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Shallow-Water Benthic Communities on California's Outer Continental Shelf

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ABSTRACT: Benthic macroinvertebrates and macrophytes were studied at depths from about 20 to 30 m on Cortes and Tanner Banks, 180 km offshore from San Diego, California, USA. The structure of these communities is described in terms of percentage cover, biomass, species diversity, and species evenness. Two distinctly different communities were present. The shallow-water community was best developed above 25 m depth, and dominated by the southern sea palm *Eisenia arborea* which formed dense stands on ridges and pinnacles. The community below 30 m was characterized by the encrusting red coralline alga *Lithophyllum proboscideum*. Remote from shore and weather-beaten, Cortes and Tanner Banks harbor subtidal communities whose relative species abundances differ from those of comparable depths near the southern California mainland and Channel Islands.

INTRODUCTION

Cortes and Tanner Banks are the tops of undersea mountains that rise abruptly from ocean basin depths approximately 180 km west of San Diego, California, USA (Fig. 1). Projecting into the mainstream of the California Current, Cortes and Tanner Banks have a combined area of approximately 33,900 ha (99 nautical miles^2) of high-relief rocky shoals less than 100 m deep, lying within 5 km of the 750-m isobath. The habitat available for shallow-water marine life on these banks is 37 % greater in area than the subtidal flanks (to 100 m depth) of San Clemente Island, the nearest California Channel Island. Far from shore and exposed to the full force of open ocean storms, the Banks are characterized by clear water (visibility usually greater than 20 m), strong currents (typically 0.2 to 0.7 m s^{-1}), and rough weather (waves up to 11 m high) (Ecomar, 1978). They are the first shallow submarine features on the continental shelf to interrupt the passage of deep ocean swells. Cortes and Tanner Banks lie close enough to the California coast to be colonized by propagules of nearshore marine fauna and flora. However, environmental conditions which shape development of shallow marine communities on the banks are oceanic rather than neritic in character.

During 1976 and 1977, the Pacific Outer Continental Shelf Office of the US Bureau of Land Management (BLM) sponsored the first comprehensive study of the subtidal ecology of these remote areas. This report summarizes the results of shallow-water descriptive community studies conducted jointly for the BLM by Science Applications, Inc. and by the University of California.

MATERIALS AND METHODS

Four study sites, two on Cortes Bank and two on Tanner Bank, were selected after a preliminary bathymetric and visual inspection. The sites were chosen to be representative of major habitat types, level enough for photographic transect methods, located near bathymetrically distinct bottom features to aid relocation, shallow enough to permit SCUBA diving without decompression, and adequately deep to permit divers to work in comparatively calm conditions on the bottom despite rough surface weather. Each site was

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marked with surface and subsurface buoys and with acoustic pinger systems on the sea floor. Sites were visited in September, October, and December 1976, and April and May 1977.

Three surveying methods were employed: photography, *in situ* observation, and harvest sampling, all done by SCUBA divers. A photographic technique, the point intercept method (Littler, 1971), provided quantitative information on standing crops of subtidal organisms. Two 20 × 1-m transects and about a dozen permanently marked quadrats were established at each site. Field notes furnished additional information on species not seen in photographs, and included observations of organisms (e. g., fish) not sampled by other methods. Some organisms were collected as voucher specimens to confirm visual and photographic identifications, and to generate as complete a species list as possible. Twelve 1-m^2 quadrats were harvested at each site to provide data on biomass and to identify small or cryptic species. After larger organisms in the harvest quadrats had been collected by hand, an underwater airlift captured material loosened by scraping tools. This technique worked well for all organisms except encrusting coralline algae, which could not be easily detached from the substrate.

Quadrats and transects were placed haphazardly within study sites. Due to uneven bottom topography, it was not possible to locate transects and quadrats in a statistically random fashion. As a consequence, the hydrocoral *Allopora californica* may have been underrepresented, since it tended to occur on pinnacles and cliff edges unsuitable for our sampling methods. Photographs and preserved organisms were identified taxonomically and used for biomass determinations. Percentage cover in transects and gross wet weight in harvested quadrats were selected as indices of species abundance patterns, with community summaries provided by the Shannon-Weaver diversity index (H') and the Pielou evenness index (J') (Pielou, 1966a,b).

This program emphasized visually dominant invertebrates and plants that could be readily seen and identified in the field and in photographs. Not all organisms could be identified to the species level. We believe that such taxonomic omissions had little effect upon benthic community summary statistics, since all calculations were based upon percentage cover, and most forms large enough to be seen in a photograph could be easily identified. The species list is least complete for invertebrates and plants smaller than 0.5 mm in size.

Although not censused, demersal fish associated with the rocky substrate were abundant, especially the rockfishes *Sebastes mystinus* and *S. serranoides*, the sheepshead *Pimelometopon pulchrum*, the señorita *Oxyjulis californica*, the rock wrasse *Halichoeres semicinctus*, the blackeye goby *Coryphopterus nicholsii*, the ocean whitefish *Caulolatilus princeps*, and many others. A number of open-ocean pelagic fish were seen, including the yellowtail *Seriola dorsalis*, the California flyingfish *Cypselurus californicus*, the blue shark *Prionace glauca*, another unidentified large carcharinid or lamnid shark, and others. Many sea lions (*Zalophus californicus*) were observed feeding on the fish and leaping out of the water.

RESULTS

The results of this study will be described site-by-site. As neither strong nor consistent temporal changes were present for most species, the data from each site will be presented as single values averaged over all sampling visits. An overview of visually dominant species at each site is illustrated in Figure 2.

