Pacific Science (1978), vol. 32, no. 3

The Distribution, Abundance, Community Structure, and Primary Productivity of Macroorganisms from Two Central California Rocky Intertidal Habitats[1]

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ABSTRACT: A wave-exposed sea stack and a protected boulder beach at Cayucos Point, California, were compared in terms of their intertidal biota on 17–18 February 1973. The major differences between the two sites appear to be due largely to differences in the shearing forces of waves and habitat structure. The mosaic of crevices, rivulets, and angled substrates in conjunction with a broad gradual slope and reduced wave action at the boulder beach habitat resulted in a predominance of macrophytes and a zonational pattern related to both horizontal location on the shore and vertical tidal level, while sessile macroinvertebrates with zonal patterns closely correlated to tidal height dominated the sea stack. Upward shifts in comparable vertical zones at the sea stack were clearly correlated with increased wetting higher on the shore due to waves and splash, in agreement with similar findings by other workers. The most abundant macrophytes at both sites were blue-green algae and *Endocladia muricata*, although the other abundant species were different at each site. Five sessile macroinvertebrates (*Mytilus californianus*, *Chthamalus fissus*, *C. dalli*, *Balanus* (*Balanus*) *glandula*, and *Pollicipes polymerus*) dominated the sea stack, while only three sessile species (*Anthopleura elegantissima*, *C. fissus*, and *C. dalli*) were prevalent on the boulder beach. Of the mobile macroinvertebrates, *Tegula funebralis* was the most numerous species at the boulder beach whereas the limpets *Acmaea* (*Collisella*) *scabra* and *A.* (*Collisella*) *digitalis* occurred most abundantly on the sea stack. Although a greater number of taxa and higher species richness values were recorded at the boulder beach, the evenness index and Shannon's index indicated a higher diversity on the sea stack. At the boulder beach, 12 species assemblages were defined by cluster analysis, while only 6 such groups were identified on the sea stack. The boulder beach macrophytes contributed approximately one-third more to total community primary production than did those of the sea stack (169.7 versus 116.5 net mg C m^{-2} h^{-1}), due mainly to the greater cover and concomitant production by Cyanophyta and fucalean Phaeophyta.

MUCH OF THE PUBLISHED ECOLOGICAL information on the rocky intertidal has been based, with several exceptions (e.g., Littler and Murray 1974, 1975), primarily on work done at rocky headland habitats along open coastal regions subjected to intensive wave exposure. However, considerable portions of the California rocky intertidal coastline consist of boulder beaches that have varying degrees of substrate stability and that receive somewhat reduced wave shock. The structure of biotic communities on rocky shores is profoundly affected by the degree of exposure to wave action. Lewis (1968) described two consequences of increased wave action: (1) the elevation of species' vertical ranges on a given shore (as a result of increased wave height

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and splash zone spray); and (2) the marked change in the composition of the biota from sheltered shores dominated by algae (particularly the Fucales), to exposed shores dominated by barnacles, mussels, and limpets. Elevation of species' ranges on exposed shores was demonstrated by Jones and Demetropoulos (1968), who determined the vertical positions of the dominant biota along a quantified wave-shock gradient. Atobe and Saito (1974) additionally have reported the elevation of algal species' ranges on a wave-exposed coastline relative to a sheltered site. The compositional differences between exposed and sheltered shores have been documented from many localities (Lewis 1964, Ricketts et al. 1968, Stephenson and Stephenson 1972). Exposed coastal areas were considered by Reynolds and Mathieson (1975) to have more productive and more diverse algal populations than sheltered areas.

During their worldwide travels, Stephenson and Stephenson (1972) visited the Pacific Grove region of central California during 1947 and were impressed by the range of exposures to wave action that existed along the coast. The species composition and vertical distribution under exposed and sheltered conditions were compared qualitatively by Stephenson and Stephenson (1972), and their observations support the general differences cited by Lewis (1968). Although Jones and Demetropoulos (1968) provided excellent data from the coast of Wales, subsequent studies of a quantitative nature that compare exposed and sheltered portions of the shore have not been undertaken in an area such as central California. In this paper we contrast the standing stocks, community structure, and primary productivity of a wave-washed, steeply sloping sea stack (rocky headland separated from the shoreline by coastal erosion) and a nearby sheltered, gently sloping boulder field at Cayucos Point in central California in an attempt to document quantitatively the marked biological differences that exist between these two types of prominent rocky intertidal habitats. Additionally, the sampling program was undertaken at a time when the sea otter *Enhydra lutris* L. was just becoming reestablished near the study area. Because its populations have increased dramatically to controversial levels in the Cayucos region during recent years (California Department of Fish and Game, personal communication), the potential value of this research as a pre-otter baseline should be considered. The only published studies on intertidal biota in the vicinity of Cayucos Point include a collection of algal floristic records from San Luis Obispo County by Sparling (1971) and a 2-year survey by Burge and Schultz (1973) of the Diablo Cove area (approximately 32 km to the south of Cayucos Point) prior to warm-water discharge from a nuclear power plant.

STUDY AREA

Cayucos Point faces southwestward into Estero Bay (Figure 1). The sea stack and boulder beach study sites are identified in Figure 2 at the southern and western portion, respectively, of the point. Observations at the time of the study (17–18 February 1973), in addition to subsequent observations from 1973 to 1976 and aerial photographs taken on 13 April 1975, indicated prevailing northwesterly seas. As a result, the boulder beach is characteristically protected to seaward by a large rocky promontory (Figure 2), while the sea stack is inundated by large breakers during high tide periods throughout most of the year. There was no indication of substrate instability at the boulder beach site studied here since no recently overturned boulders were observed.

Physical data for Cayucos Point are not available to our knowledge; however, for Diablo Cove the annual temperature ranges from 9.0° to 17.0°C (Abbott and North 1971). Mean monthly temperatures during 1970 and 1971 at Diablo Cove were found by Burge and Schultz (1973) to range from lows of 9.0° to 10.5°C during March–June to highs of 14.5° to 16.0°C during August–October. Nearshore temperature and salinity data during 1960–1969 were reported (Wyllie and Lynn 1971) for surface waters at CalCOFI Station 77.50 (approximately 13.0 km southwest of Cayucos Point). The monthly mean

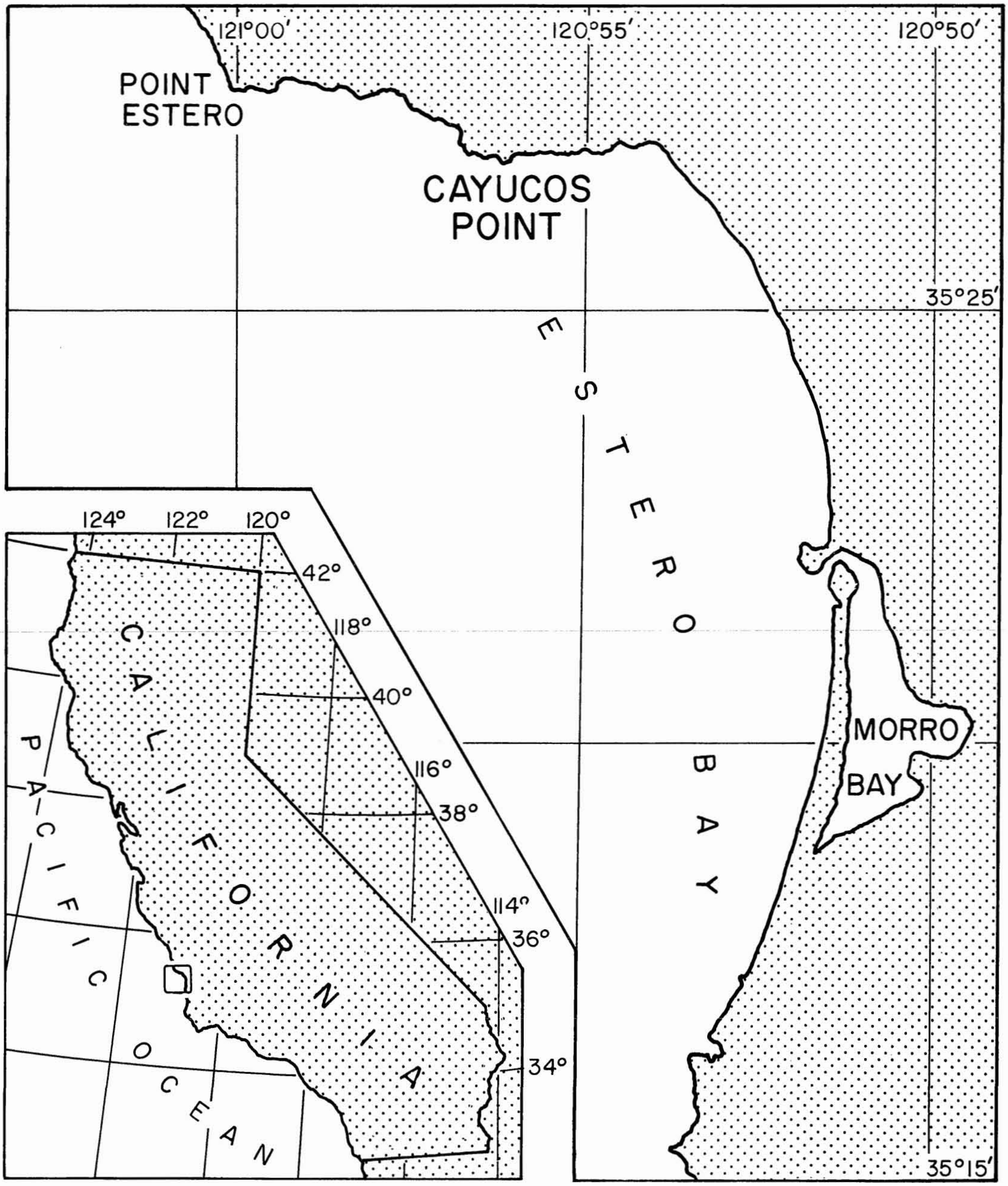

FIGURE 1. Location of Cayucos Point in Estero Bay, central California.

