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Distribution of Benthic Infaunal Communities in the Vicinity of Point Conception, California

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Abstract - Between 1982-1984, soft-bottom infaunal benthic assemblages were investigated along the shelf and slopes of the Santa Maria and Santa Barbara Basins, near Pt. Conception, California. These efforts were part of a longterm study to determine possible impacts of oil and gas developments. Data analysis delineated five communities whose distribution varied with depth and location along the coast. These spatial trends corresponded better with overlying dissolved oxygen (DO) values and sediment grain size, rather than with other environmental factors. Evaluation of data from this and other subtidal studies along the west coast of North America indicates that dissolved oxygen levels below 4 mg/l appear to have an important effect on regulating the distribution of infaunal communities.

Introduction

Pt. Conception (Fig. 1) is recognized as a biogeographic boundary (Brusca & Wallerstein 1979) or transition zone (Newman 1979) for many intertidal and shallow-water marine organisms between the cold and warm temperate regions along the west coast of North America. Comparable information regarding deeper benthic species and communities is less definitive, since previous studies have focused on one region or the other, rather than across the boundary zone (SAIC 1986).

Proposed development of oil and gas resources in the Santa Maria and Santa Barbara Basins, situated respectively north and east of Pt. Conception (Fig. 1), has required a comprehensive, quantitative survey to assess potential impacts on shelf, slope and basin infaunal communities. This long-term investigation provides an opportunity to examine the distribution of the deeper benthic species and communities in the two regions.

The purpose of this initial field study (termed Phase I) was to characterize the benthic habitat, both physically and biologically, in the Santa Maria and Santa Barbara Basin areas in order to provide a basis for subsequent, long-term monitoring during Phases II and III. This paper presents some of



Figure 1. Bathymetric features of the Santa Maria Basin and Santa Barbara Basin in the vicinity of Pt. Conception.

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Figure 2. Distribution of stations, samples and associated communities.

the results of Phase I and compares the distribution of infaunal communities in and between the two areas with corresponding environmental factors that may regulate the communities' distribution. Preliminary interpretation of some of this data has been provided in Smith & co-author's (1988).

Methods and Materials

Field and Laboratory: Field studies were conducted between November 1982 and January 1984 along a grid of 98 stations, extending from Pt. Estero to Gaviota (Fig. 2). Stations ranged in depth from 50 m along the shelf to 1,100 m on the slopes. At each station, between one and four replicate 0.1m² box cores were obtained. Only complete samples with undisturbed sediments were processed by sieving through both 0.5 and 1.0 mm screens and fixing with 10% formalin in sea-water. The samples were later sorted in the laboratory into

major taxa, wet weighed to the nearest 0.01 gram and identified to the lowest practical taxonomic level. Species' identifications were verified by experts and voucher collections were deposited in the Smithsonian Institution and the Santa Barbara Museum of Natural History.

A small portion of each core also was collected for analysis of abiotic parameters, including sediment grain size and chemistry (Table 1). Details regarding field and laboratory methodologies are provided in the final project report (SAIC 1986). Although dissolved oxygen (DO) values were not measured during the investigation, applicable values were obtained from each basin during other studies (Lynn *et al.* 1982; Sholkovitz & Gieskes 1971).

Data Analysis: Data analysis examined both the physical and biological data to compare the two basins and to determine what environmental factors might be controlling the distribution of the infaunal communities.

The mean levels of the physical and chemical sediment measurements, as well as community parameters from the two basins, were compared using analysis of variance (ANOVA). The

Table 1. List of grain size and chemistry parameters measured.

Parameter	Units
Water Depth	meters
Grain size Parameters	
Mean	phi
Mode	phi
Sand	percent
Clay	percent
Sharp & Fan	
Sorting index	-
Standard deviation	phi
Sediment Chemistry	
Organic carbon	percent dry weight
Barium	mg/g
Chromium	mg/g
Total hydrocarbon	mg/g dry weight
Total aromatic	
hydrocarbons	mg/g dry weight
Total alkane	
hydrocarbons	mg/g dry weight
Oil pollution index	-

community parameters included number of species, total abundance and the Shannon-Wiener species diversity index (H; Pielou 1969).

