SUBTIDAL PLANT AND ANIMAL COMMUNITIES OF THE SOUTHERN CALIFORNIA ISLANDS[1]

Michael Neushul
University of California, Santa Barbara

W. D. Clarke[2]
GM Defense Research Laboratories

D. W. Brown
University of California, Santa Barbara

I. INTRODUCTION

The subtidal communities along the west coast of North America are particularly rich in species, including some unique elements found nowhere else in the northern hemisphere. The extensive forest-like beds of the giant kelp, *Macrocystis* spp., are particularly luxuriant off southern California; in the shallow sublittoral regions around the Southern California Islands occur nearly two-fifths of the 54 square miles of major kelp beds recorded for this area. The complexity and dimensions of these undersea forests (Dawson et al., 1960; McFarland and Prescott, 1959) compare with those of tropical rain forests, and they are of great importance in understanding the biogeography of the area.

The benthic flora and fauna of the mainland coasts of California have been given increasing attention by biologists in recent years, largely in studies of real and potential pollution problems from sewer outfalls and the effects of kelp harvesting upon these subtidal communities (North et al., 1964, 1965, in press; Turner et al., 1964, 1965). At the same time, the subtidal plant and animal communities of the Southern California Islands have not been extensively explored. This paper describes some of the shallow communities that can be reached with SCUBA (Self-Contained Underwater Breathing Apparatus), particularly those of

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2. Current address: Westinghouse Ocean Research Laboratory, San Diego.

Anacapa Island, and discusses their floristic and faunistic relationships with the mainland.[3]

II. BIOGEOGRAPHY OF THE SOUTHERN CALIFORNIA ISLANDS

Dana (1858) first separated the marine areas north and south of Point Conception on the basis of temperature differences. Hedgpeth (1957) discussed this and later work concerning the floral and faunal break at Point Conception in his review of marine biogeography. Hydrographic studies (Reid et al., 1958; Schwartzlose, 1963; Reid, 1965) have revealed the general temperature structure and current patterns probably responsible for this biogeographic break offshore from Point Conception. The break in the flora and fauna, however, is not so complete and clean-cut as was previously believed. For instance, isolated areas of warm-water flora have been found as far north as Vancouver Island, Canada (Scagel, 1963); and cold-water flora and fauna have been found as far south as the central coast of Baja California in regions of upwelling (Dawson, 1951; Hubbs, 1960).

The Southern California Islands are an important link in the biogeography of the Pacific coast of North America. Their location, astride a major break in the marine environment on this coast, makes their flora and fauna extremely significant in understanding the biogeography of the coast as a whole.

The benthic algae and their animal associates on the underwater shelves of these islands are far better measures of the average marine climate than are the drifting plankton because the species composition of the plankton depends almost entirely on the type of water present. Thus, plankton samples taken from waters adjacent to the islands could be misleading because of vagaries of water circulation or seasonal changes in the environment. On the other hand, samples of benthic plants and organisms will indicate the biogeographic affinities of an island because they are long-lived and must be able to survive the extremes of the marine climate throughout the year. In assembling distributional data relating to the biogeographical regions north and south of Point Conception, we have drawn on Scagel (1963) and Dawson, Neushul, and Wildman (1960) for information on flora, and on Schmitt (1921), and Roedell (1953), as well as our own observations for information on fauna. The benthic biology of the Point Conception - Hueneme shelf, including areas below 150 feet not considered here, has been reviewed recently by Jones (1964).

3. The materials and methods used in the exploratory studies at Anacapa Island are discussed elsewhere (Neushul, 1965, in press; Clarke and Neushul, in press.)

The oceanic circulation in the region of the Southern California Islands (Schwartzlose, 1963; Reid, 1965) is very complicated. The cold California Current sweeps south along the central California coast as far as Point Conception where the coast line swings abruptly eastward. The current fails to follow the coast, continuing instead in a southeasterly direction. The eastern edge of this current beyond Point Conception bathes San Miguel Island with cold water, some of which is deflected into the Santa Barbara Channel. As a result, the water immediately north of both Santa Rosa and Santa Cruz islands to the east of San Miguel is colder throughout much of the year than the water along the opposite mainland coast. The main stream of the California Current continues its southeasterly direction to San Nicolas Island, where some of the water from its eastern edge enters a semipermanent counterclockwise gyre lying between San Nicolas Island and Santa Rosa and Santa Cruz islands to the north. Thus, San Miguel, the western half of Santa Rosa, and San Nicolas are all strongly influenced by the cold California Current; whereas, Santa Barbara Island, Santa Cruz, Anacapa, and the eastern half of Santa Rosa receive both cold water from the California Current and warmer water from the south, moving up along the Southern California coast. Farther south, Santa Catalina and San Clemente islands are bathed throughout the greater part of the year by the warmer southern waters. Currents and circulation in the island area are further complicated by local upwelling in the summer months.