temperatures at this offshore station ranged from a low of 10.0° to 11.0°C (typically occurring in May) to a high of 14.0° to 15.0°C (usually recorded for October), while salinities ranged from a low of 33.2 to 33.4‰ (January) to 33.6 to 34.0‰ (between February and September). The present study took place during the transition from the Davidson Current period to the colder upwelling period (Bolin and Abbott 1963). The relative constancy of water temperature is due principally to the extended upwelling

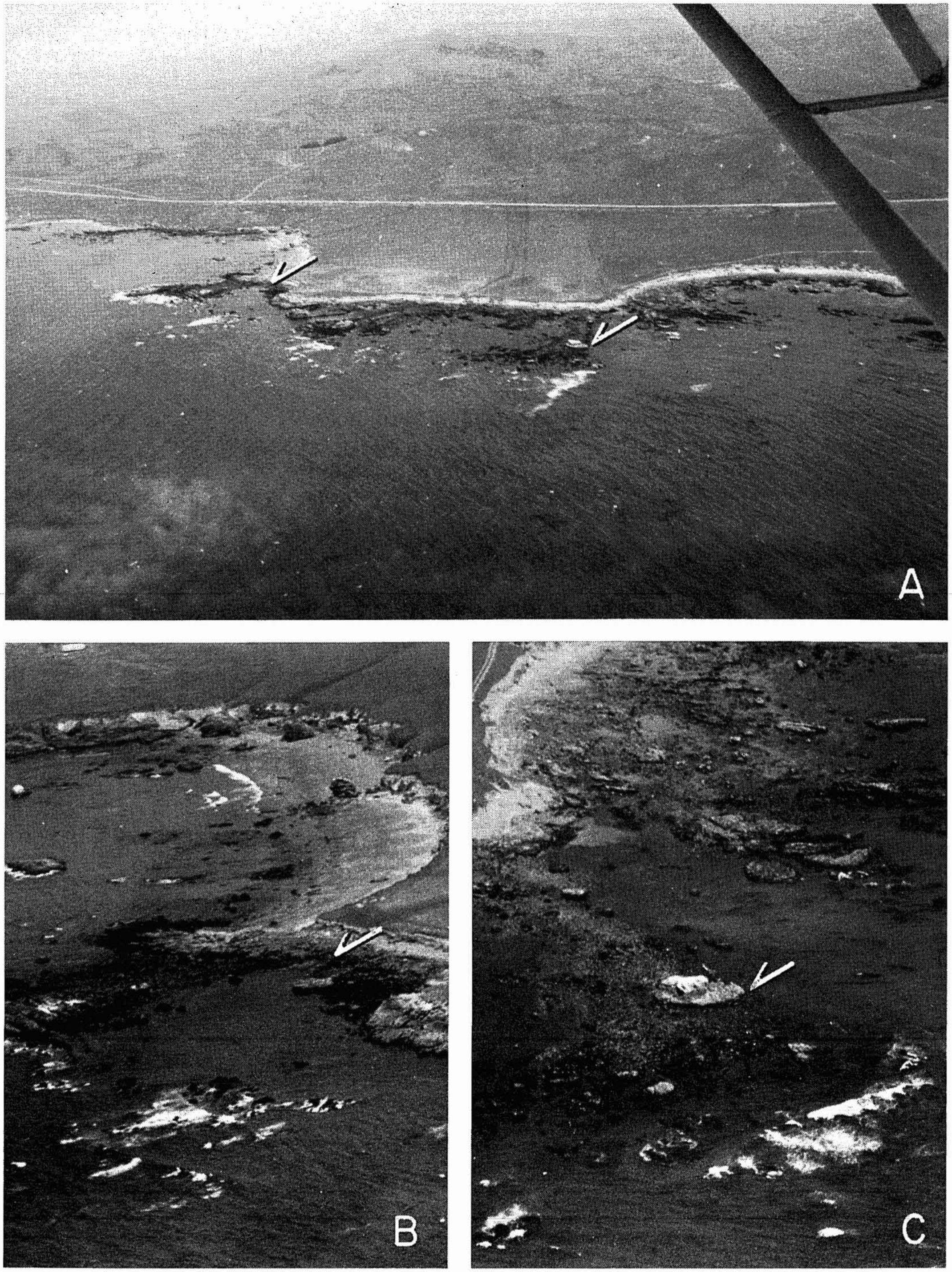

FIGURE 2. *A*, aerial photograph of Cayucos Point; *B*, boulder beach; *C*, sea stack. Study sites are indicated by arrows. Note the wave patterns and protected nature of the boulder beach (parts *A* and *B*).

season, which lasts until about September (Bolin and Abbott 1963), with concomitant cool summer temperatures.

MATERIALS AND METHODS

Patterns of distribution and abundance of the macroepibiota (i.e., those organisms recognizable with the unaided eye) were determined at both study sites with reference to tidal height. The photographimetric (nondestructive) method of sampling, described in detail elsewhere (Littler 1971, Littler and Murray 1975), was used to assess cover, density, and frequency. Two transect lines were established at each study site by laying ruled metal tapes from haphazardly selected points at 90° angles with reference to the water line. On the protected boulder beach site (Figure 2), two transect lines (transects I and II) 24 meters long were laid out parallel to each other at 220° from magnetic north. These lines were separated by a distance of 2.0 meters, ranging from the tidal levels of −0.15 to +1.68 meters (relative to 0 datum at Mean Lower Low Water, MLLW). The slope of the boulder beach over which the transect lines passed averaged 4.4°. At the sea stack site (Figure 2), two transect lines (transects III and IV) were positioned in parallel at 125° from magnetic north. The lines were 1.0 meter apart and extended from −0.15 to +2.90 meters. Due to the steep slope (22.4°) of the seaward-facing surface of the sea stack, the transects only extended 8 meters in length.

Rectangular quadrats (30 × 50 cm) were placed on both sides of the metal tapes at 1-meter intervals, giving 90 samples at the boulder beach site and 32 samples at the sea stack. Vertical heights of the quadrats with respect to MLLW were determined using a stadia rod and inclinometer. Photographs of the numbered quadrats were taken at right angles to the substrate using Kodak High-Speed Ektachrome (ASA 160) slide film with Nikonos underwater cameras and electronic strobe units. More than one photograph of a given quadrat was taken in many cases to assess the multilayered structure of algal canopies. Each canopy was photographed in turn and moved aside until the epilithic organisms had been photographed, often yielding total cover values greater than 100 percent in some samples. Two teams of taxonomic specialists, one for the macrophytes and one for macroinvertebrates, carefully counted the animals and diagrammed the cover and location of macroorganisms in each quadrat. Tape recorders were used also as a rapid method of taking field notes. The recordings and diagrams were used subsequently to minimize the number of taxonomic problems encountered while scoring the color transparencies in the laboratory.

Cover was determined from the photographs by a point–intercept method. Color transparencies (35 mm) of the quadrats were projected through a panel of glass onto a sheet of white paper containing red dots spaced at 2.0-cm intervals. The transparencies were projected without regard to the field of dots so as to provide unbiased estimates of cover. The dots intercepting each species were then summed and a given species cover was determined as the percentage of the total number of dots contained within each quadrat. Each quadrat was scored twice by this technique and the results were averaged. Species present in a given quadrat but not intercepted by a dot were arbitrarily given a cover value of 0.1%. Cover values (the percentage cover for each species), density values (numbers of individuals per 1.0 m^2 for macroinvertebrate species), and frequency values (the percentage of quadrats in which a given species occurred) were averaged for those quadrats within each 0.15-meter tidal height interval. Overall cover, density, and frequency values were calculated for each species as the grand mean of all 0.15-meter interval averages.

The community parameters of diversity, stratification, and species assemblage associations were analyzed using the cover and density data. Three measures of species diversity were calculated: Shannon's (Shannon and Weaver 1962) index ($H' = \Sigma\, p_i \log_e p_i$), an index of species richness ($D' = (s-1)/\log_e N$) after Margalef (1968), and an index of evenness ($J' = H'/\log_e s$) after Pielou

TABLE 1

MEAN COVER AND FREQUENCY COMPARISONS OF MACROPHYTE SPECIES FOR TRANSECTS I AND II (BOULDER BEACH) AND III AND IV (SEA STACK)

