2. When box cores and trawls at the Farallon Slope site were compared between 2300 and 3075 m, the average number of ophiuroids collected per m^2 for box cores was 14.6 ± 2.4 ($n = 28$ box cores) whereas the average number collected per m^2 for trawls was 0.06 ± 0.11 ($n = 17$ trawls).

Cumulative species curves showed that ophiuroids at the Farallon Slope study site had been adequately sampled with 6–7 trawls (Fig. 8a) and 10–11 box cores (Fig. 6b) below 2300 and 2005 m, respectively. The curves also indicate there was less variation in the number of species collected among trawls than among box cores (by smaller standard deviations).

Box cores failed to sample almost 50% of the ophiuroid species collected by trawls below 2300 m, and many of those missed were abundant in trawls (Fig. 12). *Ophiocten hastatum*, for instance, was the third most abundant species collected in trawls and *Ophiosphalma glabrum* the fifth. Neither species ever was collected in box cores. Several species, such as *Amphiura diomedeae* and *Amphiura otteri*, were relatively more abundant in box cores than in trawls. The most notable similarity between trawl and box core collections was the dominance of *Amphiura carchara*. Percent similarity (sum of minimums, Sanders, 1960) of relative abundances between trawl and box core distributions was 60%.

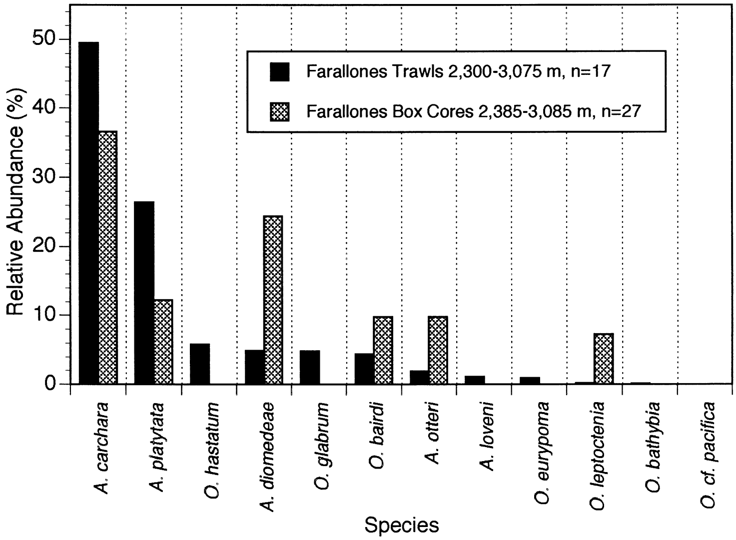

Fig. 12. Relative abundances of ophiuroid species collected with box cores and trawls below 2300 m at the Farallon Slope Area 5.

4. Discussion

4.1. Comparison of sampling methods

A combination of lifestyle habits and morphological characteristics make ophiuroids a difficult taxon to adequately sample with a single class of collecting gear. Members of the families Amphiuridae and Amphilepididae are infaunal or semi-infaunal, living in burrows or lightly covered with sediment. Ophiuridae and Ophiacanthidae tend to be epifaunal, remaining exposed on the sediment or clinging to sessile epifauna or rocky outcrops (Gage and Tyler, 1991; Gordon Hendler, pers. comm.). Members of the family Asteronychidae such as *Asteronyx loveni* are generally epizoic on gorgonians or pennatulids (Fujita and Ohta, 1988). In addition, ophiuroid species range in size from disk diameters of only a few millimeters to over 40 mm. As their name suggests, all brittle stars have fragile morphologies, although robustness varies among species.

A comparison of box core and trawl samples collected below 2300 m at the Farallon Slope study site highlights some of the unique sampling problems presented by deep-sea ophiuroids. While it took only 10–11 box cores to sample adequately the ophiuroid assemblage as shown by cumulative species curves between 2000 and 3000 m on the continental slope off central California (Fig. 6), they missed almost 50% of the ophiuroid species collected by trawls within this same depth range and area, including very abundant ones, indicating they in fact did not adequately sample this entire ophiuroid assemblage (Fig. 12). Box cores are primarily designed to sample small infaunal organisms and adequately sampled only those ophiuroid species which were smaller, less patchy, or more abundant. It appears that the 0.1 m^2 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, 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. It took only six to seven trawls to adequately sample almost twice the number of ophiuroid species at this same study site (Figs. 8 and 12). A maximum of 1268 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.