The shallow-water benthic biota of the Southern California Islands seem to reflect the prevailing oceanographic conditions. Those islands with both northern and southern elements (eastern Santa Rosa, Santa Cruz, Anacapa, and Santa Barbara) lie in a region of variable mixing between cold California Current water from the north and warmer water from the south. The greater northern (San Miguel, San Nicolas, and the western half of Santa Rosa) or southern (Santa Catalina and San Clemente) affinities of the communities that occur on the other islands are explained by the more persistent circulation features of the area. (See contribution by A. W. Ebeling in this symposium for discussion of the planktonic communities.)

For the past two years, we have been making a study of the distributions of organisms on Anacapa Island from the lower limits of the intertidal zone down to a depth of 40 meters along a marked survey line (Clarke and Neushul, unpublished manuscript). The biotic changes with depth along this carefully surveyed profile (figs. 1A-1D) – as striking in some ways as those noted to the north and south of Point Conception - include three recognizable zones of vegetation: (1) a shallow zone, extending from the intertidal down to about eight meters, dominated by *Eisenia arborea*,

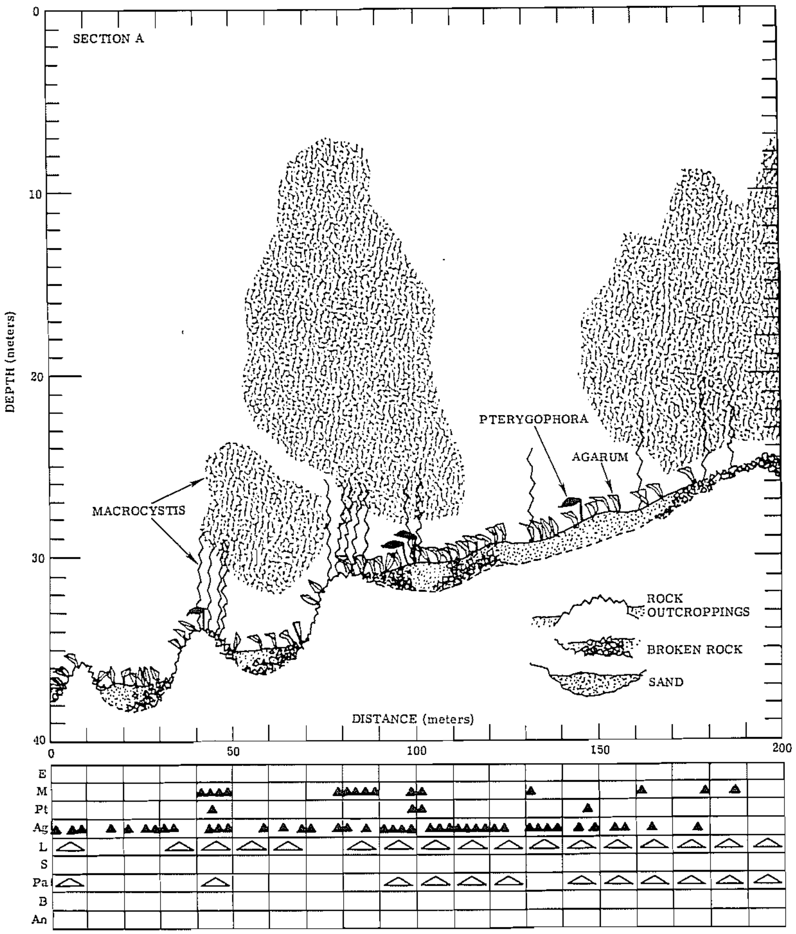

Fig. 1A

(Figs. 1A – 1D
Transect off Anacapa Island, California, showing the types of bottom and indicating the distributions of the major plants. The occurrences of the different plants are indicated by symbols which are identified in the figure. The shaded areas above the bottom represent *Macrocystis* plants that lean over the survey line because of a current flowing from west to east. The table at the bottom of the figure indicates the occurrences per two and one-half meter section of four plants: E, *Eisenia arborea;* M, *Macrocystis pyrifera;* Pt, *Pterygophora californica;* Ag, *Agarum fimbriatum;* and the presence or absence per ten meter section of six animals: L, *Lytechinus anamesus;* S, *Strongylocentrotus franciscanus* and S. *purpuratus;* Pa, *Patiria miniata;* B, *Botruanthus benedini;* An, *Anthopleura xanthogrammica.