Species abundance data from the 1.0 mm screen in the first replicate at each station were used in the community analysis. Spatial community patterns were studied using ordination and cluster analyses. The ordination technique utilized was local nonmetric multidimensional scaling (Prentice 1977), which was based on the Bray-Curtis dissimilarity index, followed by the step-across procedure (Williamson 1978). The species abundance values were transformed by a square root and standardized by the species mean for values preater than zero. Species occurring in fewer than four stations were not used in the computations. The flexible clustering method was used during cluster analysis, with the flexible coefficient beta set at the usual value of -0.25 (Clifford & Stephenson 1975). The dissimilarity values used in the cluster analysis of the stations were the distances between the stations in the ordination space; dissimilarities used in the cluster analysis of the species were the distances between the weighted average positions of the respective species in the ordination space. Additional details on the ordination and cluster analysis methods are found in SAIC (1986) and Smith & co-author's (1988).

Ordination analysis displays the samples as points in a multidimensional space. The distances between the points in the space are proportional to the dissimilarity of the communities found in the corresponding samples. Samples that contain similar communities will be closer together in the ordination space than samples that contain very dissimilar communities.

Community differences are largely caused by environmental differences and the dimensions (axes) of the ordination space are usually correlated with environmental gradients. To form hypotheses as to which environmental gradients might be causing observed community differences, the ordination axis scores (coordinates of the points on the axes) were used as dependent variables in multiple regression analyses; the environmental measurements (depth, chemical and sediment parameters) were in turn used as independent variables. To simplify the analysis, the allsubsets independent variable selection procedure was utilized (SAS PROC RSQUARE; SAS 1985).

Cluster analysis was used to form groups of stations that contained similar benthic communities. The relationships between the station groups and the species were examined with a two-way matrix. In this matrix the rows and columns are rearranged to fit the order in the cluster analysis dendrograms of the species and the stations, respectively (Kikkawa 1968; Clifford & Stephenson 1975; Smith & Greene 1976). The rearrangement of rows and columns places similar stations and species in adjacent rows and columns, which makes it easy to see patterns of species among stations. To save space, the two-way coincidence table is presented in a summarized form with the percentages of each species group within each station group indicated with symbols.

Results

Analysis of the physical and hydrographic characteristics of the two basins indicates variability within and between basins. Bathymetrically the Santa Maria Basin has a wider shelf that drops down to slope depths even greater than that sampled at 1,100 m (Fig. 1). This basin includes a sea valley (at slope depths below 600 m) situated between shallower shelf depths closer to shore and the relatively shallow Santa Lucia Bank located further offshore. South of the sea valley, off Pt. Arguello, the shelf is narrower. The slope here includes a series of shallow subtidal tributaries leading into deeper submarine canyons. This basin, filled with sediments and lacking a surrounding sill to trap water, is a geographic rather than a hydrographic basin. In contrast, the smaller Santa Barbara Basin, situated between the mainland and

Table 2. List of species by groups delineated by classification analysis. See Figure 5 for relationships among species groups and communities. (Continued on next page.)

SPECIES GROUP A

Ninoe sp. a Harmothoe nr. lunulata Kurtziella beta Lumbrineris tetraura Prionospio sp. a Amphicteis scaphobranchiata Procampylaspis sp. a Amphissa undata Leptosynapta sp. b Byblis veleronis Foxiphalus similis Tellina carpenteri Lumbrineris cruzensis Cadulus quadrifissatus Terebellides reishi Cossura rostrata

SPECIES GROUP B

Amphioplus strongyloplax Amphiodia urtica Cuspidaria parapodema Cylichna diegensis Bittium fetellum Nephtys ferruginea Cyclocardia ventricosa Synchelidium shoemakeri Acila castrensis Diastylis paraspinulosa Paraprinospio pinnata Chloeia pinnata Paranemertes sp. a Heterophoxus oculatus