North Cortes

The North Cortes study site was situated on the top of one of the many extended ridges that divided the sea bottom into valleys (depth about 30 m) and parallel crests (depth about 20 m). These ridges were covered with dense stands of the southern sea palm *Eisenia arborea*, whose density decreased with depth on the sides of the ridges. Strong currents and surge kept the ridges relatively free of unconsolidated sediment.

Beneath the meter-high canopy of *Eisenia arborea* at the study site was an understory of smaller brown and red algae, including *Dictyota flabellata*, *Pachydictyon coriaceum*, and *Rhodymenia* spp. Prominent invertebrates were the jewel anemone *Corynactis californica*,

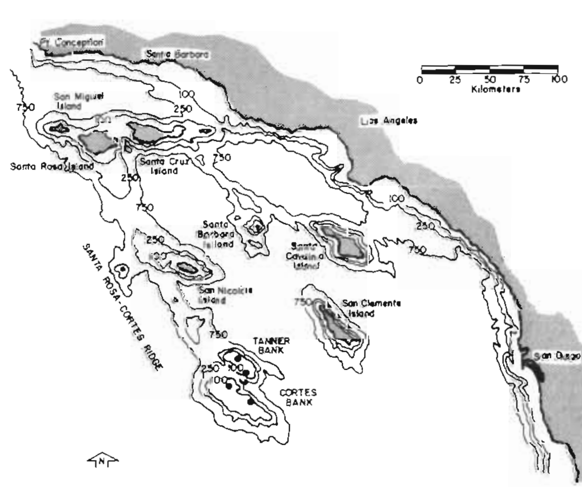

Fig. 1. Locations of study sites (dots) on Cortes and Tanner Banks with respect to other southern California continental shelf features. Contours are in meters

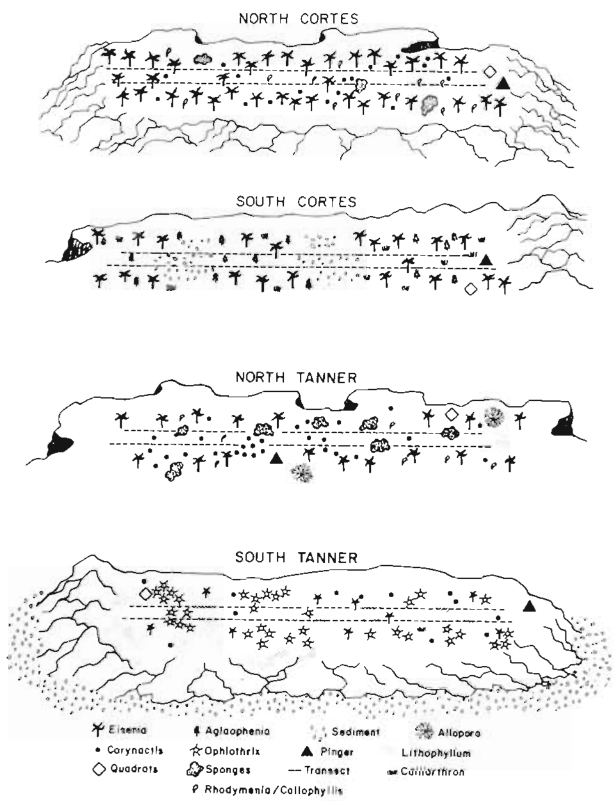

Fig. 2. Schematic illustration of study sites, showing topography and visually dominant organisms symbolically represented

the hydroids *Aglaophenia* spp. and *Abietinaria* spp., the barnacle *Balanus tintinnabulum californicus*, the pelecypods *Modiolus* spp., *Hiatella artica*, and *Chlamys hastata*, and the sponge *Tethya aurantia*. Cracks and crevices on the sides of the ridge sheltered the spiny lobster *Panulirus interruptus*, the crab *Cancer jordani*, and the sea urchin *Strongylocentrotus franciscanus*.

The two transect lines paralleled the axis of the ridge, covering a visually rather homogeneous area. In all, 94 macrophyte taxa and 46 macroinvertebrate taxa were recognized (Fig. 3A, Table 1). Phyla with the most taxa among the macrophytes and macroinvertebrates were Rhodophyta and Mollusca, respectively (Fig. 4). *Eisenia arborea* was the dominant alga in terms of percentage cover (48 %), while *Corynactis californica* (13 %) and various sponges (7 %) were the most abundant macroinvertebrates (Fig. 5). Total macrophyte cover was 109 % (overstory plus understory), compared to total macroinvertebrate cover of 31 %. Diversity (H') averaged 0.61, 1.31, and 1.65 for macroinvertebrates, macrophytes, and the two combined, respectively (Fig. 3B). Corresponding values for evenness (J') were 0.23, 0.44, and 0.46 (Fig. 3C).

The total wet weight averaged 5855 g m^{-2} (Fig. 3D), of which 5156 g (88 %) was due to *Eisenia arborea* (Fig. 6). As with percentage cover in the transects, *Corynactis californica* had the highest wet weight (94 g m^{-2}) among the macroinvertebrates harvested. *Strongylocentrotus franciscanus*, by contrast, had the second highest macroinvertebrate wet weight (85 g m^{-2}) although its average percentage cover was very low (<0.1 %). *S. franciscanus* was relatively uncom-