On the other hand, trawl data underestimated densities of ophiuroids on the continental slope at the Farallones. A comparison of box cores and trawls at the Farallon Slope site between 2300 and 3075 m showed that trawls collected on average 243 times fewer ophiuroids per m^2 than did box cores. This was confirmed by camera sled observations at the Farallon Slope where the mean abundance of ophiuroids was 2.2 per 100 m^2 in trawls compared to 69 per 100 m^2 in camera sled photographs (Craig, 1997). The camera sled data also provide an underestimate of the ophiuroids that are buried and therefore not visible in photographs. While it was impossible to tell whether or not trawls were continually engaged on the bottom, and there is some evidence they may not have been when comparing other phyla (Craig, 1997), ophiuroids were undoubtedly lost through the net due to their small size and fragile morphologies.

Some of the differences in species relative abundance patterns between box cores and trawls is attributable to morphological differences among species. *Ophiosphalma glabrum*, the largest ophiuroid found in this study with a disc diameter of up to 40 mm, was collected in trawls but not in box cores. The 0.1 m^2 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. They also may be more likely to avoid the sampler (Gordon Hendler, pers. comm.). *Amphiura otteri*, a very fragile species, was collected intact in box cores and rarely taken in trawls. *Asteronyx loveni* probably was collected in trawls but not box cores because it is almost always found above the sediment surface attached to seawhips. Box cores and trawls each had limitations so that neither were sufficient to completely sample the entire ophiuroid assemblage on the continental slope.

4.2. Bathymetric distribution

Deep-sea ophiuroids have been found to be rather eurybathic compared to other macrofauna (Tyler, 1980; Gage and Tyler, 1982,1991). Indeed, the reported depth ranges for most ophiuroid species found in this study exceeded that examined here (Table 1). Despite this, species distribution and abundance patterns still showed changes with depth off central California (Table 2, Fig. 5). Box core data showed two general faunal breaks between 550 and 3085 m, at about 1000 and about 2000 m (Fig. 2). Ophiuroids collected with trawls between 2300 and 3300 m showed a general faunal break at about 2700 m (Fig. 9). The position of the faunal break detected with trawls, however, must be interpreted with caution because few of the 29 trawls were taken between 2300 and 2700 m, and trawls sampled depth intervals ranging between 5 and 325 m (mean of 107 m) per trawl. Precise locations remain unclear due to the overlapping depths sampled by trawls.

Only two ophiuroid species, *Ophiura leptoctenia* and *Ophiacantha normani*, were collected in great enough numbers with box cores to show clear depth related trends (Table 2, Fig. 4). They were most abundant between 1000 and 2000 m, with a peak at about 1500 m. These same species are very abundant in the Santa Catalina Basin off southern California (Smith and Hamilton, 1983). Irregular patterns of the other 10 species may have been an artifact of insufficient data, so their distributions are not considered here.

Depth-related distribution patterns of ophiuroids are presumably influenced by the interplay of physical and biological factors. These may 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), variations in sediment characteristics such as grain size and organic content that supply both habitat and food (Sokolova, 1959,1972; Tyler, 1980; Carey, 1981; Sibuet, 1985), mode of larval dispersal (Schoener, 1972; Tyler, 1980), and predation and competition (Gage and Tyler, 1982). In this study, two physical phenomena were examined that could affect ophiuroid distribution. These were dissolved oxygen levels and sediment grain size and organic content. These factors may in turn affect the distribution of other organisms that interact with ophiuroids either as potential prey items or as potential predators or competitors.

Off the coast of central California, a well-developed seasonal upwelling system leads to high planktonic productivity in surface waters. As this phytodetritus sinks to the ocean floor it creates a changing pattern of dissolved oxygen with depth and an oxygen minimum zone (OMZ) centered around 800 m (Fig. 4; Thompson, 1983; Vercoutere et al., 1987). Dissolved oxygen concentrations can strongly influence the distribution of macro- and microfauna that in turn exert effects on bottom sediment characteristics (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 was found between about 500 and 1000 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 (Table 2, Fig. 4). It is impossible to tell whether ophiuroids were responding to low oxygen levels, or were absent from the OMZ purely as an artifact of insufficient sampling, especially when 20 of the 68 box cores throughout the depth range sampled contained no adult animals. These results are consistent, however, with Thompson (1983) who found that the OMZ off Big Sur in central California was devoid of ophiuroids. Two box cores within the OMZ did contain juvenile ophiuroids. Juvenile organisms often are 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. Gage and Tyler (1981) found similar results for ophiuroids in the Rockall Trough, but attributed the seasonal non-viable settlement there to unkown causes.