Dougaloplus amphacantha Amphiura acrystata Sarsonuphis parva Cossura candida Mysella cf. aleutica bepoxynius bicuspidatus Spiophanes missionensis Tharyx tesselata Mooreonuphis nebulosa Kurtzia arteaga Euphilomedes producta Nereis procera Eblersia beterochaeta Nemocardium centifilosum Monobrachium parasitum Amphichondrius granulosus Diastylis sp. a Photis californica Golfingia minuta Laonice cirrata Amphipholis squamata Exogone lourei Decamastus gracilis Amygdalum pallidulum Rhodine bitorquata Praxillella pacifica Travisia brevis Glycera capitata Sternaspis fossor Spiochaetopterus costarum Tomburchus redondoensis Ophiura lutkeni Thysanocardia nigra Spiophanes berkeleyorum Gnathia crenulatifrons Pholoe glabra Silophasma geminatum Artacamella hancocki Parvilucina tenuisculpta Rocinella angustata Ninoe palmata Volvulella californica Maera danae Pinnixa occidentalis Travisia pupa Ampelisca macrocepbala Nephtys punctata Balcis rutila Ampelisca pacifica Anobothrus bimaculatus Niccippe tumida Leptognathia sp. b Axinopsida serricata Scleroconcha trituberculata Ampelisca agassizi Pectinaria californiensis Ampelisca brevisimulata Levensenia gracilis

Ampelisca pugetica

several of the northern Channel Islands, includes a sill at 475 m off Pt. Conception and is relatively shallow, reaching maximum depths of 620 m.

The grain size distribution of the sediments in the two basins was similar (Fig. 3). Analysis of mean grain size indicates that sands were found closer to the mainland, as well as farther offshore, at shallower depths off the Santa Lucia Bank and along the northern Channel Islands. Mean grain size was smaller (silts) at intermediate distances offshore, extending south and then east from the sea valley in the Santa Maria Basin, into the floor of the Santa Barbara Basin.

The percent of organic carbon associated with the sediments in the two basins correlated with depth ($r^2 = 0.67$) and several grain size

parameters, including mean phi ($r^2 = 0.65$) and percent clay ($r^2 = 0.62$). High organic carbon values were found in both the northern portion of the Santa Maria sea valley and along the floor of the Santa Barbara Basin (Fig. 3). Lower values were found in the Santa Maria Basin, associated with the submarine canyon system and further north.

Hydrographic values from the two basins were taken from CalCOFI data collected over a 28 yr period (1950-1978) at one station in each basin (Lynn et al. 1982). Values presented are means over four seasonal sampling periods during each year, at depths between the surface and 500 m in the Santa Maria Basin and. between the surface and only 300 m in the shallower Santa Barbara Basin. Temperatures

SPECIES GROUP C

Melinna heterodonta Onuphis iridescens Pista nr. Fasciata Eunice americana Hesperonoe laevis Monoculodes emarginatus Harpiniopsis fulgens Amphissa bicolor Myriochele gracilis Lyonsiella alaskana SPECIES GROUP D Scalibregma inflatum Minuspio cirrifera Tubulanus pellucidus Adontorhina cyclia SPECIES GROUP E Rhachotropis distincta Leucon magnadentata Nephtys cornuta franciscana Sigambra tentaculata Limifossor fratula Heteromastus filobranchus Ampharete arctica Falcidens bartmanae Cadulus californicus SPECIES GROUP F Laonice apellofi Harpiniopsis epistomata Mitrella permodesta Mysella sp. d Bathymedon covilhani Huxleyia munita Nucula tenuis

Rhachotropis clemens Pentamera pseudocalcigera Brissopsis pacifica Brisaster latifrons Saxicavella pacifica Phoxocephalus bomilis Eudorella pacifica Philomedes dentata Liljeborgia cota Goniada annulata Tharyx sp. g Araphura sp. b Galeommatidae Genus A,sp. a Terebellides californica Calocarides quinqueseriatus

Dentalium rectius Glycinde armigera Bugula neritina Perigonimus repens Listriella albina Ampelisca unsocalae Munnopsurus sp. a Allia antennata Macoma carlottensis