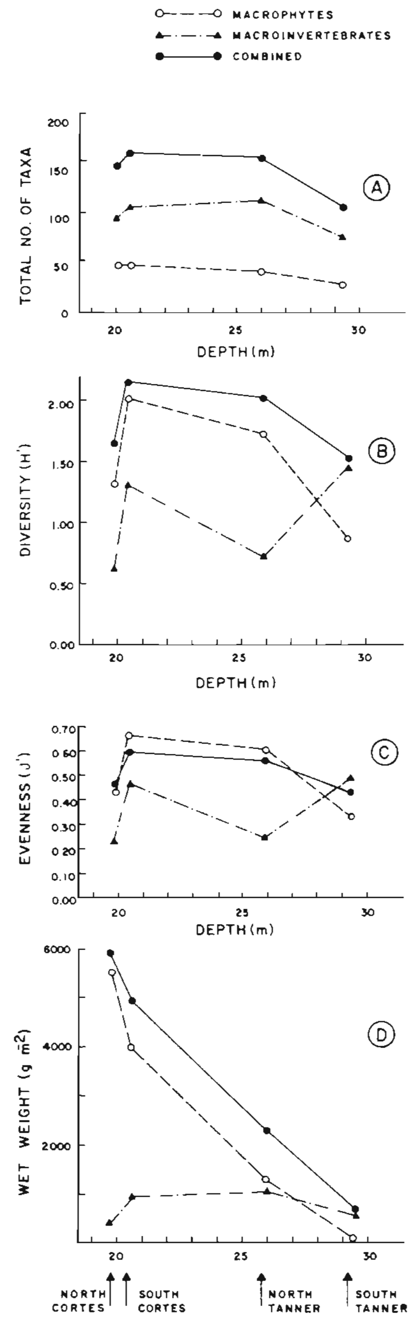

Fig. 3. Distribution of (A) total taxa, (B) species diversity, (C) species evenness, and (D) wet weight, as a function of depth at each study site

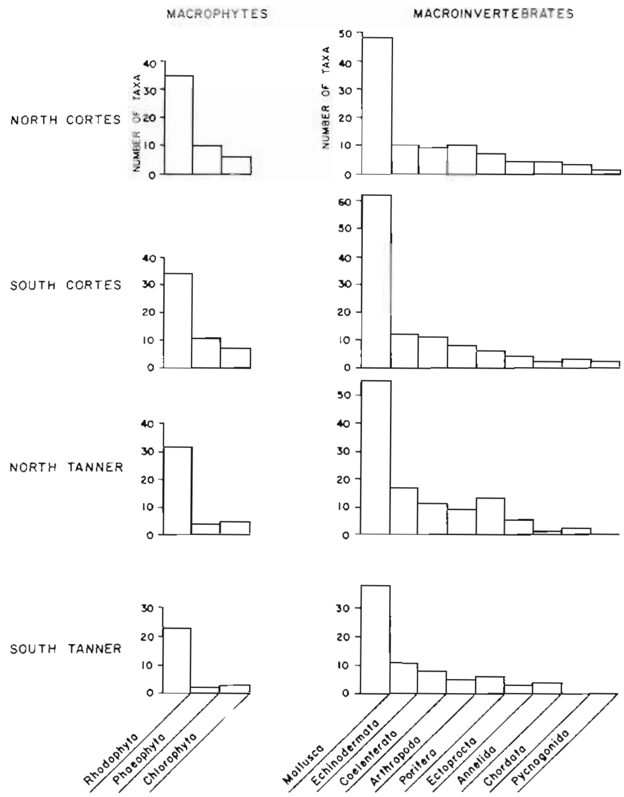

Fig. 4. Distribution of biota by number of taxa identified in major macrophyte and macroinvertebrate groups

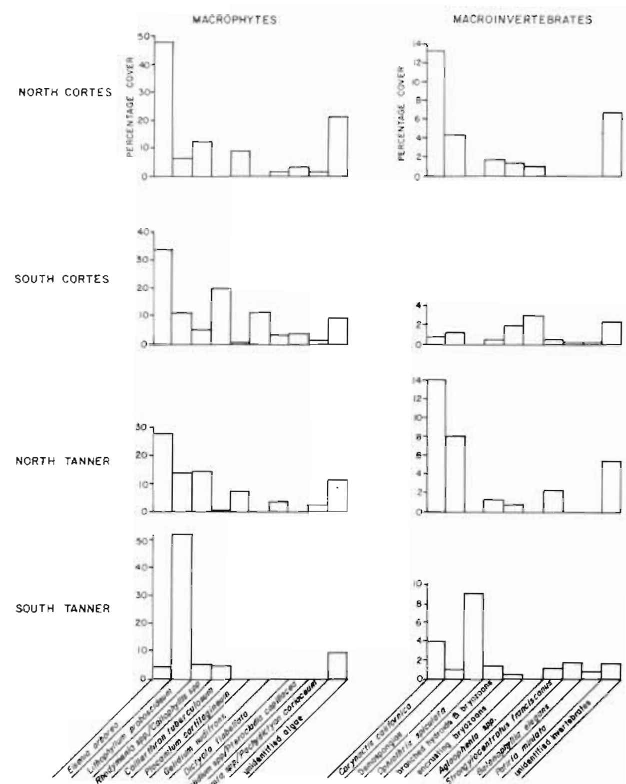

Fig. 5. Distribution of abundance in transects by percentage cover of dominant macrophytes and macroinvertebrates

mon, but a few of these large urchins happened to occur within the harvested quadrats, accounting for their high recorded biomass figure at the North Cortes site.

South Cortes

The South Cortes study site was located within view of the US Coast Guard buoy on Bishop Rock. Just slightly deeper than the North Cortes site, South Cortes (between 20 and 21 m) was surrounded by ridges covered with *Eisenia arborea*, but included many rock outcrops which projected between depressions filled with shifting, coarse unconsolidated sediment. The two transects and the quadrats were located in the somewhat protected area below the crests of nearby ridges. The flora and fauna of South Cortes may best be described qualitatively by treating the large rock outcrops and the areas beneath them separately.