* Dense kelp bed surveyed is indicated by large "A" in fig. 1C.)

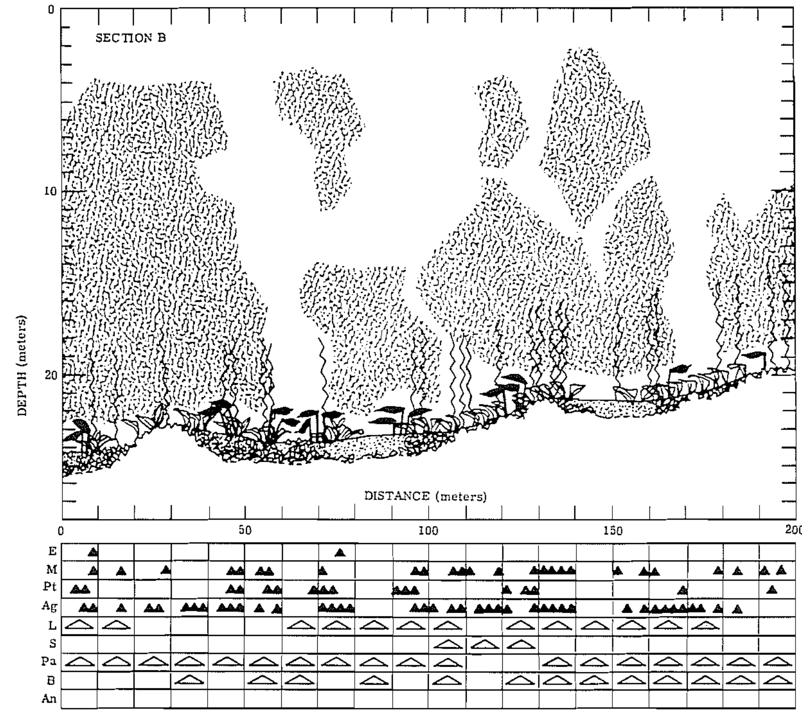

Fig. 1B

Laminaria farlowii, and *Phyllospadix torreyi;* (2) a broad mid-depth zone extending from eight meters down to about 34 meters densely populated with *Macrocystis pyrifera, Agarum fimbriatum,* and *Pterygophora californica*; and (3) a deep zone extending from about 34 meters down to the lower limit of vegetation, characterized by small red algae and scattered plants of *Agarum fimbriatum.* (Similarly, some species of animals are associated with one zone or another.)

Dawson and Neushul (unpublished manuscript) have examined algal collections from along the Anacapa Island survey line; and, as would be expected from the mixed hydrography of the area, both northern and southern species were found. Of the total of 80 algal species discussed, six are reported as new to science, four showed range extensions from north of Point Conception, while 23 are listed as being new northern range extensions of southern species. From these findings and the analysis in the Appendix below, it appears that Point Conception is more of a barrier to southern forms spreading north than it is to northern forms spreading south.

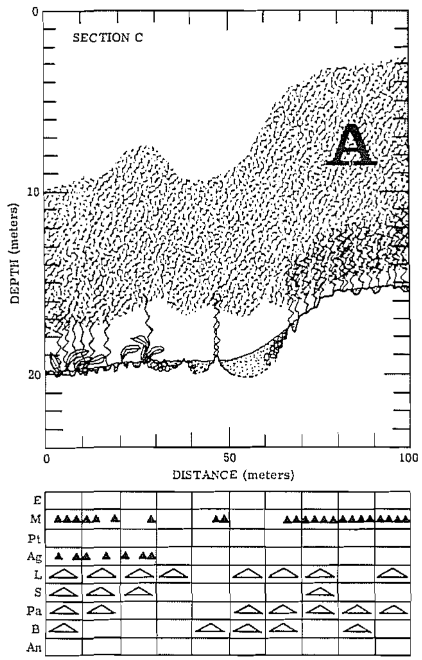

Fig. 1C

Crustose coralline algae and benthic diatoms were not treated by Dawson and Neushul, but the smaller red and brown algae that are common along the line were studied carefully. As an indication of size and numbers of species in these smaller plant assemblages, 13 of these were more than 10 centimeters high, 23 were less than 10 centimeters but more than one centimeter high, and 44 species were less than one centimeter high.