Monoculodes glyconica

Glycera branchiopoda

Ecylsippe trilobatus

Saturnia nr. ritteri

Leiochrides sp. a

Eucranta nr. anoculata

Brada pluribranchiata Harmothoe scriptoria Maldane sarsi Arbynchite californicus Cirrophorus branchiatus Ophelina acuminata Diastylis pellucida Monoculodes latissimanus Pseudbarpinia excavata

Tharyx sp. c Podarkeopsis glabrus Lepidasthenia longicirrata Micrura alaskensis

Paraphoxus oculatus Prionospio lobulata Cerebratulus californiensis Brada villosa Nuculana conceptionis Tritella tenuissima Subadyte sp. b Stegocephalus hancocki

Phyllochaetopterus limicolus Byblis barbarensis Listriolobus hexamyotus Leitoscoloplos sp. a Anobothrus sp. a Ophiomastus sp. a Nucula exigua

in the Santa Barbara Channel ranged from 17.2°C on the surface to 6.0°C at 500 m. On the average, temperatures were 0.5°C significantly higher (P < 0.05) than in the Santa Maria Basin. Salinities in the Santa Barbara Channel ranged from 33.42 % on the surface to 34.29 at 500 m. On the average, salinities were 0.10 %, significantly higher per depth (P < 0.05) than in the Santa Barbara Basin.

Dissolved oxygen values also were examined over the same 28 yr period but only for the seasonal minima in July. These readings (Lynn et al. 1982) were obtained from the surface in both basins, but only to 300 m in the Santa Barbara Basin compared with 500 m in the

Santa Marina Basin. Dissolved oxygen values from a second study, down to 574 m during July 1970 in the Santa Barbara Basin, also were examined (Sholkovitz & Gieskes 1971). Since these latter values agreed with the CalCOFI results at overlapping, shallower depths, data from the two sources were combined to provide a comparison of basins at comparable depths. Values in the Santa Maria Basin ranged from 6.90 mg/l on the surface to 0.5 at 500 m (Fig. 4), and were on the average 0.4 mg/l higher than in the Santa Barbara Basin. Therefore, comparable DO levels were found at 25-150 m shallower in the Santa Barbara Basin than in the Santa Maria Basin.



Figure 3. Distribution of grain size particles and percentage organic carbon in basin areas in the vicinity of Pt. Conception.

Biological Communities: Sample processing resulted in the identification of 996 taxa, dominated by polychaetes (434), crustaceans (288), mollusks (154) and other groups (120). The deletion of taxa not identified to species and those occurring in less than four of the samples resulted in the delineation of 179 species used in the community analyses (Table 2).

Results of cluster analysis indicate the presence of five station groupings and six species groupings (Fig. 5). These groupings are summarized in a two-way contingency matrix to show species groups in association with station groups. The organisms associated with each species group are provided in Table 2.

An aerial map indicates communities are distributed generally along an onshoreoffshore gradient (Fig. 2). A cross sectional diagram of the two basins with depth, viewed from offshore, shows the relationship of the communities more clearly (Fig. 6). The dashed lines show the level of similarity among these communities. The major break Figure 4. Profiles of dissolved oxygen values in both the Santa Maria and Santa Barbara Basins. Insert shows an oxygen profile further north at greater depths in central California, as a reference (from Thompson *et al.* 1985)

0.5

1.0

Dissolved Oxygen (mg/l)

0.

5.0

5.0

among communities occurred at 500 m and separated both the Santa Maria deep slope community and the Santa Barbara Basin community from other communities located at shallower depths. The shallow shelf community occupied outer shelf depths (30-200 m) and extended along the coast through both basins. A sub-shelf community occupied the next depth interval (200-350 m) only in the Santa Maria Basin. The upper slope community occupied comparable depths north and east of the sub-shelf community. Depths greater than 500 m were inhabited by a lower slope community in the Santa Maria Basin and an ecologically similar basin community east of Pt. Conception.