On the outcrops were dense patches of *Eisenia arborea* forming a canopy about 1 m high. Below this canopy lived many small and medium sized foliose brown and red algae such as *Dictyota* spp., *Pachydictyon coriaceum*, *Cystoseira neglecta*, and *Rhodymenia* spp. Invertebrates in the understory community

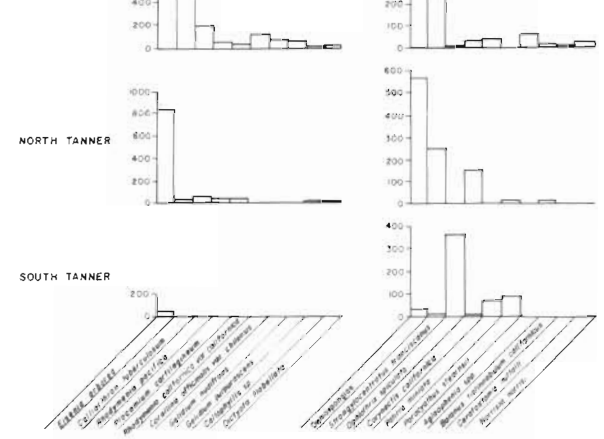

Fig. 6. Distribution of abundance in harvested quadrats by wet weight of dominant macrophytes and macroinvertebrates

included *Aglaophenia* spp., *Corynactis californica*, *Balanus tintinnabulum californicus*, and many sponges and tunicates.

Eisenia arborea was less dense in the areas below the rock outcrops. The brown alga *Laminaria farlowii* formed huge sheets lying along the bottom in some locations, while elsewhere articulated coralline algae such as *Corallina officinalis* var. *chilensis* and *Calliarthron tuberculosum* occurred together. Exposed rocks were covered with the encrusting red coralline alga *Lithophyllum proboscideum*. Invertebrates included the forms mentioned above as well as larger species such as the crabs *Pugettia dalli*, *Cancer jordani*, and *Loxorhynchus crispatus*; the sea stars *Pisaster giganteus*, *Henricia leviuscula*, and *Patiria miniata*; the urchins *Strongylocentrotus purpuratus* and *S. franciscanus*; and numerous gastropods, especially *Norrisia norrisi*. Cnidarians in this habitat included the solitary corals *Balanophyllia elegans* and *Paracyathus stearnsii* and the large red anemone *Tealia* sp. Spiny lobsters *(Panulirus interruptus)* and abalones (*Haliotis* spp.) inhabited crevices in rock outcrops. In all, 45 macrophyte taxa and 108 macroinvertebrate taxa were recognized (Fig. 3A, Table 1). Rhodophyta was the largest division among the algae while Mollusca was the largest invertebrate phylum in terms of numbers of species (Fig. 4).

Eisenia arborea was the dominant alga by percentage cover in the transects (34 %), while *Calliarthron tuberculosum*, *Lithophyllum proboscideum*, and *Gelidium nudifrons* were also prominent (Fig. 5). Total macrophyte cover (overstory plus understory) was 127 %, while total macroinvertebrate cover was 11 %. *Aglaophenia* spp. and encrusting bryozoans were the most abundant macroinvertebrates by percentage cover, but together they occupied little more than 5 % of the substrate. Diversity (H') for macroinvertebrates, macrophytes, and both combined averaged 1.31, 2.02, and 2.16 respectively (Fig. 3B). Corresponding evenness (J') values were 0.47, 0.67, and 0.60 (Fig. 3C).

In the harvested quadrats, *Eisenia arborea* and *Calliarthron tuberculosum* dominated all other macroalgae by wet weight (Fig. 6). The total average biomass at this station was 4871 g m^{-2} (Fig. 3D), of which 43 % was due to *E. arborea*, 25 % to *C. tuberculosum* and 12 % to various sponges plus *Strongylocentrotus franciscanus*.

North Tanner

The North Tanner study site was located at a depth of almost 26 m near the edge of a plateau. Adjacent to the plateau the bottom dropped abruptly to depths of more than 40 m. The transects ran roughly parallel to the edge of this underwater cliff and crossed a few low walls and ridges. Several major habitat types were found in the study area. Along the tops of the ridges and on the cliff edge *Eisenia arborea* formed a canopy in which large heads of the hydrocoral *Allopora californica* were growing. These areas were swept by particularly strong currents and had little unconsolidated sediment. Beneath the algal canopy were smaller brown and red algae, as well as *Corynactis californica* and various sponges. Below the ridge tops, in flat areas only a few meters deeper, *A. californica* did not occur and *E. arborea* was sparse. There was, instead, a low-profile community of algae and invertebrates with the most space covered by a smooth layer of *Lithophyllum proboscideum*. Breaks in this coralline crust were usually occupied by patches of *C. californica* and of the green alga *Codium hubbsii*. Other common macroalgae included *Opuntiella californica* and numerous articulated coralline reds. Hydroids, sponges, bryozoans, and solitary corals were also distributed in patches on the crust, while echinoderms such as *Henricia leviuscula* and *Strongylocentrotus franciscanus* roamed its surface.