SPECIES	MEAN COVER (%) I–II	MEAN COVER (%) III–IV	MEAN FREQUENCY (%) I–II	MEAN FREQUENCY (%) III–IV
Blue-green algae	47.6	31.7	98	84
Endocladia muricata (Post. & Rupr.) J. Ag.	21.7	10.8	71	47
Pseudolithoderma nigra Hollenb.	8.7	0.5	70	12
Pelvetia fastigiata (J. Ag.) DeToni	7.8	—	28	—
Rhodoglossum affine (Harv.) Kyl.	7.5	1.0	41	16
Hesperophycus harveyanus (Decne.) S. & G.	6.0	—	27	—
Hydrolithon decipiens (Fosl.) Adey	5.8	0.6	68	12
Gigartina papillata (C. Ag.) J. Ag.	5.1	1.0	56	12
Gigartina agardhii S. & G.	3.4	—	37	—
Corallina officinalis var. *chilensis* (Dec.) Kütz.	1.6	9.4	28	44
Phyllospadix torreyi Watson	1.2	5.6	10	22
Gigartina canaliculata Harv.	1.0	4.8	22	28
Lithophyllum proboscideum (Fosl.) Fosl.	0.8	4.8	13	38
Lithothamnium pacificum (Fosl.) Fosl.	0.6	0.3	17	9
Fucus distichus ssp. *edentatus* (de la Pyl.) Powell	0.4	—	4	—
Gastroclonium coulteri (Harv.) Kyl.	0.4	2.6	10	16
Gigartina leptorhynchos J. Ag.	0.4	—	23	—
Cryptosiphonia woodii (J. Ag.) J. Ag.	0.3	—	15	—
Egregia menziesii (Turn.) Aresch.	0.3	4.4	1	25
Gelidium coulteri Harv.	0.2	—	9	—
Gymnogongrus linearis (C. Ag.) J. Ag.	0.2	—	3	—
Neoagardhiella baileyi (Kütz.) Wynne & Tay.	0.1	—	2	—
Callithamnion pikeanum Harv.	0.1	—	2	—
Centroceras clavulatum (C. Ag.) Mont.	0.1	—	1	—
Cladophora graminea Coll.	0.1	0.1	21	6
Colpomenia sinuosa (Roth) Derb. & Sol.	0.1	—	1	—
Cryptopleura violacea (J. Ag.) Kyl.	0.1	1.3	5	16
Gelidium nudifrons Gard.	0.1	—	1	—
Iridaea flaccida (S. & G.) Silva	0.1	3.2	2	31
Laurencia pacifica Kyl.	0.1	0.3	1	6
Laurencia spectabilis Post. & Rupr.	0.1	—	1	—
Melobesia mediocris (Fosl.) Setch. & Mason	0.1	—	1	—
Peyssonnelia sp.	0.1	0.6	3	22
Porphyra lanceolata (Setch. & Hus) Smith	0.1	—	2	—
Porphyra perforata J. Ag.	0.1	0.1	1	25
Prionitis lanceolata (Harv.) Harv.	0.1	1.2	1	28
Ralfsia sp.	0.1	—	2	—
Rhodymenia sp.	0.1	—	2	—
Ulva californica Wille	0.1	0.1	1	3
Ulva expansa (Setch.) S. & G.	0.1	—	4	—
Unidentified Rhodophyta	0.1	—	2	—
Corallina vancouveriensis Yendo	—	5.9	—	41
Iridaea cordata var. *splendens* (S. & G.) Abb.	—	3.1	—	22
Calliarthron tuberculosum (Post. & Rupr.) Dawson	—	0.9	—	16
Gigartina spinosa (Kütz.) Harv.	—	0.4	—	16
Botryoglossum farlowianum (J. Ag.) DeToni	—	0.3	—	9
Callithamnion sp.	—	0.1	—	3
Nienburgia sp.	—	0.1	—	3
Total cover	123.0	95.2		

TABLE 2

MEAN COVER (%) AND FREQUENCY (%) COMPARISONS OF SESSILE MACROINVERTEBRATE SPECIES FOR TRANSECTS I AND II (BOULDER BEACH) AND III AND IV (SEA STACK)

SPECIES	MEAN COVER (%) I–II	MEAN COVER (%) III–IV	MEAN FREQUENCY (%) I–II	MEAN FREQUENCY (%) III–IV
Chthamalus fissus (Darwin 1854) and *C. dalli* (Pilsbry 1916)	2.4	4.3	13	53
Anthopleura elegantissima (Brandt 1835)	2.3	—	63	—
Balanus (*Balanus*) *glandula* (Darwin 1854)	0.1	3.2	2	53
Mytilus californianus (Conrad 1837)	—	5.6	—	41
Pollicipes polymerus (Sowerby 1833)	—	4.1	—	44
Balanus (*Semibalanus*) *cariosus* (Pallas 1788)	—	0.3	—	12
Tetraclita (*Tetraclita*) *squamosa rubescens* (Darwin 1854)	—	0.1	—	19
Haliclona sp.	—	0.1	—	12
Plocamia karykina (de Laubenfels 1927)	—	0.1	—	3
Total cover	4.8	17.8		

(1969). Assemblages or groups of organisms at each site were determined objectively from a matrix of similarity values (correlation coefficients) for all possible pairs of quadrat samples by the weighted-pair grouping method of cluster analysis. This method was adapted from Sokal and Sneath (1963).

Primary production was determined in situ for the dominant (in terms of cover) macrophytes at both sites. The work was done on 19 February 1973 between 10:50 AM and 2:50 PM under completely overcast skies (20,500–64,500 lux). The handling of algae and other methods were identical to those described by Littler and Murray (1974). For each macrophyte, productivity was calculated from dissolved oxygen values as milligrams of carbon fixed per square meter of thallus area per hour (mg C m^{-2} h^{-1}), using a photosynthetic quotient of 1.20. The production budgets for the two sites were calculated using the overall percentage cover and net primary productivity per square meter for each of the dominant species.

RESULTS

Mean Cover, Density, and Frequency

The dominant macrophytes in terms of cover (Table 1) at both the boulder beach site and the sea stack were blue-green algae (47.6 and 31.7 percent, respectively) and *Endocladia muricata* (21.7 and 10.8 percent, respectively). Macrophytes of secondary importance included five species at the sea stack (*Corallina officinalis* var. *chilensis*, *C. vancouveriensis*, *Gigartina canaliculata*, *Phyllospadix torreyi*, and *Lithophyllum proboscideum*), contributing a total cover of 30.5 percent; and six different species at the boulder beach (*Pseudolithoderma nigra*, *Pelvetia fastigiata*, *Rhodoglossum affine*, *Hesperophycus harveyanus*, *Hydrolithon decipiens*, and *Gigartina papillata*), which accounted for a total cover of 40.9 percent. Of these, the two fucalean forms *Pelvetia fastigiata* and *Hesperophycus harveyanus* were not sampled at the sea stack, while *Corallina vancouveriensis* was not collected at the boulder beach. In general, mean frequency values for each species at each site (Table 1) paralleled the cover values. The predominance of algae at the boulder beach site is indicated by the higher total mean cover (123.0 versus 95.2 percent) and the greater number of taxa (41 versus 28).

Data on the sessile macroinvertebrates (space occupiers) are presented as cover (Table 2), and for the mobile species as density (Table 3). Nine sessile species representing a total cover of 17.8 percent were recorded from the sea stack (Table 2). Most of the cover was attributable to the mussel

TABLE 3

MEAN DENSITY (NUMBER PER 1.0 m^2) AND FREQUENCY (%) COMPARISONS OF MOBILE MACROINVERTEBRATE SPECIES FOR TRANSECTS I AND II (BOULDER BEACH) AND III AND IV (SEA STACK)

	MEAN DENSITY		MEAN FREQUENCY (%)	
SPECIES	I–II	III–IV	I–II	III–IV
Tegula funebralis (A. Adams 1855)	84.9	0.9	83	3
Acmaea (*Collisella*) *limatula* (Carpenter 1864)	3.3	0.2	24	3
Acmaea (*Collisella*) *scabra* (Gould 1846)	2.4	112.3	18	59
Acmaea (*Collisella*) *pelta* (Rathke 1833)	2.3	4.6	12	28
Acmaea (*Collisella*) *asmi* (Middendorf 1847)	1.9	—	12	—
Pagurus spp.	1.6	—	13	—
Acmaea (*Notoacmea*) *scutum* (Rathke 1833)	1.3	0.2	7	3
Littorina planaxis (Philippi 1847)	0.7	4.8	5	16
Acanthina punctulata (Sowerby 1825)	0.6	—	6	—
Nucella emarginata (Deshayes 1839)	0.6	0.6	7	6
Tegula brunnea (Philippi 1848)	0.6	2.3	5	16
Ocenebra circumtexta (Stearns 1871)	0.5	—	6	—
Acmaea (*Collisella*) *digitalis* (Rathke 1833)	0.5	36.9	4	44
Pisaster ochraceus (Brandt 1835)	0.4	—	5	—
Mopalia muscosa (Gould 1846)	0.2	—	6	—
Nuttallina californica (Reeve 1847)	0.1	0.9	3	9
Crepidula adunca (Sowerby 1825)	0.1	0.2	1	3
Cyanoplax hartwegii (Carpenter 1855)	0.1	—	1	—
Olivella biplicata (Sowerby 1825)	0.1	—	1	—
Ocenebra sp.	0.1	—	1	—
Mitrella carinata (Hinds 1844)	0.1	—	1	—
Acmaea (*Collisella*) *strigatella* (Carpenter 1864)	0.1	1.5	1	13
Acmaea (*Notoacmea*) *insessa* (Hinds 1843)	—	0.4	—	6
Tonicella lineata (Wood 1815)	—	0.4	—	6
Littorina scutulata (Gould 1849)	—	0.4	—	6
Leptasterias hexactis (Stimpson 1862)	—	0.4	—	6
Lottia gigantea (Sowerby 1834)	—	0.2	—	3
Fissurella volcano (Reeve 1849)	—	0.2	—	3
Total density	102.5	167.4		

Mytilus californianus and the barnacles *Chthamalus fissus*, *C. dalli*, *Balanus* (*Balanus*) *glandula*, and *Pollicipes polymerus*. Only four sessile invertebrates, with a total cover of 4.8 percent, were present in the boulder beach transects (Table 2); one of these, *Anthopleura elegantissima*, was absent from the sea stack samples. For the mobile macroinvertebrates (Table 3) a single species, *Tegula funebralis*, dominated the boulder beach habitat with a mean density of 84.9 individuals per square meter. The 21 remaining species from the boulder beach had mean densities less than 3.4 m^{-2}. The dominant species from the sea stack (Table 3) were the limpets *Acmaea* (*Collisella*) *scabra* and *A*. (*Collisella*) *digitalis*, with mean densities of 112.3 m^{-2} and 36.9 m^{-2}, respectively. The 16 remaining species had mean densities lower than 4.9 m^{-2}. Largely because of the higher limpet abundances, the total mean density of mobile macroinvertebrates was higher for the sea stack (167.4 m^{-2}) than for the boulder beach (102.5 m^{-2}).