Ordination analysis provides an ecological. view of the relationships among all stations comprising the five communities (Fig. 7). The



Figure 5. Simplified two-way matrix of station and species groups. A list of all species used in the calculations is provided in Table 2.

distribution of communities in multidimensional space is plotted along the first two axes which displayed the greatest amount of ecological variability. Situated along the left side of axis 1 was the shelf community which occupied the shallowest depths. At the opposite end of axis 1 was the most ecologically distant community, the basin community at the bottom of the Santa Barbara Basin (though not occurring at the greatest depths surveyed). The distribution of samples and communities along axis 2 does not show any apparent geographic or bathymetric pattern. A summary of biological characteristics of each community is presented in Table 3. Shallower communities and communities with higher dissolved oxygen had higher richness (number of species), total abundance of organisms (number of specimens) and diversity levels (Shannon-Wiener).

Regulating Factors: Regression analyses (Table 4) showed that depth was most highly correlated with the community variation expressed along ordination axis 1 ($r^2 = 0.77$). Weaker correlations were found for organic carbon ($r^2 = 0.53$) and percent clay ($r^2 = 0.26$).



Figure 6. Cross-sectional view from off-shore of the subtidal area in the vicinity of Pt. Conception showing the distribution of the five benthic, infaunal communities delineated in this study

The correlation between axis 1 and depth is somewhat consistent with the distribution of station groups in Figure 7, where the shallowest shelf group is found at the negative end of axis 1 and deeper slope and basin groups are found toward the positive end. However, the fact that the basin group at the far right is not found at the deepest water depths indicates that some factor other than depth may be influencing the community changes corresponding with this axis. Dissolved oxygen (DO), which was not measured as part of this field study, appears to follow this gradient along axis 1. DO values are highest in the shallower shelf groups at the negative end of axis 1 and lowest in the Santa Barbara Basin community at the extreme positive end of the axis.

The relationship between DO and infaunal communities also can be seen in a plot of communities along an oxygen and a depth gradient of the two basins (Fig. 8). The shallowest community, located on the shelf, occupied the highest DO levels. The sub-shelf and upper slope communities occupied similar depths in the Santa Maria Basin and overlapped somewhat in DO level. The lower slope community in the Santa Maria Basin occupied the greatest depths surveyed but not the lowest DO levels. Finally, the basin community in the Santa Barbara Basin, located at the extreme end of the ecological gradient along axis 1 (Fig. 7), was associated with the lowest DO levels but not the greatest depths (Fig. 8).

Axis 2, representing secondary environmental factor(s), corresponded somewhat with sediment parameters of sand and clay (Table 4). Communities located higher up along axis 2 were found either nearshore (shelf) or further offshore along the slopes of the Santa Maria Basin where sand was more abundant (Fig. 3). Communities lower down along axis 2 were located in areas such as the Santa Barbara Basin, where sand was less abundant.

Discussion

Physical Factors: The Santa Maria Basin is deeper, has both a sea valley and a system of submarine canyons, and is, therefore, bathymetrically more complex than the Santa Barbara Basin in the vicinity of Pt. Conception. The percent sand was greatest in shallow, shelf waters in both basins and relatively shallow waters located offshore.

The organic content of the sediments varied more within than between basins. Values were highest in the sea valley of the Santa Maria Basin and the floor of the Santa Barbara Basin. This distribution is attributed to finer particle size with greater surface area for attachment. One area at sea valley depths, between Pt. Sal and Pt. Arguello, had low values of organics.



Figure 7. Distribution of stations and communities in ordination space, according to the first two axes.

Small but significant hydrographic differences were noted between the two basins. The Santa Barbara Basin had significantly (P < 0.05) higher temperatures but lower salinities per depth, and lower dissolved oxygen levels than the Santa Maria Basin, even above the sill. Comparable DO levels have been recorded farther north ($36^{\circ}25'N$) off Pt. Sur (Brownkoew & Greene 1981; Churgin & Haminski 1974). They reported an oxygen minimum zone (DO< 0.05) between 500 m and 1,000 m, with lowest levels around 700 m. Hydrographic differences north and east of Pt. Conception, long recognized at shallower depths, extend to slope and basin depths as well.