A total of 38 macrophyte taxa and 111 macroinvertebrate taxa were identified at North Tanner (Fig. 3A, Tabel 1). Rhodophyta contained the most macrophyte taxa, while Mollusca had the most macroinvertebrate taxa (Fig. 4). *Eisenia arborea* was the dominant alga in the transects (28 % cover) (Fig. 5). *Lithophyllum proboscideum* and *Rhodymenia* spp./*Callophyllis* spp. (indistinguishable in photographs) each accounted for about half as much cover as *E. arborea*. Total macrophyte cover was 93 % (overstory plus understory). Total macroinvertebrate cover was 33 %, of which *Corynactis californica* (14 % cover) and sponges (8 % cover) were most prominent. Diversity (H') for macroinvertebrates, macrophytes, and both combined averaged 0.72, 1.72, and 2.02, respectively (Fig. 3B). Corresponding evenness (J') values were 0.25, 0.61, and 0.57 (Fig. 3C).

The average harvested quadrat contained 2271 g m^{-2} wet weight (Fig. 3D), divided nearly equally between macrophyte and macroinvertebrate biomass. *Eisenia arborea* was the dominant macrophyte (845 g m^{-2}), while sponges, *Corynactis californica*, and *Stronglycentrotus franciscanus* together accounted for 979 g m^{-2} (Fig. 6).

South Tanner

The South Tanner site was the deepest of the four stations, located on top of a short ridge at a depth of more than 29 m. Compared to the other sites, South Tanner looked barren due to the low physical relief and the paucity of large, erect algae. The whole site appeared pinkish-purple in color due to extensive cover by *Lithophyllum proboscideum.* Closer examination revealed a striking invertebrate community. Thousands of brittle stars *(Ophiothrix spiculata)* carpeted the bottom, while the orange cup coral *Balanophyllia elegans* was in great abundance on the smooth surfaces. The two transects at this site ran over a physically fairly homogeneous area. Except for a very gentle rise near the ends of the transects, the rocks were quite flat. The ridge lay parallel to other ridges at similar depths but was separated from them by a bed of coarse unconsolidated sediment at a depth of about 40 m.

The species assemblage at South Tanner was similar to that described above for the coralline crust at North Tanner, wi h the addition of high densities of the echinoderms *Ophiothrix spiculata, Patiria miniata, Strongylocentrotus purpuratus,* and *S. franciscanus.* Four species of large gastropods were also common: the chestnut cowrie *Cypraea spadicea,* the queen turban *Tegula regina,* the ringed top shell *Calliostioma annulatum,* and the brick-red top shell *Astraea gibberosa.* Twenty-six macrophyte taxa and 72 macroinvertebrate taxa were identified (Fig. 3A, Table 1). Rhodophyta and Mollusca, once again, were the phyla with the greatest number of taxa (Fig. 4). The brown macroalgae were represented by only two species (*Eisenia arborea* and *Laminaria farlowii*) at this deep site.

Lithophyllum proboscideum dominated algal cover (51 %), while *Ophiothrix spiculata* (9 %) and *Corynactis californica* (4 %) were the most visible macroinvertebrates in the transects (Fig. 5). Total coverage was 85 % for the macroalgae and 22 % for the macroinvertebrates. Diversity (H') for macroinvertebrates, macrophytes, and both combined averaged 1.47, 0.88, and 1.52, respectively (Fig. 3B). Corresponding evenness values were 0.49, 0.34, and 0.43 (Fig. 3C).

Ninety percent of the biomass in the harvest quadrats at South Tanner was due to macroinvertebrates. The total wet weight averaged 675 g m^{-2} (Fig. 3D), of which *Ophiothrix spiculata* alone accounted for 365 g m^{-2} (Fig. 6).

COMPARISON AMONG STATIONS AND DISCUSSION

Two contrasting subtidal communities on Cortes and Tanner Banks could be distinguished in this study. At the North Cortes study site and in general in shallow areas less than 25 m deep, the *Eisenia arborea* forest community was most common, with its associated understory algae (*Dictyota flabellata, Pachydictyon coriaceum, Plocamium cartilagineum,* and *Rhodymenia* spp.) and invertebrates (*Corynactis californica, Aglaophenia* spp. and *Abietinaria* spp.). At the South Tanner study site and at other areas deeper than 25 m, a community dominated by a smooth, hard crust of *Lithophyllum proboscideum* and, in patches, *Corynactis californica, Paracyathus stearnsii, Balanophyllia elegans,* and *Ophiothrix spiculata* was characteristic. The clear dichotomy between *Eisenia arborea* forest and encrusting coralline communities was best observed on tall pinnacles in the area surrounding the South Tanner site. The tops of these pinnacles were covered with *E. arborea* and *Allopora californica.* A short distance down were bands of *Corynactis californica* interspersed with *Lithophyllum proboscideum* dotted by solitary corals. Below 25 m, even on flat ledges, the coralline crust community remained dominant; if *E. arborea* was present, it was sparse, and individual plants appeared greatly reduced in size compared to the 1-m tall plants seen at shallower locations.

Other surveys of Cortes and Tanner Banks have described similar communities in less detail (Smith, 1976; Ecomar, 1978). A recent submersible survey reported these two communities may be seen at some locations at greater depths as well as two other communities on rocky substrates: a community dominated by the brown algae *Agarum fimbriatum* and *Laminaria farlowii* from 40–60 m, and a deep community (89–149 m) characterized by ophiuroids and by the crinoid *Florometra serratissima* (Interstate Electronics Corporation, 1979).

Community biomass on Cortes and Tanner Banks decreased sharply with depth at our four stations (Fig. 3D). The decrease in biomass was due to changes in macrophyte biomass, primarily. While macrophyte biomass exceeded macroinvertebrate biomass at the shallower stations on Cortes Bank, the two were nearly equal at the transitional North Tanner site, and macroinvertebrate biomass exceeded algal biomass at the deepest station, South Tanner.