Vertical Distribution and Abundance

The macrophytes and sessile macroinvertebrates at the boulder beach site (Figure 3) did not show pronounced vertical zonational patterns. The only forms that were abundant throughout the 1.8-meter vertical range sampled were the blue-green algae. Of the major species, *Endocladia muricata*, *Hesperophycus harveyanus*, *Pelvetia fastigiata*, and the barnacles *Chthamalus fissus* and *C. dalli* were

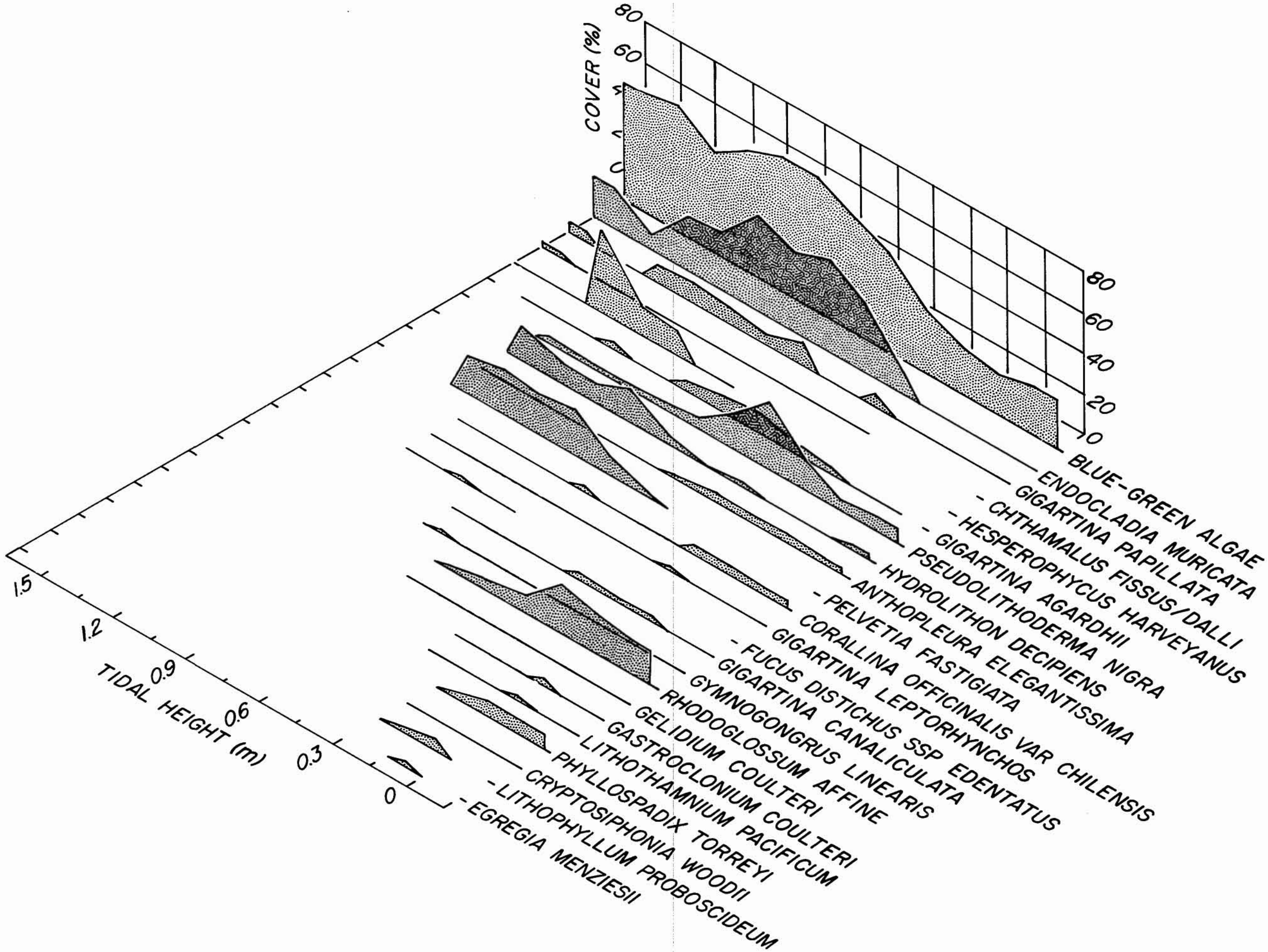

FIGURE 3. Percentage cover of major macrophytes and sessile macroinvertebrates as a function of tidal height at the boulder beach.

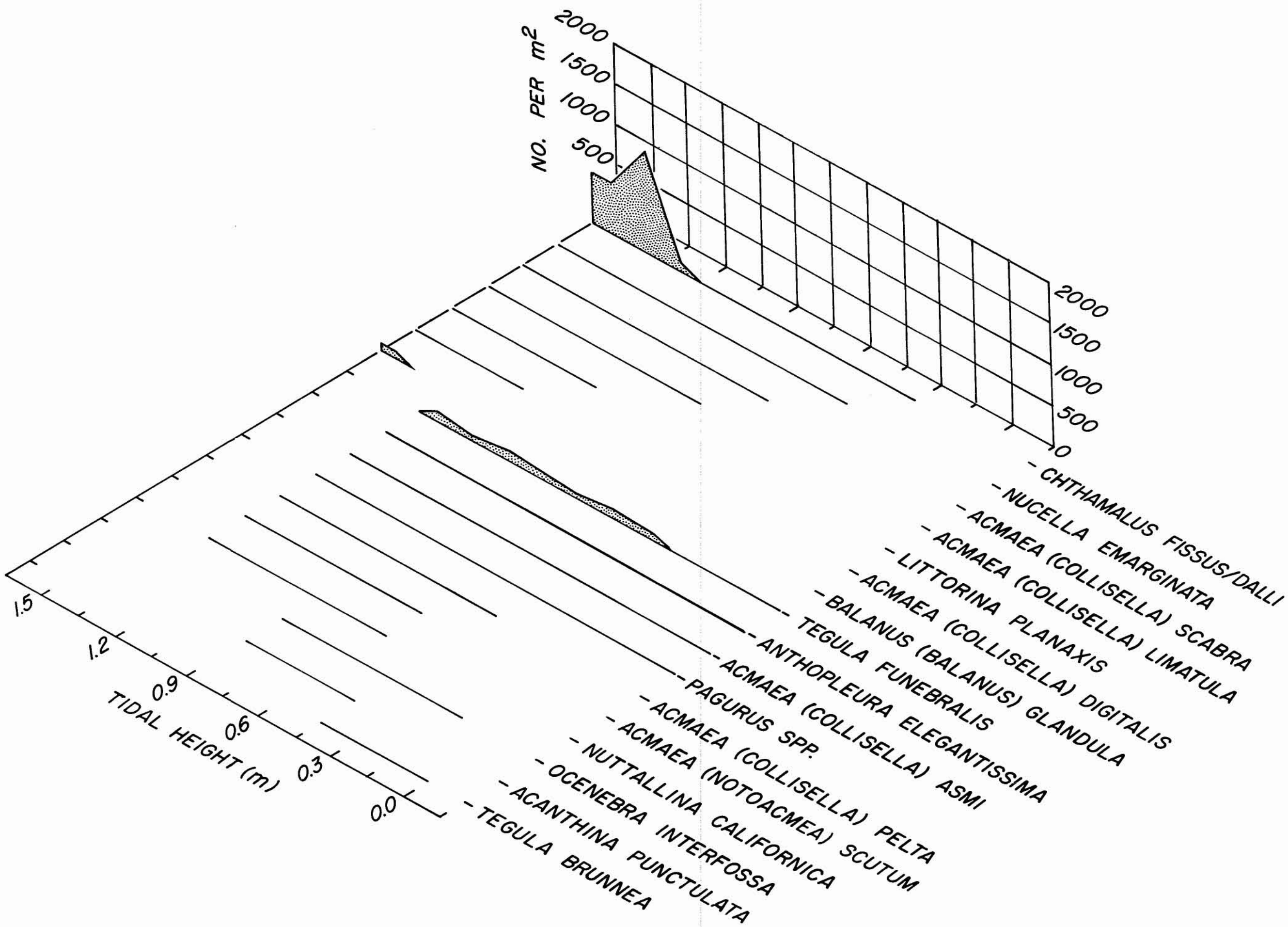

FIGURE 4. Density (number per square meter) of macroinvertebrates as a function of tidal height at the boulder beach.