Many of the smaller red algae that occur near the lower limit of plant distribution on the survey line are found both north and south of Point Conception; living as they do under such extreme conditions, these plants seem to be as little affected by the hydrographic differences found on either side of Point Conception as are those plants of the intertidal environment (Scagel, 1963). The organisms inhabiting these marginal living areas are apparently subjected to additional environmental stresses that outweigh those found in the more even marine climate at intervening depths north and south of Point Conception. Thus, the greatest differences in the benthic flora on either side of this point are found in the broad mid-depth zone extending roughly from 8 to 30 meters where the environment is less variable and the controlling factors that determine the plant species are probably hydrographic differences in the marine environment.

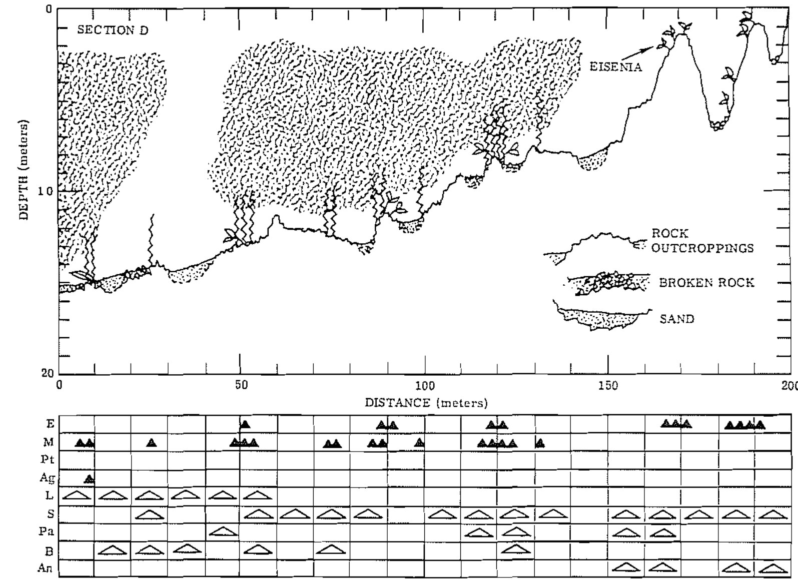

Fig. 1D

III. ENDEMISM AND EVOLUTION OF THE SOUTHERN CALIFORNIA ISLANDS BIOTA

The Southern California Islands provide diverse shallow-water environments which have a few endemic species (see Appendix). The low amount of marine endemism agrees well with that found in the terrestrial floras (see contribution by P. H. Raven in this symposium). Distance between islands, or between an island and the mainland, is probably not nearly so effective a barrier in preventing dispersal of marine organisms as it is for terrestrial organisms since the majority of benthic organisms found in shallow-water environments have pelagic stages during some part of their life cycle. The small number of endemics listed in the Appendix supports this conclusion. If the distance is great enough, however, the number of common species drops while the number of endemics rises. Certainly, in comparison with the Southern California Islands, the marine flora and fauna of Guadalupe Island reflect their greater isolation, particularly in the high number of endemics.

The distribution and speciation of Rhodophyta (Dixon, 1963) and Phaeophyta (Powell, 1963) can be discussed only in general terms. However, there are evidences of some endemic species and subspecies among the larger Phaeophyta of the Southern California Islands: Silva (1957) and Chapman (1961) discuss

Egregia laevigata f. *insularis*, a plant limited to the northern islands; Dawson (1962), and Parker and Dawson (1964) deal with the phenotypic variation and speciation of the elk kelp, *Pelagophycus*, for the area; and Parker and Bleck (in press) are suggesting that *Pelagophycus giganteus* is an exclusively insular form, distinctive from *P. porra* of mainland coasts.