Two species, *Ophiura leptoctenia* and *Ophiacantha normani*, were primarily responsible for a large increase in ophiuroid abundance at the lower edge of the OMZ (Table 2, Fig. 4), possibly reflecting an OMZ “edge effect” (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 consisting of bacteria (Thompson, 1983; Mullins et al., 1985; Vercoutere et al., 1987). This may in turn lead to higher abundances of potential prey items.

When the partial pressure of dissolved oxygen is below about 2.8 mg/l, an oxygen value associated with the dysaerobic biofacies, it becomes a first-order ecological factor affecting the distribution of marine benthos (Tyson and Pearson, 1991). Dissolved oxygen levels rose above 2.8 mg/l in this study below about 2000 m, and the environment changed from dysoxic to oxic (Fig. 4). This depth also was where the largest change in ophiuroid species composition and relative abundance patterns were found, primarily due to decreases in the abundances of *Ophiura leptoctenia* and *Ophiacantha normani* (Table 2, Figs. 4 and 5).

The pattern of decreasing sediment grain size and increasing sediment organic content with increasing water depth found in this study is consistent with sediment data from the continental slope northwest of Point Sur, CA (Vercoutere et al., 1987). In addition, these authors found that the total organic carbon (TOC) content of surface sediments parallels the distribution curve for dissolved oxygen versus water depth. While ophiuroid species may be responding differentially to the partial pressure of dissolved oxygen, they also may be responding to increases in the amount of available food as a consequence of organically enriched sediment. Finer sediments are thought to contain more food due to the increased grain surface area to grain volume available for microbial activity, and have been shown to support higher densities of deposit-feeders at a given water depth (Wheatcroft, 1992).

Many 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). Pearson and Gage (1984) attributed slight dissimilarities in diet between Rockall Trough species to differences in lifestyle. The more motile, epifaunal Ophiuridae showed the greatest variety in food items. The diets of most of the ophiuroid species collected in this study have never been examined. However, the two ophiuroid species dominant between 1000 and 2000 m, *Ophiura leptoctenia* and *Ophiacantha normani*, appear to be mobile scavengers (Tyler, 1980; Smith and Hamilton, 1983; Smith, 1985; Hendler, 1996). *Amphiura carchara* and *Amphiura diomedeae*, the two ophiuroid species dominant between 2000 and 3000 m, are both members of the family Amphiuridae, species of which generally are microphageous deposit or suspension feeders (Warner, 1982).

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 predatory species with depth. He concluded that food quality and supply is a regulator of faunal abundance and energy use in the deep sea and suggested that as depth increases and prey density decreases, organisms will become less specialized feeders and will tend toward deposit-detrital and omnivorous feeding. This trend also has been suggested by others (Sokolova, 1959; Sibuet, 1985; Gage and Tyler, 1991). Where there is sufficient oxygen at the sea floor, variations in sediment organic content and its associated communities may play an important role in ophiuroid distribution by affecting the food supply (Carney et al., 1983; Levin et al., 1991).

Biological controls such as predation and intra- and interspecific competition may help regulate 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). Smith (1985) found that at least three predators, the rockfish *Sebastes altivelis*, the asteroid *Nearchaster aciculosus*, and the crab *Paralomis multispina*, were drawn to high concentrations of the ophiuroid *Ophiacantha normani* attracted to bait in water depths of 1,300 m in Santa Catalina Basin. 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 4260 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 13 asteroid species were collected between 500 and 3000 m, the depth range of this study.

4.3. Spatial and local zoogeographic distribution

Small-scale patchiness of ophiuroids on the continental slope off central California was reflected by the large percentage of box cores that contained no adult ophiuroids (29%; Fig. 4), by the high variance-to-mean ratios of species abundances in most depth intervals (Table 2), and by the highly significant values of Morisita's Index of Dispersion for species collected with box cores (Table 3). Large-scale patchiness was evident in the large variance-to-mean ratios of species abundances collected with trawls within each of the three sampling areas (Table 4), and also was supported by camera-sled observations (Hecker Environmental Consulting, 1992). Camera-sled transects frequently traveled through areas 300 m long or more where ophiuroids were apparently abundant, then equal distances where few were seen (Susan Craig and Lisa Weetman, pers. comm.).