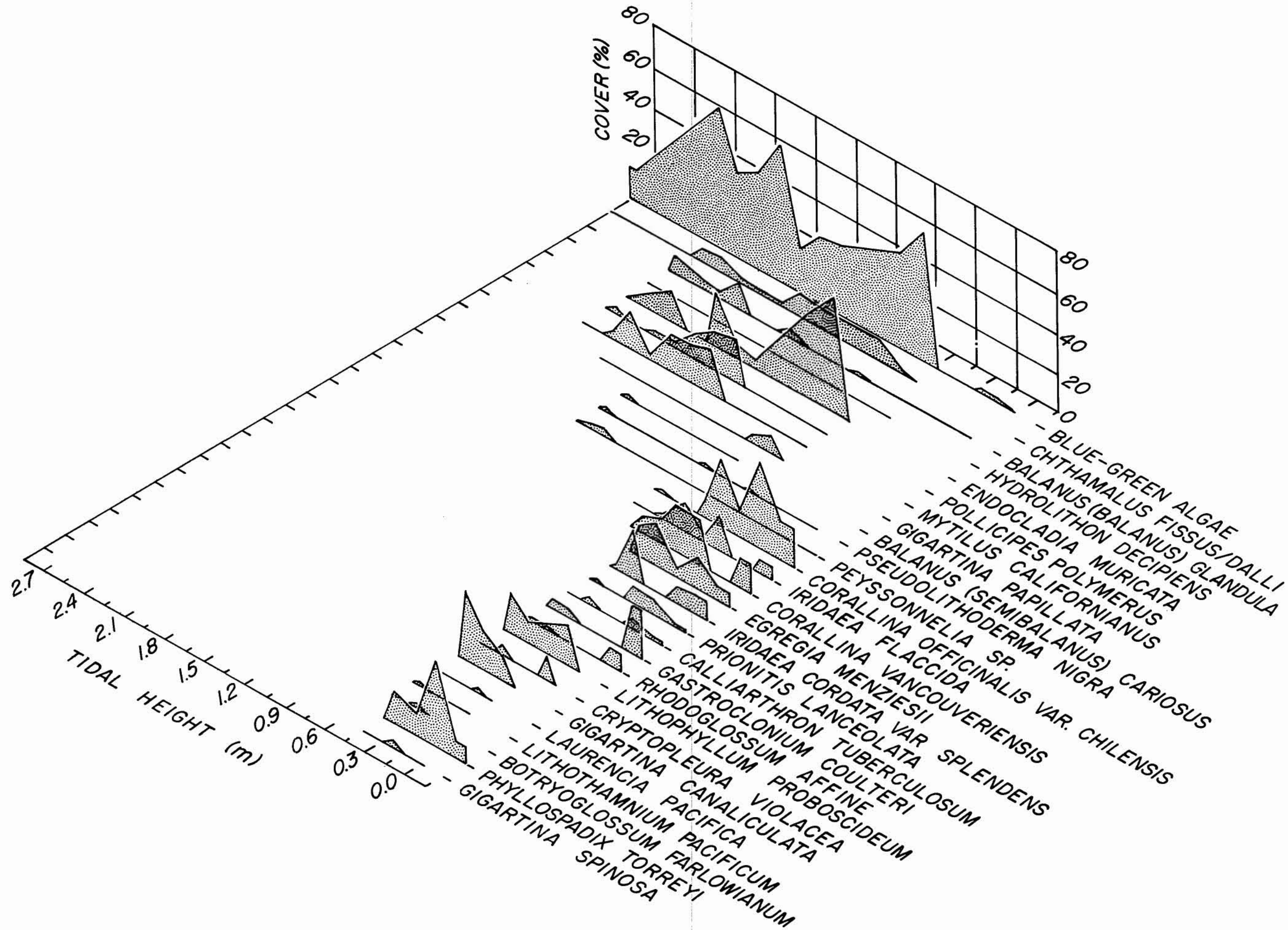

FIGURE 5. Percentage cover of major macrophytes and sessile macroinvertebrates as a function of tidal height at the sea stack.

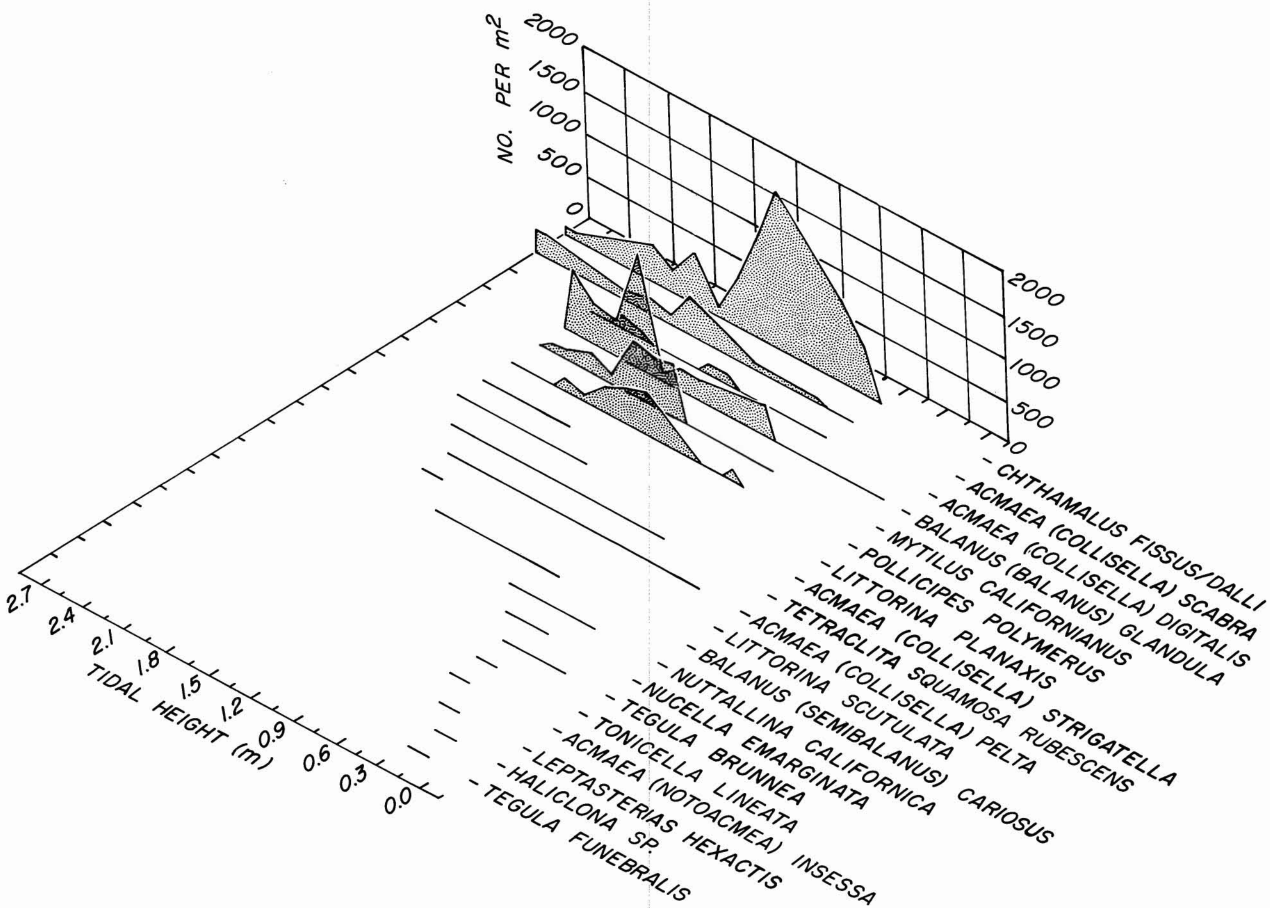

FIGURE 6. Density (number per square meter) of macroinvertebrates as a function of tidal height at the sea stack.

TABLE 4

COMPARISONS OF SPECIES DIVERSITY (SPECIES RICHNESS, EVENNESS, AND SHANNON'S INDEX) BETWEEN THE BOULDER BEACH (TRANSECTS I AND II) AND SEA STACK (TRANSECTS III AND IV) SITES FOR THE TOTAL MACROBIOTA AND THE MACROPHYTES AND MACROINVERTEBRATES TREATED SEPARATELY

	SPECIES RICHNESS (D′)		EVENNESS (J′)		SHANNON'S INDEX (H′)	
	I–II	III–IV	I–II	III–IV	I–II	III–IV
Total macrobiota (% cover)	9.18	7.40	0.61	0.78	2.59	3.10
Macrophytes (% cover)	5.62	3.93	0.58	0.80	2.15	2.66
Macroinvertebrates, sessile species (% cover)	1.28	2.43	0.71	0.73	0.78	1.51
mobile species (density)	7.68	5.28	0.29	0.37	0.90	1.07
all species (density)	6.95	4.78	0.44	0.51	1.40	1.67

abundant only above +0.46 meter. Species that were prominent mainly below +0.46 meter included *Rhodoglossum affine*, *Phyllospadix torreyi*, and, to a lesser extent, *Corallina officinalis* var. *chilensis*, *Anthopleura elegantissima*, *Lithothamnium pacificum*, and *Lithophyllum proboscideum*. Among the macroinvertebrates (Figure 4), the majority of species distributions were confined to the shore above +0.30 meter, while the majority of algal species (Figure 3) extended below this level.

Aside from the reduced number of macrophyte species (Table 1) and the increased number of sessile macroinvertebrate species (Table 2) at the sea stack site, a conspicuous difference between the two habitats was the vertical expansion of species distributions on the sea stack (Figures 5, 6). This expansion resulted in the apparent separation (at about +0.61 meter) of species distributions into upper-shore and lower-shore groupings. The dramatic decrease in abundance of blue-green algae below the +0.61-meter level (Figure 5) may be compared to their continued abundance (20–50 percent cover) below this level on the boulder beach (Figure 3). At the sea stack, substrate space below +0.61 meter appeared to be partitioned (Figure 5) primarily among a number of macrophytes, including *Corallina officinalis* var. *chilensis*, *C. vancouveriensis*, *Egregia menziesii*, *Iridaea cordata* var. *splendens*, *Gastroclonium coulteri*, *Lithophyllum proboscideum*, *Gigartina canaliculata*, and *Phyllospadix torreyi*. Marked differences in the composition of the macroinvertebrate fauna between the upper shore at the boulder beach site and at the sea stack are illustrated by a comparison of Figures 4 and 6. Aside from the widely distributed *Tegula funebralis*, only *Chthamalus fissus* and *C. dalli* were abundant at the boulder beach (Figure 4). While these two barnacles represent the most abundant forms at the sea stack (Figure 6), *Balanus* (*Balanus*) *glandula*, *Pollicipes polymerus*, *Mytilus californianus*, *Acmaea* (*Collisella*) *scabra*, and *A.* (*Collisella*) *digitalis* were also important constituents of the sea stack community above +0.61 meter.