The total number of macrophyte taxa (all sampling methods) declined with depth (Fig. 3A). However, the number of macroinvertebrates and macrophytes combined showed a pattern in which the two sites intermediate in depth (South Cortes and North Tanner) had higher numbers of taxa than the shallowest or deepest sites. This same pattern emerged when diversity was plotted against depth (Fig. 3B). The shallowest and deepest sites had the lowest H' values (based on percentage cover along the transects) while the intermediate-depth stations were the most diverse. The values of H' largely reflected macrophyte diversity, since algal cover was generally much greater than invertebrate cover.

Table 1. Macrophyte and macroinvertebrate taxa identified at Cortes and Tanner Banks. Refer to text for explanation of sampling methods and omission of some invertebrate groups. NC: North Cortes, SC: South Cortes, NT: North Tanner, ST: South Tanner

	NC	SC	NT	ST
MACROPHYTES				
CHLOROPHYTA				
Codium cuneatum	×	×	×	
Codium hubbsii	×	×	×	×
Codium setchellii	×			
Derbesia marina		×		
Halicystis ovalis	×	×	×	×
Unidentified chlorophyte spp.		×		
PHAEOPHYTA				
Colpomenia sp.	×	×		
Cystoseira osmundacea/neglecta	×	×		
Dictyopteris undulata	×	×		
Dictyota binghamiae	×	×	×	
Dictyota flabellata	×	×		
Eisenia arborea	×	×	×	×
Laminaria farlowii	×	×	×	×
Pachydictyon coriaceum	×	×	×	
Zonaria farlowii	×	×		
RHODOPHYTA				
Asparagopsis taxiformis			×	×
Bossiella orbigniana ssp. *dichotoma*	×	×	×	×
Bossiella orbigniana ssp. *orbigniana*		×		
Botryocladia pseudodichotoma	×	×	×	×
Calliarthron tuberculosum	×	×	×	×
Callophyllis firma	×		×	×
Callophyllis sp.				
Carpopeltis bushiae		×		
Carpopeltis divaricata		×		
Ceramium spp.				×
Coeloseira compressa	×		×	
Corallina officinalis var. *chilensis*	×	×	×	
Corallina vancouveriensis		×		
Cryptopleura corallinara	×			
Cryptopleura crispa		×		
Cryptopleura spp.	×	×	×	×
Gelidium nudifrons	×	×		
Gelidium purpurascens	×	×		
Gelidium robustum	×			
Gelidium spp.	×		×	
Gigartina sp.			×	
Griffithsia pacifica		×	×	
Gymnogongrus leptophyllus			×	
Halymenia coccinea			×	
Herposiphonia plumula	×	×	×	×
Heterosiphonia erecta	×	×		
Laurencia spectabilis	×			
Laurencia spp.	×	×		
Lithothamnium pacifica				×
Lithophyllum proboscideum	×	×	×	×
Lithophyllum spp.	×	×	×	×
Microcladia coulteri		×		
Nienburgia andersoniana		×		
Opuntiella californica	×	×	×	×
Ozophora spp.		×	×	
Plocamium cartilagineum	×	×	×	×
Polysiphonia acuminata	×			
Polysiphonia hendryi var. *hendryi*			×	
Polysiphonia spp.			×	×
Pterosiphonia baileyi	×	×	×	
Pterosiphonia dendroidea	×	×	×	×
Rhodoglossum affine	×		×	
Rhodymenia californica var. *attenuata*	×			
Rhodymenia californica var. *californica*	×	×	×	×
Rhodymenia pacifica	×	×	×	×
Rhodymenia sp.	×			
Unidentified crustose rhodophyte sp.	×	×	×	×
Unidentified epiphytic encrusting coralline spp.	×	×	×	×
Unidentified epizoic encrusting coralline spp.	×		×	×
Unidentified foliose rhodophyte spp.	×	×	×	×
MACROINVERTEBRATES				
PORIFERA				
Demospongiae				
Haliclona sp.			×	
Hynectyon hyle				×
Microciona parthena			×	
Mycale psila			×	
Myxilla incrustans			×	
Penares cortius		×	×	
Plocamia karykina	×	×	×	
Plocamilla illgi			×	
Stelleta estrella	×		×	
Suberites ficus	×	×	×	×
Tethya aurantia	×		×	×
Calcarea				
Leucandra heathi	×	×	×	×
COELENTERATA				
Hydrozoa				
Abietinaria sp., near *expansa*				×
Abietinaria spp.	×	×	×	×
Aglaophenia diegoensis	×			
Aglaophenia sp.	×	×	×	
Allopora californica			×	×
Sertularella solitaria			×	
Sertularella turgida			×	
Sertularella spp.			×	
Unidentified branched hydroid spp.	×	×	×	×
Anthozoa				
Anthopleura xanthogrammica		×		
Balanophyllia elegans	×	×	×	×
Charisea sp.		×		
Corynactis californica	×	×	×	×
Epiactis prolifera	×	×		
Paracyanthus stearnsii	×	×	×	×
Tealia coriacea		×		
Tealia sp.	×	×	×	×
ECHINODERMATA				
Asteroidea				
Henricia leviuscula	×	×	×	×
Mediaster aequalis			×	
Orthasterias koehleri				×
Patiria miniata		×	×	×
Pisaster giganteus	×	×	×	×
Echinoidea				
Strongylocentrotus franciscanus	×	×	×	×
Strongylocentrotus purpuratus	×	×	×	×
Ophiuroidea				
Amphipodia occidentalis	×			

Table 1. (Continued)