Comparisons of relative abundance patterns of ophiuroid species among the Farallon Slope, Pioneer Canyon and Monterey Canyon indicated that animals were more evenly distributed among species at the Monterey Canyon site (Fig. 11). Although many of the same species were found at all three locations, species relative abundance patterns differed 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, suggesting a more homogeneous environment in Monterey (Fig. 8).

The nature and causes of ophiuroid dispersion patterns within as well as between geographic areas may be complex even for a single species, and may vary over both space and time and in response to density. Grassle et al. (1975) attributed patchiness of the surface deposit feeding deep-sea ophiuroid *Ophiosphalma lymani* at low densities to avoidance of disturbed areas on the sea floor, but at high densities individuals were observed to actively space themselves so that the tips of their arms were not touching. At 4100 m in the Northeast Pacific, Lauerman et al. (1996) found that ophiuroids on three different substrates, hard substrate, *Paradiopatra* tubes and soft sediment, exhibited both random and aggregated distributions on various spatial scales, and showed substantial large scale heterogeneity on spatial scales of meters to several kilometers. They suggested that this spatial variability may be related to numerous physical and biological factors including heterogeneity of the sediment surface that affects fluid motion and deposition of particulate organic matter, current speed, food supply, and reproductive behavior.

Local topographic variation and differences in the depositional environment may have influenced ophiuroid abundance patterns in this study within as well as between sites. 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 and more discrete faunal patches and areas of zonation. 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, soft sediment environment and animals were more evenly distributed (Nybakken et al., 1992b; Hecker Environmental Consulting, 1992; Susan Craig and Lisa Weetman, pers. comm.). Box core sampling at the Farallones site identified three depositional sites of low kinetic energy 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 canyon's steeper sides or flanks (Blake et al., 1992; SAIC, 1992). These apparent small and large scale variations in topographic relief that regulate the distribution of sediment grain size and concentrations of organic matter may also influence the spatial distribution of ophiuroids by affecting current regimes, nutrient availability and biological activity.

Intraspecific associations between ophiuroids and both seapens and holothurians also shed light on potential causes of spatial variation within and between sites. Camera-sled data showed that small white ophiuroids often were found in association with seapen beds (Order Pennatulacea) at the Farallon Slope site (Hecker Environmental Consulting, 1992). Sessile, filter-feeding seapens presumably are successful where water currents carry abundant food (Gary Williams, pers. comm.). While ophiuroids were frequently 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. Large seapen beds were quite common at the Farallon Slope (Hecker Environmental Consulting, 1992), but seapens were sparse in Monterey Canyon and never were found in large beds (Nybakken et al., 1992b; Susan Craig and Lisa Weetman, pers. comm.). This possibly may reflect differences in water motion between these two sites (Craig, 1997).

Interestingly, the occurrence of ophiuroids was inversely related to the occurrence of elasipodid holothurians. Ophiuroids were either absent or present only in low numbers in areas where large herds of elasipodid holothurians were found, and where there were large numbers of ophiuroids there were no epifaunal holothurians (Craig, 1997). Out of the 29 trawl samples collected in this study, the only two without brittle stars were collected in Monterey Canyon and each contained close to 3000 holothurians, the majority being *Scotoplanes globosa*, *Peniagone* cf. *incerta*, and *Elpidia* cf. *theeli* (Nybakken et al., 1992a,b). Camera sled photographs confirmed that lack of brittle stars was not purely an artifact of trawl sampling (Susan Craig and Lisa Weetman, pers. comm.).

Elasipodid holothurians are opportunistic mobile surface deposit feeders that thrive in organic-rich environments and often are found in large herds in or near canyon systems in unstable sedimentary environments (Hansen, 1975; Billett, 1991). Gage and Tyler (1991) have postulated that large-bodied epifaunal deposit feeders such as elasipodid holothurians are successful in low energy flow regimes, areas where current speeds would likely be too slow to suspended organic matter into the water column. It may also be that the sheer numbers of holothurians excluded ophiuroids by disturbance.