Species Richness, Evenness, and Diversity

Although a greater number of taxa and higher species richness values were obtained at the boulder beach (Table 4), the evenness index and Shannon's index indicate a higher diversity at the sea stack site. The greater number of taxa from the boulder beach (67 versus 55) is reflected in the higher values for species richness (9.18 versus 7.40). Upon considering the macrophyte and macroinvertebrate components of the community separately, the number of macrophyte taxa was found to be greater at the boulder beach (41 versus 28), as was species richness (5.62 versus 3.93). Similarly, slightly more taxa of mobile macroinvertebrates occurred at the boulder beach site (22 versus 18), resulting

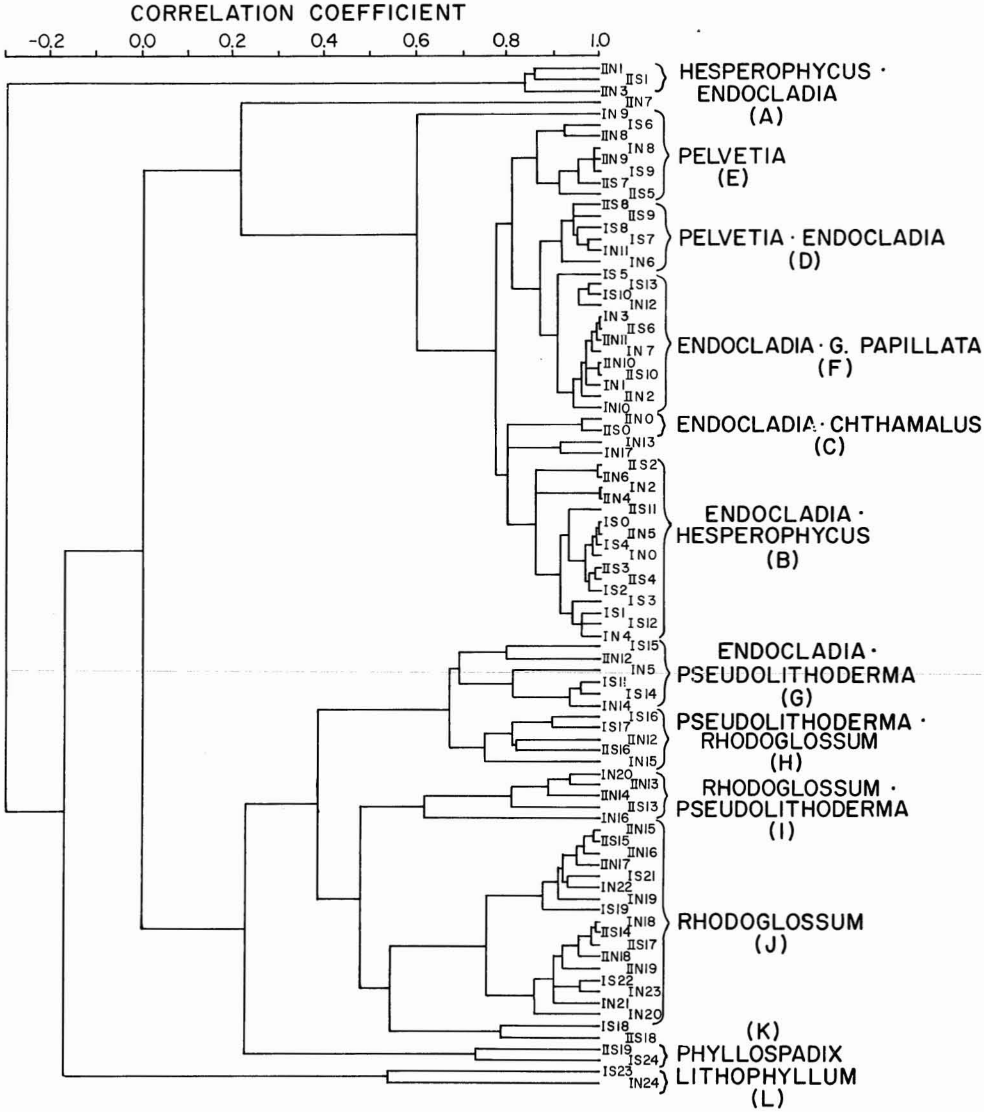

FIGURE 7. Cluster analysis results for boulder beach quadrats (using percentage cover data), expressed as a dendrogram. Dominant cover organisms from the quadrats in each cluster group are given to the right of the dendrogram.

in a higher richness value (7.68 versus 5.28). However, the numbers of sessile macroinvertebrate taxa were higher at the sea stack (9 versus 4), which was reflected in greater species richness (2.43 versus 1.28).

On the basis of the evenness component of species diversity, results were obtained (Table 4) that were opposite to those determined using either the numbers of taxa or the richness measure. The sea stack had a higher evenness than the boulder beach for the total macrobiota (0.78 versus 0.61), as well as for the macrophytes (0.80 versus 0.58) and macroinvertebrates (0.51 versus 0.44) treated separately. Diversity computations using Shannon's index (Table 4) were in agreement with the evenness values, i.e., higher values at the sea stack for the total macrobiota (3.10 versus 2.59), macrophytes (2.66 versus 2.15), and macroinvertebrates (1.67 versus 1.40).

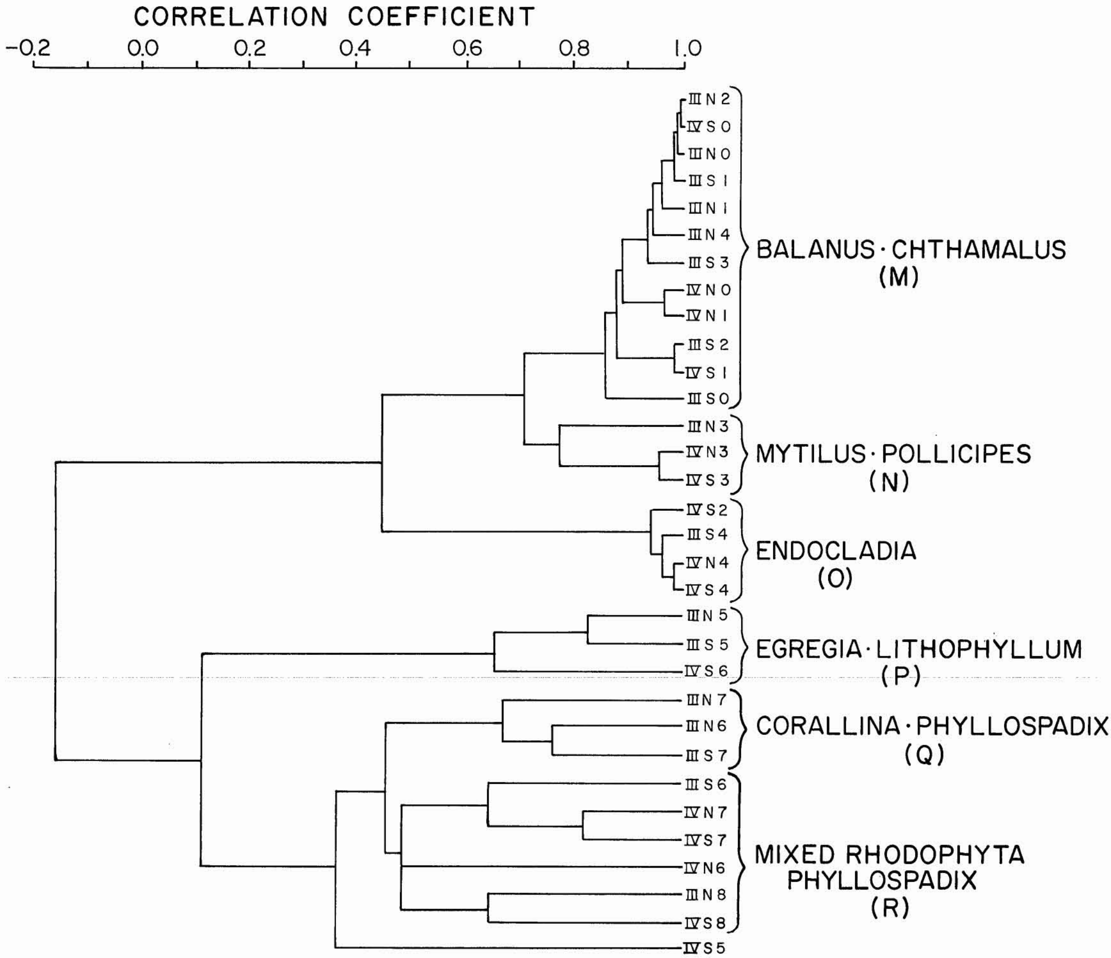

FIGURE 8. Cluster analysis results for sea stack quadrats (using percentage cover data), expressed as a dendrogram. Dominant cover organisms from the quadrats in each cluster group are given to the right of the dendrogram.

Community Classification

Community structure at the boulder beach and sea stack sites was determined by cluster analysis. Cluster groups were objectively identified from the resultant dendrograms (Figures 7, 8), and the dominant organisms in the quadrats comprising a particular cluster group were determined by inspection of the raw cover data and used to characterize that group. At the boulder beach (Figure 7), 12 such cluster groups were recognized. These fell into two large groupings: one containing a series of upper beach quadrats (the *Hesperophycus–Endocladia*, *Endocladia–Hesperophycus*, *Endocladia–Chthamalus*, *Pelvetia–Endocladia*, *Pelvetia*, and *Endocladia–Gigartina papillata* cluster groups), and the other comprising a series of lower beach quadrats (the *Endocladia–Pseudolithoderma*, *Pseudolithoderma–Rhodoglossum*, *Rhodoglossum–Pseudolithoderma*, *Rhodoglossum*, *Phyllospadix*, and *Lithophyllum* cluster groups). At the sea stack (Figure 8), seven cluster groups were recognized, three of which belonged to an upper beach grouping (*Balanus–Chthamalus*, *Mytilus–Pollicipes*, and *Endocladia*), and the remaining four (*Egregia–Lithophyllum*, *Corallina–Phyllospadix*, mixed Rhodophyta–*Phyllospadix*, and mixed Rhodophyta) com-