Biological Communities: The distribution of infaunal communities along the shelf, slope and basins varied primarily with depth as reported in southern California by Thompson & Jones (1987). A secondary spatial trend involved changes alongshore, particularly off Pt. Conception.

Table 3. Biotic characteristics of the five infaunal communities delineated in the Santa Maria and Santa Barbara Basins. Values are for 1.0 mm screen organisms taken from 0.1 m^2 box core.

Community	Depth (m)	DO	Species	Specimens	Diversity	Characteristic Species
1. Shelf	30-175	2.0	68	236	2.91	Amphiodia urtica
2. Sub-shelf	200-350	1.3	32	81	2.90	Spiophanes berkeleyorum
3. Upper Slope	200-450	0.7	25	57	2.83	Brisaster latifrons
4. Lower Slope	500-1100	0.2	23	44	2.67	Nuculana conceptionis
5. Basin	500-600	0.1	10	27	1.69	Mitrella permodesta



Figure 8. Distribution of the five benthic, infaunal communities relative to depth and oxygen levels in the Santa Maria and Santa Barbara Basins.

Regulating Factors: Evidence indicates that a primary factor regulating the distribution of the five communities in the area was DO. Community abundance values (species, specimens and diversity values) also corresponded strongly with DO values. The Santa Barbara Basin community had the lowest mean number of species, specimens and diversity index, as well as the lowest dissolved oxygen levels, but these values were not recorded at the greatest depths investigated.

Areas at or below shelf depths (200 m) were exposed to DO values below 4 mg/l, a level in which other studies have reported an important effect on benthic infaunal organisms. Rosenberg (1977) noted that when the DO levels dropped from 9 to 4 mg/l the number of species and biomass both decreased. In Alaskan fjords, community structure and community abundance values both correspond with grain size and total organic carbon when DO levels were above 4 mg/l; however, when DO levels dropped below 4 mg/l, species and total abundance values in each community decreased (VTN 1982). In a study off Pt. Sur in central California ($36^{\circ}30'N$), stations were examined along a depth gradient from 400 to 12,090 m (Thompson *et al.* 1985). The abundance of all taxa decreased in the oxygen minimum zone (DO< 0.5 mg/l), between 500 and 1,000 m, as reported here.

Individual benthic species have displayed anatomical or physiological changes in areas of low oxygen levels. Some species of mollusks (Lucinoma and Parvilucina), found in the Santa Barbara Basin, have been reported to contain enzymes adapted to low oxygen, high sulfide environments (Felbeck et al. 1981). Increased surface area for respiration has been reported in echinoids (Thompson pers. comm.) and polychaetes (Montagne pers. comm.) in areas of lower DO levels, regardless of depth. Davis (1977) reported that gamete development in the polychaete Neanthes is inhibited at oxygen levels below 4 mg/l. Thompson (1982) reported that at deep, low oxygen depths off southern California, the number of sub-surface deposit feeders decreased. This trend could be due to lower oxygen values within the sediments.

Ordination axis 2 corresponded best with two grain size parameters, percentage of sand and clay. These are two parameters that have traditionally been thought to regulate benthic communities. The importance of sand may be due to it's greater permeability for water and therefore oxygen exchange (Weston 1988). Organic carbon, another factor which has been noted to regulate benthic communities, did not correspond strongly along either axis.

In articles published since the submittal of this paper, there is further evidence that oxygen levels correspond strongly with the distribution of infaunal benthic communities along the west coast of North America. These articles include studies by Thompson & Jones (1987) in southern California, Kanter & co-author's (1989) in central and northern California and Hyland & co-author's (1991) within the Santa Maria Basin.

Conclusion

Soft-bottom infaunal samples were taken along a grid of stations in the Santa Barbara and Santa Maria Basins to characterize the environment prior to monitoring the potential impacts of oil and gas development. Sediment grain size and organic carbon levels were similar between basins, but varied within basins. Significantly higher temperatures, lower salinities and lower oxygen levels were present in the Santa Barbara Basin, even above sill depth.