The Monterey Submarine Canyon is one of the largest submarine canyons on the west coast of North America, and 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). These factors probably lead to greater sediment and organic accumulation from both down-canyon flow and settlement of phytodetritus from planktonic blooms. Indeed, massive amounts of phytodetritus were observed with camera sled photographs in Monterey Canyon at depths greater than 3000 m, and these accumulations were much greater than anything seen at the Farallon Slope (Craig, 1997). Monterey Canyon also had the highest mean abundance of ophiuroids among the three geographic locations sampled (Table 4). While some abyssal epibenthic megafaunal species feed selectively on phytodetrital material (e.g. Kaufmann and Smith, 1997), the incorporation of phytodetritus into deep-sea sediments also is an important factor affecting faunal abundances (Smith et al., 1994).

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 the Monterey Canyon most likely reflects these disparities.

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. 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, 1981; 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 off central California, more intensive sampling is needed during different seasons within the same study location, as well as seasonal sampling with box cores. It has been shown that infrequent and essentially instantaneous surveys of the abyssal sea floor may give biased views of epibenthic megafaunal community structure (Lauerman et al., 1996).

Acknowledgements

This study could not have been completed without the help of numerous individuals. G. Hendler provided invaluable advice and encouragement throughout the course of research as well as verified all taxanomic identifications, made available specimens in his collection at the Natural History Museum of Los Angeles County, and engaged in hours of helpful discussion about the manuscript. R. Mooi at the California Academy of Sciences Department of Invertebrate Zoology and Geology also provided ophiuroid specimens for verification of identifications. Many others gave generous support in the field and laboratory including J. Blake, S. Craig, B. Hecker, B. Hilbig, G. Moreno, S. Osborn, L. Smith-Beasley, L. Weetman, I. Williams, and the crews of the R/V *Wecoma* and the R/V *Point Sur*. This manuscript benefitted from discussions with G. Caillet, M. Foster, D. Pawson, and G. Williams as well, and the critical reviews of G. Hendler and an anonymous reviewer. Support for this project was provided by the U.S. Navy through W. VanPeters, and by Science

Applications International Corporation (SAIC) through J. Blake under subcontract to PRC Environmental Consulting, Inc.. Additional support was provided by the Earl and Ethel Meyers Foundation and the David and Lucille Packard Foundation. The U.S. Navy and U.S. Environmental Protection Agency made available samples collected as part of deep-sea site assessment studies.

References

Alton, M.S., 1972. Bathymetric distribution of the echinoderms off the northern Oregon coast. In: Pruter, A.T., Alverson, D.L. (Eds.), The Columbia River Estuary and Adjacent Ocean Waters. University of Washington Press, Seattle, pp. 475–537.

Andrew, N.L., Mapstone, B.D., 1987. Sampling and the description of spatial pattern in marine ecology. Oceanography and Marine Biology Annual Review 25, 39–90.

Astrahantseff, S., Alton, M.S., 1965. Bathymetric distribution of brittlestars Ophiuroidea collected off the northern Oregon coast. Journal of the Fisheries Research Board of Canada 22, 1407–1424.

Austin, W.C., Hadfield, M.G., 1980. Ophiuroidea: the brittle-stars. In: Morris, R.H., Abbott, D.P., Haderlie, E.C. (Eds.), Intertidal Invertebrates of California. Stanford University Press, Stanford, California, pp. 146–159.

Barham, E.G., Ayer, N.J., Boyce, R.E., 1967. Macrobenthos of the San Diego Trough: photographic census and observations from bathyscaphe. Trieste. Deep-Sea Research 14, 773–784.

Billett, D.S.M., 1991. Deep-sea holothurians. Oceanography and Marine Biology Annual Review 29, 259–317.

Blake, J.A., Muramoto, J., Hilbig, B., Williams I.P., 1992. Biological and sedimentological investigations of the sea floor at the proposed U.S. Navy Ocean Disposal Site. July 1991 survey (R/V *Wecoma*). Benthic biology and sediment characterization. Report prepared for PRC Environmental Management, Inc. under Navy CLEAN Contract No. N62474-88-D-5086.

Boesch, D.F., 1977. Application of numerical classification in ecological investigations of water pollution. Special Scientific Report, 77, Virginia Institute of Marine Science, EPA-600/3-77-033, pp. 114.