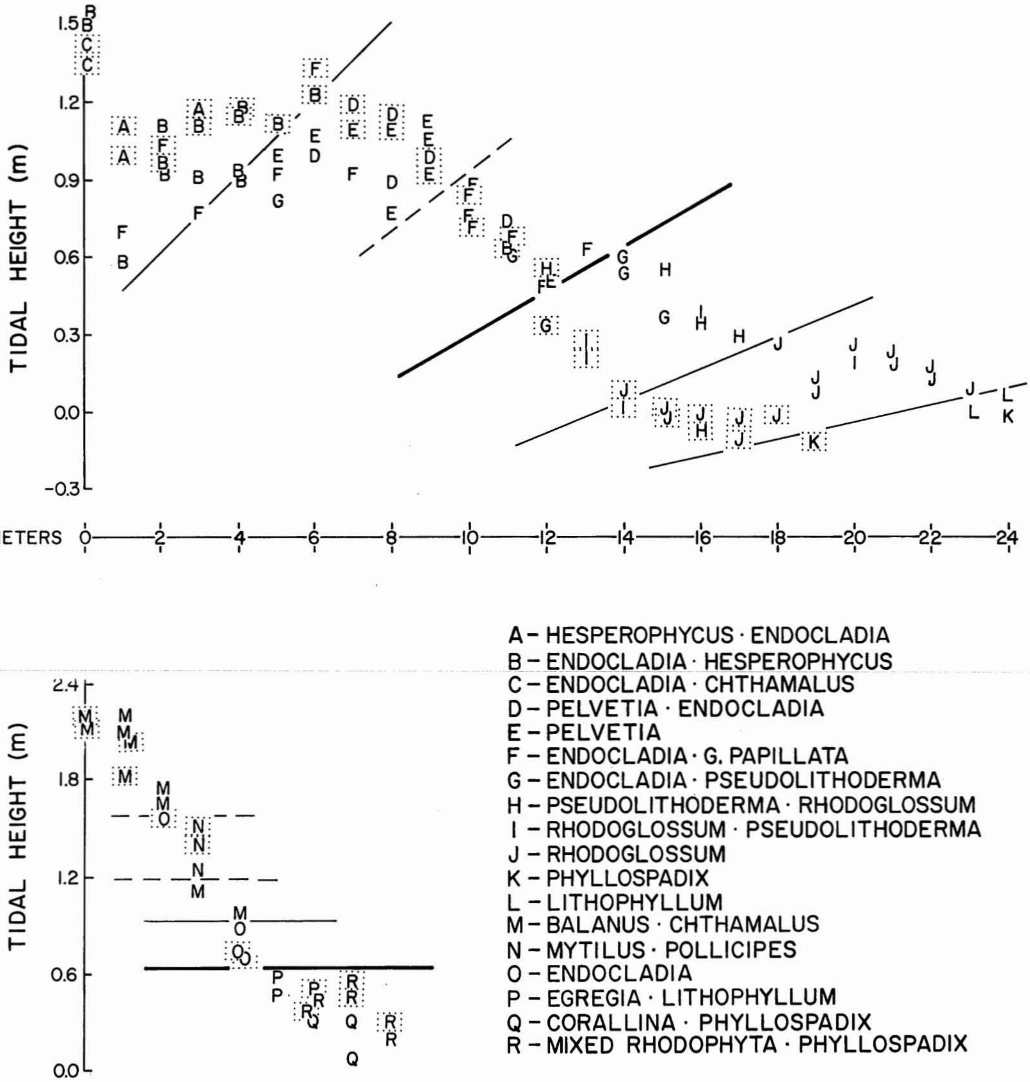

FIGURE 9. Diagrammatic locations of quadrats (identified according to cluster group) in relation to tidal height and horizontal distance along the shore at the boulder beach (upper plot) and sea stack (lower plot). Quadrats on the south transect lines at each site are enclosed by dotted lines, while those on the north transect lines are not enclosed.

prised a lower beach assemblage of quadrats.

To map the biota objectively, each quadrat (identified by its cluster group dominants) was plotted (Figure 9) by both tidal height and distance from the meter zero position along each transect line. The patterns of zonation at the two sites contrasted markedly; the zones at the sea stack were vertically distinct, while those at the boulder beach represented the product of a vertical tidal height component and a horizontal beach slope and breadth component. At the sea stack, an upper shore zone located above about +1.00 meter was dominated by *Balanus* and *Chthamalus*. This zone was interrupted between +1.20 and +1.70 meters by a *Mytilus–Pollicipes* band. An *Endocladia* community described a zone extending from +1.00 to +0.60 meter. All three of these cluster groups belonged to the larger upper shore quadrat assemblage identified in the dendrogram (Figure 8), which was sharply set off from the lower shore grouping of three clusters at +0.60 meter (Figure 9). The lower shore assemblage included *Egregia–Lithophyllum*, *Corallina–Phyllospadix*, and mixed Rhodophyta–*Phyllospadix* groups. Although the *Egregia–Lithophyllum* group was distinct from the other two groups in the dendrogram (Figure 8), the three were not vertically separated (Figure 9). At the boulder beach, the upper shore was dominated by *Hesperophycus* and *Endocladia*, which together with *Chthamalus* described a zone between meters 0 and 5 along the transect lines (Figure 9). Overlapping this zone vertically, but seaward of it, was a second zone in which *Endocladia* remained abundant but *Pelvetia* replaced *Hesperophycus*. Further to seaward, at about meter 10, an *Endocladia–Gigartina papillata* zone was identified. Interestingly, this last cluster group included four quadrats higher on the shore that were situated between the boulders and were consequently at a lower tidal level. The preceding three zones were separated in the cluster analysis (Figure 7) as an upper beach assemblage distinct from a lower beach quadrat grouping at +0.60 meter (Figure 9). The lower beach grouping occurred seaward of about meter 12, where one of the transect lines continued for 12 meters at a gradual slope, and the other dropped off abruptly (over a 2-meter distance) to MLLW at meter 14 and extended 5 meters further to seaward. As a result, three lower beach zones were evident that were related more to the tidal level component than the horizontal component. The first of these was dominated by *Pseudolithoderma* and *Rhodoglossum*, with *Endocladia* still conspicuous in the upper portion. The second zone was dominated by *Rhodoglossum* and the third zone included quadrats that contained either *Phyllospadix* or *Lithophyllum* as the dominant macrophyte species.

Primary Productivity

Contributions of the dominant macrophytes by taxonomic group to overall net primary production at the boulder beach and sea stack are given in Table 5. The boulder beach macrophytes proved to be about a third more productive than those of the sea stack (169.7 versus 116.5 mg C $m^{-2}h^{-1}$). This difference can be accounted for by the greater cover and concomitant production at the boulder beach by blue-green algae (80.9 versus 53.9 mg C $m^{-2}h^{-1}$) and Phaeophyta (39.3 versus 5.9 mg C $m^{-2}h^{-1}$). Of the latter group, the fucalean species *Pelvetia fastigiata* and *Hesperophycus harveyanus*, which produced 23.4 and 12.0 mg C $m^{-2}h^{-1}$, respectively, did not contribute importantly to community productivity at the sea stack. The large brown alga *Egregia menziesii* was a more prevalent producer at the sea stack (5.7 mg C $m^{-2}h^{-1}$) than at the boulder beach (0.4 mg C $m^{-2}h^{-1}$), as was the angiosperm *Phyllospadix torreyi* (3.4 versus 0.7 mg C $m^{-2}h^{-1}$). Contributions to total primary productivity by Rhodophyta were nearly the same for the two communities (48.8 and 53.3 mg C $m^{-2}h^{-1}$). However, *Rhodoglossum affine*, *Hydrolithon decipiens*, *Gigartina papillata*, and *G. agardhii* were major producers only at the boulder beach, whereas the coralline algae *Corallina officinalis* var. *chilensis*, *C. vancouveriensis*, and *Lithophyllum proboscideum*, along with *G. canaliculata*, were more important at the sea stack. *Endocladia muricata* was a major producer in both habitats but contributed only half as much organic carbon production on the sea stack as at the boulder beach (11.9 versus 23.9 mg C $m^{-2}h^{-1}$). Chlorophyta were so low in abundance that they contributed only a negligible amount to total community productivity at both sites.

DISCUSSION

The major differences between the two sites would appear to be due largely to differences in the shearing forces of waves and the relative degree of habitat structure between the two sites. As shown by this study and others (Lewis 1964, Stephenson and Stephenson 1972), macroinvertebrates such as barnacles, mussels, and limpets come to dominate the middle and upper intertidal

TABLE 5

MEAN COVER (%) AND NET PRODUCTION RATES (mg C m^{-2} h^{-1}) OF DOMINANT MACROPHYTES (>2% TOTAL COVER) FOR TRANSECTS I AND II (BOULDER BEACH) AND III AND IV (SEA STACK)

DIVISION AND SPECIES	COVER		PRODUCTIVITY	
	I–II	III–IV	I–II	III–IV
Angiospermae				
Phyllospadix torreyi	1.2	5.6	0.7	3.4
Chlorophyta				
Cladophora graminea	0.1	0.1	—	—
Ulva californica	0.1	0.1	—	—
Ulva expansa	0.1	—	—	—
Total	0.3	0.2		
Cyanophyta				
Blue-green algae	47.6	31.7	80.9	53.9
Phaeophyta				
Pseudolithoderma nigra	8.7	0.5	3.5	0.2
Pelvetia fastigiata	7.8	—	23.4	—
Hesperophycus harveyanus	6.0	—	12.0	—
Fucus distichus ssp. *edentatus*	0.4	—	—	—
Egregia menziesii	0.3	4.4	0.4	5.7
Colpomenia sinuosa	0.1	—	—	—
Ralfsia sp.	0.1	—	—	—
Total	23.4	4.9	39.3	5.9
Rhodophyta				
Endocladia muricata	21.7	10.8	23.9	11.9
Rhodoglossum affine	7.5	1.0	3.8	0.5
Hydrolithon decipiens	5.8	0.6	2.3	0.2
Gigartina papillata	5.1	1.0	2.6	0.5
Gigartina agardhii	3.4	—	13.3	—
Corallina officinalis var. *chilensis*	1.6	9.4	1.6	9.4
Gigartina canaliculata	1.0	4.8	0.3	1.4
Lithophyllum proboscideum	0.8	4.8	0.8	4.8
Lithothamnium pacificum	0.6	0.3	—	—
Gastroclonium coulteri	0.4	2.6	0.2	1.6
Gigartina leptorhynchos	0.4	—	—	—
Cryptosiphonia woodii	0.3	—	—	—
Gelidium coulteri	0.2	—	—	—
Gymnogongrus linearis	0.2	—	—	—
Neoagardhiella baileyi	0.1	—	—	—
Callithamnion pikeanum	0.1	—	—	—
Centroceras clavulatum	0.1	—	—	—
Cryptopleura violacea	0.1	1.3	—	—
Gelidium nudifrons	0.1	—	—	—
Iridaea flaccida	0.1	3.2	—	1.0
Laurencia pacifica	0.1	0.3	—	—
Laurencia spectabilis	0.1	—	—	—
Melobesia mediocris	0.1	—	—	—
Peyssonnelia sp.	0.1	0.6	—	—
Porphyra lanceolata	0.1	—	—	—
Porphyra perforata	0.1	0.1	—	—
Prionitis lanceolata	0.1	1.2	—	—
Rhodymenia sp.	0.1	—	—	—
Unidentified Rhodophyta	0.1	—	—	—
Corallina vancouveriensis	—	5.9	—	20.1
Iridaea cordata var. *splendens*	—	3.1	—	1.9