Parker and Dawson (1965) described from the upper Miocene of southern California a fossil plant, *Julescranea grandicornis*, which is intermediate between *Pelagophycus* and *Nereocystis*. They suggest that these two present-day genera are derived from *Julescranea*. The Miocene fossil marine flora of southern California (3 genera, 13 species) is associated with the higher temperatures of water of that time. It is somewhat surprising that *Macrocystis* is absent from the flora while *Julescranea* is present, particularly in view of the similar southern California habitats of *Macrocystis* and *Pelagophycus* today.

Pleistocene cooling probably accounts for the change from the dominantly cystoseiraceous fossil flora in the Miocene to the present laminarian dominated flora. The anti-tropical distribution of the marine benthos here and along the coasts of South America is discussed in relation to this cooling by Hubbs (1952) and Hedgpeth (1957).

IV. SOME UNIQUE FEATURES OF UNDER-SEA VEGETATION

In the analysis of submarine plant communities, comparisons with land vegetation are understandable. These have their limitations, however, since submerged vegetation is distinctive. Terrestrial plant life tends to develop best on unconsolidated sedimentary substrates; whereas marine vegetation favors solid rock substrates, because of the strong erosive forces resulting from currents and wave surge. This physical movement, coupled with the denseness of the watery milieu, profoundly affects the morphological structure of plants.

Plants of moderate size, such as the brown alga, *Eisenia arborea*, which occur in shallow water where wave surge is often violent, usually have resilient, leathery stipes that support the fronds, keeping them off the bottom. This favorable frond-orientation would seem to have adaptive value in reducing abrasion and in providing maximum exposure to light. The movements of individual *Eisenia* plants under various conditions of wave surge have been observed and measured in our present study (fig. 2).

Large plants like the giant kelp, *Macrocystis pyrifera* (fig. 3), which occur in deeper water, are much too big to be held up by their stipes. Their foliage is supported, instead, by small gas-filled floats at the base of each blade, buoying up the whole plant structure.

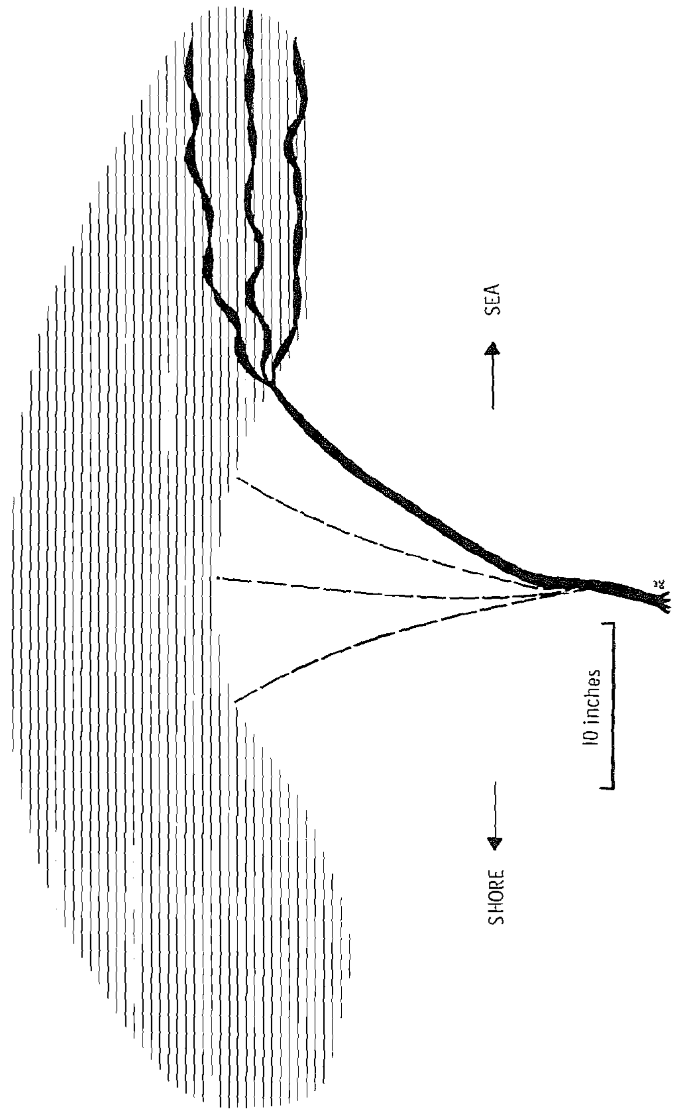

Fig. 2 Movement of *Eisenia* plant caused by wave surge at a depth of 1.5 meters. Dashed lines indicate different positions taken by the stipe in response to onshore-offshore water movements caused by wave surge. Shaded area indicates movement of fronds.