Bolin, R.l., Abbott, D.P., 1963. Studies on the marine climate and phytoplankton of the central coastal area of California, 1954–1960. California Cooperative Oceanic Fisheries Investigations Report 9, 23–45.

Breaker, L.C., Broenkow, W.W., 1989. The circulation of Monterey Bay and related processes. Moss Landing Marine Laboratories Technical Publication, 89-1, 91pp.

Carey Jr., A.G., 1972. Food sources of sublittoral, bathyal and abyssal asteroids in the Northeast Pacific Ocean. Ophelia 10, 35–47.

Carey Jr., A.G., 1981. A comparison of benthic infaunal abundance on two abyssal plains in the northeast Pacific Ocean. Deep-Sea Research 28A, 467–479.

Carey Jr., A.G., 1990. Distributional ecology of selected megaepifauna on abyssal plains adjacent to Gorda Ridge, northeast Pacific Ocean. In: McMurray, G.R. (Ed.), Gorda Ridge: A Seafloor Spreading Center in the United States Exclusive Economic Zone. Springer, New York, pp. 241–251.

Carey Jr., A.G., Stein, D.L., Rona, P.L., 1990a. Benthos of the Gorda Ridge axial valley (NE Pacific Ocean): taxanomic composition and trends in distribution. Progress in Oceanography 24, 47–57.

Carey Jr., A.G., Taghon, G.L., Stein, D.L., Rona, P.A., 1990b. Distributional ecology of benthic megaepifauna and fishes in Gorda Ridge Axial Valley. In: McMurray, G.R. (Ed.), Gorda Ridge: A Seafloor Spreading Center in the United States Exclusive Economic Zone. Springer, New York, pp. 225–240.

Carney, R.S., Haedrich, R.L., Rowe, G.T., 1983. 9. Zonation of fauna in the deep sea. In: Rowe, G.T. (Ed.), The Sea, Vol. 8. Wiley, New York, pp. 371–398.

Clark, H.L. 1911. North Pacific Ophiurans in the collection of the United States National Museum. Bulletin of the United States National Museum 75, 302pp.

Craig, S. 1997. Distribution of deep-sea invertebrate megafauna off central California. Masters Thesis, Moss Landing Marine Laboratories, San Jose State University, California, 133pp.

D'yakonov, A.M. 1954. Ophiuroids of the USSR Seas. Publication of the Zoological Institute of the Academy of Sciences of the USSR, 55, trans. Israel program for Scientific Translation (Jerusalem, 1967), 123pp.

Fujita, T., Ohta, S., 1988. Photographic observations of the life style of a deep-sea ophiuroid *Asteronyx loveni* (Echinodermata). Deep-Sea Research 35, 2029–2043.

Gage, J.D., Tyler, P.A., 1981. Non-viable seasonal settlement of larvae of the upper bathyal brittle star Ophiocten gracilis in the Rockall Trough Abyssal. Marine Biology 64, 153–161.

Gage, J.D., Tyler, P.A., 1982. Depth-related gradients in size structure and the bathymetric zonation of deep-sea brittle stars. Marine Biology 71, 299–308.

Gage, J.D., Tyler, P.A. 1991. Deep-Sea Biology: A Natural History of Organisms at the Deep-sea Floor. Cambridge University Press, New York, 504pp.

Grassle, J.F., Sanders, H.L., Hessler, R.R., Rowe, G.T., Mclellan, T., 1975. Pattern and zonation: a study of the bathyal megafauna using the research submersible Alvin. Deep-Sea Research 22, 457–481.

Hansen, B., 1975. Systematics and biology of the deep-sea holothurians. Galathea Report 13, 1–262.

Hartman, O., Barnard, J.L., 1958. The benthic fauna of the deep basins off Southern California. Allan Hancock Pacific Expeditions 22, 1–67.

Hecker Environmental Consulting, 1992. Biological and sedimentological investigations of the sea floor at the proposed U.S. Navy Ocean Disposal Site. July 1991 survey (R/V *Wecoma*). Megafaunal assemblages. Report prepared for PRC Environmental Management, Inc. under Navy CLEAN Contract No. N62474-88-D-5086.

Hendler, G., 1996. Class Ophiuroidea. In: Blake, J.A., Scott, P.H., Lissner, A. (Eds.), Taxanomic Atlas of the benthic fauna of the Santa Maria Basin and the western Santa Barbara Channel. Vol. 14 — Miscellaneous Taxa. Santa Barbara Museum of Natural History, Santa Barbara, California, pp. 113–179.