The distribution of the communities, as well as various abundance indices, corresponded more strongly with DO than with depth, organic carbon, grain size or any other parameter measured. The replacement of the deep slope, Santa Maria Basin community with an ecologically similar community in the Santa Barbara Basin is attributed to the differences in oxygen levels between the two basins. The apparent importance of DO in this area, as well as that reported in other areas along the temperate west coast of North America, provides substantive evidence that even at levels as high as 4 mg/l, oxygen levels may be more important than previously thought.

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No. V in I	Variables Model	r ^{.2}	Independent Variables in Model
Axis 1	1	0.77	Water Depth
	1	0.53	Organic Carbon
	1	0.26	Percent Clay
	1	0.19	Total Hydrocarbons
	1	0.17	Sort 25
	1	0.11	Total Aromatics
	1	0.10	Mean Grain Size
	2	0.82	Water Depth + Percent Clay
Axis 2 1 1 1 1 1 1 1	1	0.18	Sand
	1	0.17	Mode Grain Size
	1	0.13	Total Hydrocarbons
	1	0.09	Total Alkanes
	1	0.08	Mean Grain Size
	1	0.07	Oil Pollution Index
	2	0.26	Sand + Clay

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Abstract - Linckia columbiae is a sexual species that also reproduces asexually by ray autotomy. Seventy percent of L. columbiae surveyed at the Catalina Marine Science Center Marine Life Refuge, Santa Catalina Island were regenerating autotomized rays. Autotomy occurred throughout the year with the highest incidence in late summer. The incidence of autotomy correlates with growth, but not gender or depth. Regeneration experiments suggest that 3 yr, or longer, may be required for a single ray to reach the adult stage. Gametogenesis was generally confined to nonregenerating rays. Oocyte production was low and spawning occurred in late summer. Lacking evidence of recent larval recruitment at the study site, population densities and morphometric features of L. columbiae are best explained by continuous asexual reproduction.

Introduction

The variable seastar, Linckia columbiae Gray, generates new multirayed individuals from single autotomized rays (Monks 1903, 1904; MacGinitie & MacGinitie 1949). In contrast, regeneration of new individuals from fissioned segments in most fissiparous asteroids requires a portion of the central disc (Emson & Wilkie 1980). Among other species of fissiparous asteroids, fission is often a significant mode of reproduction, but the emphasis on asexual and sexual reproduction varies between populations as well as between species (James & Pearse 1969; Emson 1978; Rideout 1978; Emson & Wilkie 1980; Ottesen & Lucas 1982; Crump & Barker 1985; Mladenov et al. 1986). When fission is frequent, regeneration may limit the

extent of sexual development; gametogenesis may be diminished or absent. Because fission alters body shape and provides a source of new individuals, the incidence of fission affects other population parameters, especially morphometry and population density. The present study relates the incidence of ray autotomy in *L*. *columbiae* to population structure, growth, and sexual reproduction.

Methods

Study Sites: Pumpernickel Cove and its adjoining coastal reef are is located in the Catalina Marine Science Center Marine Life Refuge on the northwest shore near the west end of Santa Catalina Island, California. The site is an extension of steep cliffs which, underwater, give rise to boulder fields and bedrock escarpments of moderate to high relief. Patches of coarse sand and cobble occur throughout the area. The dominant community over most of the cove and reef is kelp forest, Macrocystis pyrifera, with an understory of encrusting and erect corallines, scattered small fleshy rhodophytes and various shrubby brown algae. Much of the vertical rock surface is a mosaic of encrusting corallines and sessile invertebrates. A single collection of Linkia columbiae was made from similar habitat depths of 8-15 m at Admiral's Reef near Cat Rock, Anacapa Islands, California in September 1986.

Procedures: 1. *Morphometry and Autotomy*. Data on morphometry and autotomy were taken from 10 samples, containing from 16-183 individuals between June 1985 and September 1989. Specimens were collected using scuba at the east end of Pumpernickel Cove from 6-10 m depth. For each specimen, rays were counted and identified (by number) based on the usual

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