Although depression of the surface canopy of the giant kelp has been observed, effects such as the changes in plant attitude relative to current velocity and the drag forces imparted on the plants by currents and wave surge have not been investigated.

A dense stand of kelp (shown at position A, fig. 1C) was carefully surveyed to assess the effects of currents and wave surge on the vegetation. All of the plants within a meter-wide strip on either side of the survey line for a distance of 30 meters were counted – 23 in all, having a total of 244 stipes, a density comparable to the densest stands measured on the mainland (North, 1957; Neushul, in press). A current of 0.4 meters/second will pull these plants over at an angle of 20° to 30° to the horizontal (fig. 3). The final angle taken by the plants under any given current condition is obviously a balance between the drag forces exerted by the current and the lift produced by the gas-filled floats.

With strong currents, the plants form overlapping layers of vegetation, greatly increasing shade in certain areas of the bottom. With no current, the plants float vertically to the surface, thereby changing the light and shade patterns again, since there is little overlap of one plant by another. By changing the vegetation structure, currents not only affect the light regime of smaller

Fig. 3 Photograph showing the 20° to 30° angle to the horizontal taken by the kelp plants with a current of 0.4 meters/second. Dr. Clarke is shown in the photograph. (Photograph taken by Mr. R. Pieper.)

plants living under giant kelp, they also modify the light environment of the kelp plants themselves by causing them to shade one another and by forcing them to depths where less light is available.

Currents can depress the surface canopy of these plants to a depth of 25 feet; this has been measured directly by divers with depth gages. With such a strong current, the water is generally more turbid and restricts visual observations of the canopy top to a horizontal distance of about 30 feet; but divers can extend observations to 90 feet by using a small, hand-held sonar unit to detect plants. This device can be used to measure the depth of the canopy top and to determine attitudes and positions of individual plants around a vertical line extending from the surface to the bottom.

A sample of measurements made with the hand-held sonar is given in table 1. On the day these measurements were made, the current was flowing from west to east at right angles to the survey line. In a straight line descending from the surface to the bottom, measurements were taken horizontally at the four points of the compass at a depth of 7 feet, 15 feet, 25 feet, and 45 feet (the last measurement is 5 feet above the bottom). At 7 feet and 15 feet no targets were picked up by the sonar unit except on the east range where, at a horizontal distance of 25 feet, a current meter was suspended from a skiff. At a depth of 25 feet, the top of the kelp canopy had been penetrated and on the south range at right angles to the current, targets were detected at horizontal distances of 20, 25, and 35 feet. These targets represent two or three plants, inclined across the beam of sound projected by the sonar unit and attached to the bottom upstream on the right. Up-current on the west range, no plants were detected within the ranging limits of the hand-held sonar. On the north range, again at right angles to the current, a single target was detected at a distance of 60 feet, a plant attached to the bottom upstream on the left. Down-current on the east range, a target was detected at a distance of 35 feet, a plant attached to the bottom upstream from the point where the measurements were being made (since it was not detected at a depth of 45 feet on the east range and passed overhead outside the beam of the sonar unit). Two other targets were detected on the east range, however, at a depth of 45, 60, and 75 feet away. On the south and north ranges at the 45-foot depth, the plants "seen" were not the same plants as those on the south and north ranges at the 25-foot level, because the distances to the individual plants were different.

The pull exerted by currents on *Macrocystis* plants was measured, after severing the plants from the bottom, by attaching one end of a spring scale to the basal dichotomy of the plant and the

Table 1. Measurements of kelp plants made with hand-held sonar unit (see text for explanation).

Depths in feet at which readings were taken	Horizontal Distances in Feet from hand-held sonar to kelp plants (current velocity 0.19 meters/second)			
	South Range (across current)	West Range (up current)	North Range (across current)	South Range (down current)
7	–	–	–	25*
15	–	–	–	25*
25	20, 25, & 35	–	60	35
45	5 & 10	(no reading taken)	25 & 80	60 & 75

*This target is a current meter suspended from a skiff.

Table 2. Measurements of pull on kelp plants under different current and wave surge conditions (see text for explanation).