	NC	SC	NT	ST
Amphipholis pugetana			×	
Amphipholis squamata		×	×	×
Amphipholis spp.	×		×	
Ophiactis simplex	×	×		
Ophiocantha spp.	×		×	
Ophioeryptus spp.			×	
Ophioncus granulosus			×	
Ophionereis eurybrachyplax		×		
Ophioplocus esmarki		×	×	×
Ophiopteris papillosa	×		×	×
Ophiothrix spiculata	×	×	×	×
Holothuroidea				
Parastichopus parvimensis		×	×	×
Psolus sp.		×		
ANNELIDA				
Polychaeta				
Dodecaceria concharum	×			×
Dodecaceria fewkesi	×			×
Pseudopotamilla exoyura		×		
Spirobranchus spinosus	×	×		×
Unidentified colonial tubeworm spp.	×		×	×
ECTOPROCTA				
Lichenopora sp./*Disporella* sp.	×	×	×	×
Phidolopora pacifica			×	
Unidentified branched bryozoan spp.	×	×	×	×
Unidentified encrusting bryozoan spp.	×	×	×	×
CHORDATA				
Urochordata				
Archidistoma psammion		×		
Clavelina huntsmani	×			
Distaplia occidentalis			×	
Ritterella pulchra	×			
Styela plicata		×		
Unidentified tunicate spp.	×	×	×	
MOLLUSCA				
Polyplacophora				
Callistochiton crassicostatus	×	×	×	×
Callistochiton decoratus		×		
Callistochiton sp.			×	
Chaetopleura gemma			×	×
Chaetopleura sp.				×
Cryptochiton stelleri			×	
Cyanoplex dentiens			×	×
Cyanoplex lowei	×	×		
Dendrochiton thamnoporus	×	×	×	×
Ischnochiton sp.				×
Leptochiton spp.		×		
Placiphorella velata		×		
Schizoplax brandtii			×	
Schizoplax sp.				×
Pelecypoda				
Chama pellucidea	×	×	×	
Chlamys hastata	×			
Gregariella chenui	×	×	×	×
Hiatella arctica	×	×		
Hinnites giganteus	×	×		
Kellia laperousii	×	×	×	×
Lima hemphilli	×		×	
Lithophaga plumula	×	×		×
Modiolus capax	×			
Modiolus carpenteri	×			
Modiolus neglectus	×	×	×	
Modiolus spp.	×	×		
Philobrya setosa	×	×		×
Pododesmus cepio			×	
Pododesmus pernoides		×		
Pseudochama exogyra	×	×	×	
Gastropoda = Prosobranchia				
Acmaea (Acmaea) mitra			×	×
Acmaea (Acmaea) rosacea		×		
Acmaea (Colisella) triangularis		×		
Amphissa versicolor	×	×	×	×
Astraea gibberosa	×	×	×	×
Astraea undosa		×	×	
Balcis spp.			×	
Balcis thersites		×	×	
Calliostoma annulatum			×	×
Calliostoma gemmulatum				×
Calliostoma gloriosum				×
Calliostoma supragranosum	×	×	×	×
Ceratostoma nuttalli	×	×	×	×
Cerithiopsis carpenteri	×	×	×	×
Cerithiopsis cosmia	×	×	×	
Cerithiopsis spp.	×	×	×	×
Conus californicus	×	×	×	×
Crepipatella lingulata	×	×	×	
Cypraea spadicea	×	×	×	×
Cystiscus politulus		×	×	×
Dendropoma lituella			×	
Diodora arnoldi				×
Epitonium tinctum		×		
Erato columbella	×	×		
Fusinus luteopictus		×	×	
Granulina margaritula			×	
Haliotis corrugata	×			
Haliotis sp.		×		×
Hipponix tumens		×	×	
Homalopoma paucicostatum	×	×	×	×
Homalopoma radiatum			×	
Lacuna porrecta	×			
Lamellaria diegoensis		×		
Latiaxis oldroydi	×			
Lirularia acutiscostata			×	×
Maxwellia gemma	×	×	×	
Maxwellia santarosana				×
Megathura crenulata		×	×	
Metaxia convexa		×		
Mitra idae			×	×
Mitrella aurantiaca		×	×	
Mitrella carinata	×	×	×	
Mitromorpha aspera	×		×	
Mitromorpha carpenteri		×		
Murexiella santarosana			×	
Norrisia norrisi		×		
Nucella (Thais) canaliculata			×	
Ocenebra atropurpurea	×	×	×	×
Ocenebra gracillima		×		
Parviturbo acuticostatus	×			
Seila montereyensis	×	×	×	×
Serpulorbis squamigerus	×			
Tegula regina		×	×	×
Tricolia pulloides	×	×		
Triphora catalinensis		×		
Triphora pedroana	×			
Trivia californiana		×		
Turbonilla kelseyi				×
Volvarina taeniolata	×			
Gastropoda = Opisthobranchia				
Aldisia sanguinea	×	×		
Anisodoris nobilis	×	×	×	×

Table 1. (Continued)