TABLE 5 (*Cont.*)

MEAN COVER (%) AND NET PRODUCTION RATES (mg C m^{-2} h^{-1}) OF DOMINANT MACROPHYTES (>2% TOTAL COVER) FOR TRANSECTS I AND II (BOULDER BEACH) AND III AND IV (SEA STACK)

DIVISION AND SPECIES	COVER		PRODUCTIVITY	
	I–II	III–IV	I–II	III–IV
Calliarthron tuberculosum	—	0.9	—	—
Gigartina spinosa	—	0.4	—	—
Botryoglossum farlowianum	—	0.3	—	—
Callithamnion sp.	—	0.1	—	—
Nienburgia sp.	—	0.1	—	—
Total	50.5	52.8	48.8	53.3
Grand total	123.0	95.2	169.7	116.5

zones where shearing forces of waves are high. This animal dominance at the sea stack tended to lower overall community productivity (Table 5) and to result in a marked animal/plant break between the upper and lower portions of the shore (Figure 8). On the other hand, the mosaic of crevices, angled substrates, and rivulets at the boulder beach resulted in less pronounced patterns of vertical zonation and a predominance of macrophytes, which would no doubt be physically removed if subjected to wave forces comparable to those consistently observed at the sea stack. Upward shifts in comparable zones at the sea stack were clearly correlated with increased wetting higher on the shore due to waves and splash, in agreement with similar findings by other workers (Jones and Demetropoulos 1968, Lewis 1964, Stephenson and Stephenson 1972). Reynolds and Mathieson (1975) stated that exposed sites typically have more diverse algal populations than sheltered locations. This statement is supported for the macrophytes in the present study (Table 4) by the evenness and Shannon's index data but is not supported when numbers of taxa and the richness index are used. The sea stack habitat tended to favor macrophytes structurally adapted to exist under strong shearing forces of water movement. The boulder field, on the other hand, is sheltered from such extreme water movement and, as expected, a greater number of relatively delicate frondose macrophytes were found under these conditions. The boulder beach habitat also presents a mosaic of wet rivulets and substrate exposures that increase spatial heterogeneity, which is likely to be an important factor contributing to the higher number of macrophyte taxa. It must also be appreciated that different boulder beaches show large variability in wave exposure and concomitant substrate stability. Consequently, less stable boulder fields than the one examined in this study would be expected to result in alterations to the populational patterns reported here.

Our productivity numbers (Table 5) clearly show less community production for the sea stack relative to the boulder beach habitat. These results contrast with the statement by Reynolds and Mathieson (1975) that exposed areas typically exhibit higher primary productivity than sheltered sites. We maintain that the lower primary productivity determined for the sea stack is to be predicted because, in agreement with observations elsewhere by Stephenson and Stephenson (1972), fucalean and other frondose algal stocks do not develop successfully on such areas that are subjected to the strong shearing forces of large waves. Consequently, much of the upper primary substrate normally occupied by frondose forms and Cyanophyta in calmer situations has become dominated by mussels, barnacles, and limpets at the sea stack. The community productivity values obtained (116.5 and 169.7 mg C $m^{-2}h^{-1}$ for the sea stack and boulder beach, respectively) are quite comparable to those reported for both sewage-polluted and unpolluted intertidal macrophytic communities in southern California by Littler and Murray (1974), i.e., 127.1 and 125.4 mg C $m^{-2}h^{-1}$, respectively.

Very little data has been collected that can be compared to the findings of this study. However, an excellent descriptive account of rocky intertidal habitats in the vicinity of Monterey, in central California, has been published by Stephenson and Stephenson (1972). Although these authors produced only qualitative results, their commendable thoroughness and perceptive interpretations of zonational patterns warrant placing our findings in perspective with theirs. Among the sites treated by Stephenson and Stephenson, the steeply sloping surfaces in the exposed portions of Sand Hill Cove, where a patchy mussel zone had developed, would appear to be most comparable to the sea stack site of this study. In both cases, the upper shore was dominated by *Balanus* (*Balanus*) *glandula* and sparse *Endocladia muricata*. We also found *Chthamalus fissus* and *C. dalli* to co-occur with *B.* (*Balanus*) *glandula*, although in lower abundance, along with scattered *Mytilus californianus* and *Pollicipes polymerus*. Extending into a higher region were the two species of *Chthamalus* and the two limpets *Acmaea* (*Collisella*) *scabra* and *A.* (*Collisella*) *digitalis* (Figure 6), which corresponds to the supralittoral fringe of Stephenson and Stephenson (although *Chthamalus* typically is not found in this zone). Curiously, *Littorina planaxis*, which should be the numerical dominant in the supralittoral fringe (Figure 6), occurred only below +2.44 meters in very low abundance. Below the balanoid zone was a mussel zone (from +0.76 to +1.68 meters) dominated by *M. californianus* and *P. polymerus* at both the sea stack and at the Stephensons' site. On the sea stack, *Endocladia muricata* extended toward this zone and terminated its upward range abruptly at +0.61 meter (Figure 5). Stephenson and Stephenson also indicated the presence of patches of *E. muricata* not extending above the base of the mussel zone.

In the distribution diagrams for the sea stack (Figures 5, 6), the lower limits of a number of species occurred at about the +0.60-meter level, suggesting a major zonal break. This was supported by the cluster analysis (Figure 8), which included all the quadrats above this level in a separate upper shore grouping. In excellent agreement with these results are those of Stephenson and Stephenson, who considered the base of the mussel zone to be a major divisional point between the upper and lower midintertidal zones. The lower shore (below the mussel zone) was comparable in both studies in terms of the dominant species present, although clear zonation of these species, as shown by the Stephensons, was not observed at the sea stack. The lower midintertidal zone at Sand Hill Cove was divided into a narrow upper band of articulated and crustose corallines and a lower region where *Egregia menziesii* and *Alaria marginata* overlay corallines and mixed Rhodophyta. At the sea stack, a similar zone of corallines was lacking that separated *Endocladia muricata* above +0.60 meter from *E. menziesii* below this level. Instead, the cluster analysis (Figure 8) suggests the presence of only one distinct group of quadrats, dominated by *E. menziesii* and *Lithophyllum proboscideum*, located immediately below *E. muricata* between +0.30 and +0.60 meter (Figure 9). The remaining lower shore cluster groups (*Corallina–Phyllospadix* and mixed Rhodophyta–*Phyllospadix*) showed no pattern of vertical separation and are not comparable to the lower shore at Sand Hill Cove, particularly since *Phyllospadix* was apparently lacking from the latter site.

Among the other coastal sites studied by Stephenson and Stephenson (1972), a moderately sheltered shore of gradual slope at Cabrillo Point, Pacific Grove, appears to be most comparable to the boulder beach of the present study. The absence of *Mytilus californianus* and *Pollicipes polymerus* and the marked reduction in sessile suspension-feeding invertebrates from the boulder beach compare favorably with the Cabrillo Point site. At the latter location, the Stephensons reported a distinct upper *Balanus* (*Balanus*) *glandula* zone containing patches of *Endo-*

cladia muricata and extending through the upper midlittoral zone. In contrast, our data for the boulder beach indicated a near absence of *B.* (*Balanus*) *glandula*, while the comparable upper midlittoral zone (above +0.6 meter) was dominated by *Hesperophycus harveyanus*, *Pelvetia fastigiata*, *Gigartina papillata*, and *E. muricata*. These macrophytes were closely interrelated by the cluster analysis (Figure 7) and separated more as a function of distance down the shore than by tidal level (Figure 9). It is interesting that *P. fastigiata* and *H. harveyanus* occurred at approximately the same tidal level at the boulder beach; whereas, others (e.g., Stephenson and Stephenson 1972) have clearly shown the two to form distinct bands (*Pelvetia* below *Hesperophycus*) that overlap only to a minor extent. Our interpretation for the nearly complete overlap (Figure 9) is that increased wave splash and surge at the seaward margin of the relatively flat portion of the shore between meters 0 and 9 permitted the *P. fastigiata* zone to persist higher in the intertidal. The lower midlittoral zone at Cabrillo Point consisted of an upper *E. muricata* band, followed by a broad zone of "lower balanoid turf" (i.e., a dark-colored, low-growing, red algal turf that included *Rhodoglossum affine*) with sparse *Egregia menziesii* occurring at the lower end of the turf zone (~MLLW). At the boulder beach, *E. menziesii* was present between MLLW and +0.15 meter (Figure 1). *Endocladia muricata* and *Pseudolithoderma nigra* comprised a comparable zone between about +0.30 and +0.60 meter, although a "lower balanoid turf" as such was lacking, since only one of the component species, *R. affine*, was important.

ACKNOWLEDGMENTS

We wish to thank Diane Littler, who prepared the illustrations and proofread the manuscript; Maurice Hill, who assisted with the computer-mediated cluster analysis; and James Smith, who flew one of us (R. R. S.) over the study area to take aerial photographs. The data used in this paper were reworked from photographimetric samples taken during a course taught by the authors in which the following participated as students: Ernest Christopher, Judith Connors, Richard Cook, Virginia Cooke, Wayne Dorband, William Fitt, Maurice Hill, David Jamison, Christopher Kitting, Harry Landau, Patrick O'Brien, Earl Peattie, Allan Rapp, Robert Rubin, Victoria Sork, James Stretch, Peter Tuck, Scott Verzwyvelt, James Watson, and Kirk Wentworth.

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