Hurtubia, J., 1973. Trophic diversity measurement in sympatric predatory species. Ecology 54, 885–890.

Kaufmann, R.S., Smith Jr., K.L., 1997. Activity patterns of mobile epibenthic megafauna at an abyssal site in the eastern North Pacific: results from a 17-month time-lapse photographic study. Deep-Sea Research I 44, 559–579.

Koehler, R., 1914. A contribution to the study of ophiurans of the United States National Museum. Bulletin of the United States National Museum 84, 146pp.

Krebs, C.J. 1989. Ecological Methodology, Harper and Row, New York, 654pp.

Lauerman, L.M.L., Kaufmann, R.S., Smith Jr., K.L., 1996. Distribution and abundance of epibenthic megafauna at a long time-series station in the abyssal northeast Pacific. Deep-Sea Research I 43, 1075–1103.

Levin, L.A., Huggett, C.L., Wishner, K.F., 1991. Control of deep-sea benthic community structure by oxygen and organic-matter gradients in the eastern Pacific Ocean. Journal of Marine Research 49, 763–800.

Madsen, F.J., 1961. On the zoogeography and origin of the abyssal fauna in view of the knowledge of the Porcellanasteridae. Galathea Report 4, 177–218.

Maluf, L.Y. 1988. Composition and distribution of the central eastern Pacific echinoderms. Technical Report No. 2, Natural History Museum of Los Angeles County, 242pp.

Mullins, H.T., Thompson, J.B., Mcdougall, K., Vercoutere, T.L., 1985. Oxygen-minimum zone edge effects: Evidence from the central California coastal upwelling system. Geology 13, 449–528.

Nybakken, J., Smith-Beasley, L., Summers, A., Craig, S., Weetman, L., 1992a. invertebrate megafauna collected from the proposed u.s. navy Ocean Disposal Site as determined from beam and otter trawls and camera sled samples. Report prepared for PRC Environmental Management, Inc. under Navy CLEAN Contract No. N62474-88-D-1991, 56pp.

Nybakken, J., Smith-Beasley, L., Summers, A., Craig, S., Weetman, L., 1992b. Invertebrate megafauna collected from the proposed U.S. Navy Ocean Disposal Site as determined from beam trawls taken in February–March, 1992. Supplementary report prepared for PRC Environmental Management, Inc. under Navy CLEAN Contract No. N62474-88-D-1991, 32pp.

Oliver, J.S., Kvitek, R.G., Slattery, P.N., 1985. Walrus feeding disturbance: scavenging habits and recolonization of the Bering Sea benthos. Journal of Experimental Marine Biology and Ecology 91, 233–246.

Pearson, M., Gage, J.D., 1984. Diets of some deep-sea brittle stars in the Rockall Trough. Marine Biology 82, 247–258.

Pereyra, W.T., Alton, M.S., 1972. Distribution and relative abundance of invertebrates off the northern Oregon coast. In: Pruter, A.T., Alverson, D.L. (Eds.), The Columbia River Estuary and Adjacent Ocean Waters. University of Washington Press, Seattle, pp. 444–474.

Pielou, E.C., 1966. The measurement of diversity in different types of biological collections. Journal of Theoretical Biology 13, 131–144.

Rhoads, D.C., Mulsow, S.G., Gutschick, R., Baldwin, C.T., Stolz, J.F., 1991. The dysaerobic zone revisited: a magnetic facies? In: Tyson, R.V., Pearson, T.H. (Eds.), Modern and Ancient Continental Shelf Anoxia, Geological Society of London Special Publication, Vol. 58, pp. 187–199.

SAIC (Science Applications International Corporation), 1991. Biological and sedimentological investigations of the sea floor at the proposed U.S. Navy 103 Ocean Disposal Site. Report prepared for PRC Environmental Management, Inc.

SAIC (Science Applications International Corporation), 1992. Benthic biological and sediment characterization ocean studies report for detailed physical and biological oceanographic studies for an ocean site designation effort under the Marine Protection, Research and Sanctuaries Act of 1972 (MPSRA). Report prepared for U.S. Environmental Protection Agency and U.S. Environmental Protection Agency Region IX under EPA Contract No. 68-C8-0062.