	NC	SC	NT	ST		NC	SC	NT	ST
Aplysia sp.			×		*Lophopanopeus leucomanus heathii*	×			
Cadlina luteomarginata				×	*Loxorhynchus crispatus*	×	×	×	×
Cadlina modesta		×			*Paguristes ulreyi*				×
Cadlina sparsa			×		*Pagurus hirsutiusculus*	×			
Cadlina spp.			×		*Pagurus setosus*			×	
Discodoris heathi	×				*Pagurus* spp.		×	×	×
Doriopsilla albopunctata	×	×	×		*Panulirus interruptus*	×	×		
Doris sp. (sensu lato)		×			*Paraxanthias taylori*	×	×	×	×
Flabellinopsis iodinea	×	×	×		*Pugettia dalli*	×	×		
Hermissenda crassicornis			×	×	*Pugettia richii*		×		
Phidiana pugnax	×	×			*Pugettia producta*			×	
Triopha carpenteri			×		*Pylopagurus califoriensis*	×			
Unidentified nudibranch spp.	×	×	×	×	*Pylopagurus diegensis*	×	×	×	
					Pylopagurus spp.			×	
ARTHROPODA					*Scyra acutifrons*				
Crustacea = Cirripedia									
Balanus tintinnabulum californicus	×	×	×	×	Pycnogonida				
Crustacea = Malcostraca					*Ammothea hilgendorfi*	×	×		
Cancer jordani	×	×	×		*Tanystylom intermedium*		×		

The hump-shaped trend in diversity with depth appears to be due to changes in evenness (J') rather than to differing numbers of taxa (Fig. 3C). H' is increased by greater numbers of taxa and by increased evenness in the distribution of abundance. As both Figures 3A and 3C indicate, the higher diversity values at South Cortes and North Tanner were functions of more equitable distributions of abundance among the species present. However, different environmental conditions are believed to be responsible for the high diversity at each of the two sites.

The South Cortes site differed from all of the others in having large cobbles and small boulders up to about 20 cm in diameter mixed with shelly debris in depressions around larger rocks. Water movement at this site (21 m deep) was strong enough to lift our 70 kg lead transect markers out of holes 20 cm deep and move them tens of meters away. Given this heavy surge and the presence of loose sediment, the lower-lying rocks and their attached biota must periodically be subjected to severe scouring. Abraded substrate would be available to settling organisms such as algal spores and invertebrate larvae, while the lack of a solid *Eisenia arborea* canopy would ensure high light levels for settlers. Thus mechanical disturbance may act to retard ecological succession. Higher community diversity would result from the maintenance of ecologically subdominant forms (Paine, 1966), which would be competitively excluded from a climax community such as an *E. arborea* forest.

At North Tanner the relatively high evenness and diversity values are believed to have resulted from sampling a mixture of two communities. The rather abrupt change in community composition with depth at the North Tanner site suggests that in the absence of abrasive crust disturbance, competitive interactions between *Lithophyllum proboscideum* and *Eisenia arborea* may reach a critical value at a depth near 25 m. Two lines of evidence may be cited: First, *E. arborea* is capable of living at a depth as great as 40 m in the clear water of this area, but its size decreases sharply below 30 m (Interstate Electronics Corporation, 1979). Second, *L. proboscideum* showed extremely rapid recovery rates after being scraped at South Tanner. As little as one month after we scraped off all living material in experimental quadrats, *L. proboscideum* had completely regrown over the area and no damage was visible. This observation suggests that rapid growth rates may be responsible for the dominance of *L. proboscideum* over other algae at our deep sites. North Tanner showed a mosaic of both *E. arborea* and *L. proboscideum* communities and consequently exhibited high diversity values.

The organisms reported in this study (Table 1) are also found in rocky subtidal habitats along the coast of central and southern California and on the Channel Islands. Nevertheless, the geographic, bathymetric, and hydrographic setting that makes Tanner and Cortes Banks unique oceanographic features of southern California's outer continental shelf has produced subtidal communities with different relative abundances and depth ranges from those typical of mainland and Channel Island coastal zones. For example, *Eisenia arborea* does not extend below 8 m at Anacapa Island (Neushul et al., 1967); 10 m at Santa Catalina Island (Abbott and Hollenberg, 1976); and 12 m at Corona del Mar (Lippincott, 1978), whereas it grows as deep as 40 m on Tanner Bank (Interstate Electronics Corporation, 1979). Species such as *Allopora californica* and *Cypraea spadicea*, which are often collected for souvenirs or jewelry along the coast are in much greater abundance on Tanner and Cortes Banks (Smith, 1976), as are more common species such as *Corynactis californica* (compare McLean, 1962; Pequegnat, 1964; Turner et al., 1968; Rosenthal et al., 1974). Offshore banks and islands also appear to serve as refuges for relict species (Newman and Ross, 1977) and previously undiscovered taxa, such as the monoplacophoran limpet *Vema hyalina* found near our study sites (McLean, 1979). Furthermore, some species common in rocky habitats in southern California are conspicuously absent on Cortes and Tanner Banks. These species include the giant kelp *Macrocystis pyrifera*, the palmate kelp *Pterygophora californica*, and the gorgonians *Muricea californica* (= *M. appressa*) and *M. fruticosa*. The top of Cobb Seamount, which lies 490 km off the coast of North America and is isolated by very deep water, also appears to have fewer species than the mainland (Birkeland, 1971).

Cortes and Tanner Banks lie farther offshore than any other shallow-water habitat off the coast of California or Oregon, but they are only semi-isolated biogeographically. Species with long-lived larvae could easily be carried there by currents. Moreover, Cortes and Tanner Banks are connected at a depth of 500 m to the central California mainland and the northern Channel Islands by the Santa Rosa-Cortes Ridge (Fig. 1). Prehistoric sea-level and/or tectonic changes along this relatively shallow ridge probably allowed the Banks to be populated originally by many nearshore species, even by some, such as *Allopora californica* (Ostarello, 1976) and *Balanophyllia elegans* (Gerrodette, in press), known to have extremely limited larval dispersal. The subtidal communities on Cortes and Tanner Banks as a whole may thus be characterized as a subset of mainland California fauna and flora, perhaps with closer affinities to central than to southern California.

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