Size of Plant (Number of stipes)	Type of Water Motion	Inclination of Kelp Plant to Horizontal	Maximum Pull (pounds) on Spring Scale
18	light current (velocity 0.19 m/sec) and weak wave surge	45°	5.0
26	light current (velocity 0.19 m/sec) and weak wave surge	45°	8.5
38	weak current (velocity 0.10 m/sec) and moderate wave surge	90°	20.0

other end to the bottom. The first two entries in table 2 are the pull in pounds exerted by light currents and weak surge on one plant with 18 stipes and another with 26 stipes.

Wave surge, the orbital motion imparted to water particles by passing surface waves, is much stronger than near-shore currents and reaches much higher velocities. Wave surge is not continuous in one direction, but consists of an oscillatory motion first toward the shore and then away from the shore. Since orbital motion increases towards the surface, surge forces near the top of a plant are greater than at the bottom. This means that the near-surface canopy receives most of the wave energy, transmitting it through the stipes down to the holdfast attached to the bottom. The third entry in table 2 is the maximum measured value of the pull exerted on a plant with 38 stipes under conditions of moderate wave surge and weak current.

During storms, wave surge can be very destructive, exerting greater pull on plants than their structures can withstand. Severe storms can carry away the surface canopy as well as entire plants, greatly modifying the established underwater plant communities (Zobell, 1959).

The importance of surge direction, which is generally normal to the shore because of the refraction towards shore of waves entering shallow water, is indicated in the orientation of the *Macrocystis* plants themselves. In the dense kelp that was studied, the primary dichotomy of 12 out of 13 plants was oriented at right angles to the direction of wave surge.

Although the effects of currents and wave surge are greatest in shallow water near shore, water movements occur at much greater depths, affecting the plants there as well. One of us (Clarke) observed circular areas of lighter colored sand around isolated plants of *Agarum fimbriatum* at depths of 38 to 40 meters, where the sand is disturbed by the sweeping of the long flat frond in response to currents around the axis of the plant's point of attachment.

V. CONCLUSIONS

The findings reported in this paper emphasize the mixed biota of the Southern California Islands, with respect to the biogeographic break at Point Conception. Animals in the intertidal and immediate subtidal zones down to a depth of eight meters, both on the mainland and throughout the islands, are only slightly affected by this break, probably because of the extreme environmental conditions encountered in these zones. Plants at the lower limits of vegetation and uppermost intertidal also seem to be unaffected by this barrier. It is only in the broad belt of plant and animal communities in the intermediate depths that marked differences are found. Some unique features of the subtidal vegetation of these intermediate depths are apparently adaptations to water movement.

The subtidal communities found on the islands and reflecting the complicated circulation offshore should, with further investigation, help in understanding the biogeographic barrier at Point Conception. From analyses of the organisms making up the subtidal communities, the barrier seems to be more effective in preventing southern forms from spreading north than it is in preventing northern forms from spreading south. The low number of marine endemics reported here seems to be in agreement with the findings of the terrestrial ecologists and is probably attributable to the ease with which marine forms can be transported during their pelagic stages.

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APPENDIX

1. –Northern species, unreported south of Point Conception.

   Algae - *Macrocystis integrifolia, Postelsia palmaeformis, Lessoniopsis littoralis, Nereocystis leutkeana, Egregia menziesii, Dyctoneurum californicum, Rhodomela larix, Spongomorpha coalita.*

   Fish - *Spirinchus starksi, Sebastodes melanops, Hypomesus pretiosus, Hippoglossus stenolepis.*

   Crustaceans - *Spirontocaris macrophthalma, Crangon munita, C. variabilis, Callianassa goniophthalma, Pagurus tanneri, P. setosus, Parapagurus mertensii.*

   Miscellaneous Invertebrates - *Cryptochiton stelleri, Parastichopus californicus.*

2. –Northern species, rare south of Point Conception.

   Fish - *Notorynchus maculatum, Cetorhinus maximus, Raja binoculata, Isopsetta isolepis, Lepidopsetta bilineata, Hexagrammos decagrammus, H. superciliosus, Cebidichthys violaceus, Xiphister mucosus.*

   Crustaceans - *Cryptolithodes sitchensis.*

3. –Northern species, uncommon south of Point Conception.