Sanders, H.L., 1960. Benthic studies in Buzzards Bay III. The structure of the soft-bottom community. Limnology and Oceanography 5, 138–153.

Schoener, A., 1968. Evidence for reproductive periodicity in the deep sea. Ecology 49, 81–87.

Schoener, A., 1972. Fecundity and possible mode of development of some deep-sea ophiuroids. Limnology and Oceanography 17, 193–199.

Sibuet, M., 1985. Quantitative distribution of echinoderms (Holothuroidea, Asteroidea, Ophiuroidea, Echinoidea) in relation to organic matter in the sediment, in deep sea basins of the Atlantic Ocean. In: Keegan, B.F., O'Connor, B.D.S. (Eds.), Proceedings of the Fifth International Echinoderm Conference, Galway 24–29 September 1984. Balkema, Rotterdam, pp. 99–108.

Sibuet, E.M., 1984. Interference competition between brittle-stars? In: Keegan, B.F., O'Connor, B.D.S. (Eds.), Proceedings of the Fifth International Echinoderm Conference, Galway 24–29 September 1984. Balkema, Rotterdam, pp. 639–644.

Sides, E.M., Woodley, J.D., 1985. Niche separation in three species of Ophiocoma (Echinodermata: Ophiuroidea) in Jamaica. West Indies. Bulletin of Marine Science 36, 701–715.

Smith, C.R., 1985. Food for the deep sea: utilization, dispersal, and flux of nekton falls at the Santa Catalina Basin floor. Deep-Sea Research 32, 417–442.

Smith, C.R., Hamilton, S.C., 1983. Epibenthic megafauna of a bathyal basin off southern California: patterns of abundance, biomass, and dispersion. Deep-Sea Research 30, 907–928.

Smith Jr., K.L., Kaufmann, R.S., Baldwin, R.J., 1994. Coupling of near-bottom pelagic and benthic processes at abyssal depths in the eastern North Pacific Ocean. Limnology and Oceanography 39, 1101–1118.

Sokolova, M.N., 1959. On the distribution of deep-water bottom animals in relation to their feeding habits and the character of sedimentation. Deep-Sea Research 6, 1–4.

Sokolova, M.N., 1972. Trophic structure of deep-sea macrobenthos. Marine Biology 16, 1–12.

Summers, A.C., 1993. Bathymetric, spatial and local zoogeographic distribution of ophiuroids on the continental slope off central California. Masters Thesis, Moss Landing Marine Laboratories, San Jose State University, California, 68pp.

Thompson, J.B., 1983. Analysis of macrofaunal assemblages across the oxygen minimum zone offshore of central California. Masters Thesis, California State University, Sacramento. 77pp.

Tyler, P.A., 1980. Deep-sea ophiuroids. Oceanography and Marine Biology: an Annual Review 18, 125–153.

Tyler, P.A., 1986. Studies of a benthic time series: reproductive biology of benthic invertebrates in the Rockall Trough. Proceedings of the Royal Society of Edinburgh 88B, 175–190.

Tyson, R.V., Pearson, T.H., 1991. Modern and ancient continental shelf anoxia: an overview, In: Tyson, R.V., Pearson, T.H. (Eds.), Modern and Ancient Continental Shelf Anoxia, Vol. 58. Geological Society of London Special Publication, pp. 187–199.

Vercoutere, T.L., Mullins, H.T., Mcdougall, K., Thompson, J.B., 1987. Sedimentation across the central California oxygen minimum zone: An alternative coastal upwelling sequence. Journal of Sedimentary Petrology 57, 709–722.

Vinogradova, N.G., 1959. The zoogeographic distribution of the deep-water bottom fauna in the abyssal zone of the ocean. Deep-Sea Research 5, 205–208.

Warner, G., 1982. Food and feeding mechanisms: Ophiuroidea. In: Jangoux, M., Lawrence, J.M. (Eds.), Echinoderm Nutrition. Balkema, Rotterdam, pp. 161–181.

Wheatcroft, R.A., 1991. Conservative tracer study of horizontal sediment mixing rates in a bathyal basin. California borderland. Journal of Marine Research 49, 565–588.

Wheatcroft, R.A., 1992. Experimental tests for particle size-dependent bioturbation in the deep ocean. Limnology and Oceanography 37, 90–104.