   Fish - *Psettichthys melanostictus, Platichthys stellatus, Hypsurus caryi, Embiotoca lateralis.*

   Crustaceans - *Crangon spinosissima.*

4. –Southern species, uncommon north of Point Conception.

   Fish - *Mustelus californicus, Prionace glauca, Squatina californica, Paralabrax clathratus, P. nebulifer, Leuresthes tenuis, Sphyraena argentea, Sarda chiliensis, Seriphus politus, Caulolatilus princeps.*

5. –Southern species, rare north of Point Conception.

Fish - *Heterodonius francisci, Cephaloscyllium uter, Platyrhinoidis triseriata, Urolophus halleri, Albula vulpes, Anchoa compressa, Strongylura exilis, Synodus lucioceps, Symphurus atricauda, Stereolepis gigas, Seriola dorsalis, Thunnus thynnus, Xiphias gladius, Umbrina roncador, Pimelometopon pulchrum, Medialuna californiensis, Girella nigricans.*

Crustaceans - *Panulirus interruptus, Planes minutus.*

6. –Southern species, unreported north of Point Conception.

Algae - *Chaetomorpha torta, Codium cuneatum, Coilodesme rigida, Desmarestia tabacoides, Dictyota flabellata, Dictyopteris zonarioides, Egregia laevigata, Eisenia arborea, Halidrys dioica, Macrocystis pyrifera, Pachydictyon coriaceum, Pelagophycus porra, Sargassum agardhianum, Taonia lennebackerae, Zonaria farlowii, Acrosorium uncinatum, Amphiroa zonata, Binghamia forkii, Botryocladia neushulii, Branchioglossum undulatum, Carpopeltis bushiae, Chondria nidifica, C. californica, Corallina gracilis, Cryptonemia angustata, Drouetia peltata, Gelidium nudifrons, Gigartina binghamiae, G. serrata, Gracilaria cunninghamii, Laurencia diegoensis, L. subopposita, Lithothamnium giganteum, Myriogramme caespitosa, Phyllophora clevelandii, Pogonophorella californica, Prionitis cornea, Pterochondria* pygmaea, *Pterocladia* pyramidale, *Rhodymenia arborescens, R. palmettiformis, Sciadophycus stellatus, Scinaea johnstoniae.*

Fish - *Gymnura marmorata, Anchoa delicatissima, Cetengraulis mysticetus, Cypselurus californicus, Gymnothorax mordax, Citharichthys xanthostigma, Hippoglossina stomata, Pleuronichthys ritteri, Paralabrax maculatofasciatus, Mugil cephalus, Makaira audax, Anisotremus davidsoni, Roncador stearnsi, Cheilotrema saturnum, Menticirrhus undulatus, Chromis punctipinnis, Hypsypops rubicunda, Scorpaena guttata, Porichthys myriaster.*

Crustaceans - *Pasiphaea emarginata, P. corteziana, Palaemon ritteri, Palaemonetes hiltoni, Urocaris infraspinis, Hyppolysmata californica, Spirontocaris lagunae, Alpheus barbara, A. californiensis, Synalpheus lockingtoni, Betaeus longidactylus, Crangon holmesi, Callianassa affinis, Paguristes parvus, Pylopagurus holmesi, Parlithodes californiensis, Munida hispida, Munidopsis histrix, M. aspera, Lepidops myops, Pachycheles holosericus, Cyclodorripe plana, Anasimus spinosus, Epialtus nuttalii, E. bituberculatus, Pugettia dalli, Pelia tumida, P. clausa, Cancer amphioetus, C. anthonyi, Callinectes bellicosus, Cycloxanthops rugosus, Lophopanopeus frontalis, L. lockingtoni, Xanthias latimanus, Pilumnus spinohirsutus, Heteractaea lunata, Speocarcinus californiensis, Fabia lowei, Pinnixa barnharti, Parapinnixa affinis, Grapsodius eximius, Uca crenulata, Metamysidopsis elongata.*

Miscellaneous Invertebrates - *Renilla kollikeri, Lytechinus anamesus.*

7. –Insular endemic species.

Algae - *Egregia laevigata* f. *insularis, Pelagophycus giganteus.*

Fish - *Cymatogaster gracilis.*

Crustacea - *Pontonia californiensis, Periclimenes tenuipes, Spirontocaris brachydactyla, Nectocrangon californiensis, Pinnixa tomentosa, P. hiatus.*