

ZONATION, SPECIES DIVERSITY,
AND REDEVELOPMENT IN THE ROCKY
INTERTIDAL NEAR TRINIDAD, NORTHERN CALIFORNIA

by

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INTRODUCTION

This paper presents the results of a three-year, seven-month field study on the interrelationships among ecological factors, species diversity, and the redevelopment of rocky intertidal zones near Trinidad, northern California.

Zonation

Rocky intertidal zones are tidal intervals associated with a single dominant species or characteristic group of species and have been studied as early as 1812 when Wahlenberg described the distribution of algae off the coast of Norway (Gislen, 1930). Since then terms such as associations, communities, fasciations, formations, groupings, and habitats have been used to describe zones.

Early investigators commonly determined zones solely from observations of the most conspicuous sessile species. Other researchers, who scraped intertidal rocks to examine all the organisms present, still relied on the dominant species to establish zones. Such studies have been made world-wide and many are discussed in the literature reviews of Gislen (1930), Chapman (1946), Doty (1957), Southward (1958), Zenkevitch (1963), Lewis (1964), Glynn (1966), and Stephenson and Stephenson (1972).

Researchers have made similar investigations along the west coast of North America: on Kodiak Island, Alaska (Nybakken, 1969); on Vancouver Island, British Columbia (Scagel, 1961; Stephenson and Stephenson, 1961a, 1961b, and 1972; Widdowson, 1965; and Druehl, 1967); in Puget Sound, Washington (Muenscher, 1915, 1916; Shelford and Towler, 1925; Shelford, 1930; Towler, 1930; Shelford, et al., 1935; Rigg and Miller, 1949; and Dayton, 1971); in Brookings, Oregon (Doty, 1946); near Pacific Grove, California (Hewatt, 1937; Gislen, 1943, 1944; Doty, 1946; and Stephenson and Stephenson, 1972); between Pacific Grove and Tijuana, Mexico (Gislen, 1943, 1944); and near La Jolla, California (Shelford, et al., 1935; Gislen, 1943, 1944; and Stephenson and Stephenson, 1972). Most of these studies were conducted in the vicinities of Vancouver Island - Puget Sound, Pacific Grove, and La Jolla. Comparable studies have not been found in the literature concerning the rocky intertidal beaches in the less populated area of northern California, from Tomales Bay to the Oregon border.

With the recent development of computers and numerical methods to analyze large quantities of data, zones now can be determined from analysis of all organisms present, rather than just the dominant species. Classification or cluster analysis is such a technique that has been used in taxonomy, evolution, and ecology, in which units are grouped together based on the similarity of their species compositions.

Similarity analysis, using all species present, apparently has not been used previously to form zones in the rocky intertidal although very similar studies have been made to indicate its feasibility. Wulff and Webb (1969) did use this method to form zones based solely on the macroscopic algae on wooden pilings in Gloucester Point, Virginia. Glynn (1966) found that similarity analysis of samples taken strictly from the Endocladia muricata-Balanus glandula association in Monterey, California were grouped into low, mid, and high quadrats within that zone. Field and McFarlane (1968) applied similarity analysis to samples taken from the balanoid zone exposed to differential wave action in False Bay, South Africa. Their samples were grouped according to the amount of wave exposure.

Redevelopment

Studies on the redevelopment of rocky intertidal areas from either scraped or new substrates often are concerned as to whether or not succession occurs. Succession, as summarized from Odum (1963) and recognized in this paper is 1) the sequential series of stages (seres), which 2) leads to a more stable stage (climax), and 3) involves modifications of the environment by earlier stages for the establishment of later forms.

Early researchers have applied the term succession to stages leading to a climax condition in the development of rocky intertidal

zones without considering Odum's third and critical factor. Examples of such studies are the short term investigations in La Jolla, California by Wilson (1925) and at Friday Harbor, Washington by Pierron and Huang (1926). Other researchers, such as Hewatt (1935) who followed redevelopment of a scraped Mytilus californianus zone in Monterey, California for three years, stated that some of the earliest inhabitants are essential to the seating of later forms, but did not provide evidence for this critical aspect of succession.

In contrast to those who believe that succession does occur in the rocky intertidal, Shelford (1930), on the basis of his own investigations as well as those by Wilson (1925) and Pierron and Huang (1926), stated that "there is development but probably little or no succession in the growth of the intertidal communities on rock." In support of Shelford's theory, alternative mechanisms have been proposed to explain the appearance of stages in the redevelopment of rocky intertidal zones. Kitching (1937), Bokenham (1938), and Northcraft (1948) discussed recolonization of intertidal algae in terms of differential rates of growth. Rees (1940) suggested that species comprising early stages of redevelopment were in the plankton as larvae during much of the year and were able to settle as soon as new or denuded substrates were available for colonization. Connell (1972) recently summarized that the reasons for the orderly sequence of recolonization in the rocky intertidal are the differences in the length of breeding seasons, motility of planktonic stages,

rates of growth after settlement, and ultimate size reached by species, rather than successive modifications of the environment by the organisms themselves.

Species Diversity

Species diversity, according to Margelef (1958), Lloyd and Ghelardi (1964), and Pielou (1966), as cited by Hulbert (1971) and adopted in this paper, is a numerical value which takes into account both the number of species (richness, variety) in an area as well as the relative abundance of these species (equitability). Diversity values increase with greater richness and/or equitability. Maximum diversity occurs when there are equal numbers of all species present. In contrast, if all organisms belong to the same species, diversity is zero.

Diversity values have been related to environmental conditions. Areas of low diversity according to Sanders (1969) are characterized by physical conditions which fluctuate widely and are not rigidly predictable; the organisms present are exposed to severe physiological stresses and/or new environments. Such areas are termed "physically controlled." In contrast, regions of high diversity which Sanders (1969) described as "biologically accommodated" are associated with physical conditions that are more constant and are less stressful physiologically.

In the rocky intertidal, physiological stresses due to aerial exposure probably are important factors controlling species diversity. Working on four sides of a cement piling in Southern California, Smith and Emerson (1971) reported the lowest diversities at the highest tidal elevations (physically controlled regions) due to greater aerial exposure which increased the physiological stresses associated with desiccation. Lower elevations (biologically controlled areas) with less aerial exposure had higher measures of species diversity. In high intertidal areas at several localities in California, Risk (1971) recorded higher diversities with greater substrate rugosity. Possibly, organisms on more rugose substrates are under less physiological stress from aerial exposure since the habitat retains moisture better than smooth surfaces.

Purpose

The purpose of this study was to investigate interrelationships among environmental factors, species diversity, and the redevelopment of rocky intertidal zones along seaward and landward transects near Trinidad in northern California. The following are discussed: 1) zones of visibly dominant species as compared to zones numerically determined from all organisms collected; 2) tidal elevations and other factors which might cause breaks between zones; 3) stages, causal factors, and an estimated time of redevelopment for each

zone; 4) natural changes in control areas; and 5) a proposed model for species diversity with space (zonation) and time (redevelopment).

MATERIALS AND METHODS

The study site chosen was a twelve-foot high, basic igneous rock, located on a sandy beach just south of Luffenholz County Park and two miles below the town of Trinidad in Humboldt County, northern California (Fig. 1). This outcropping (Plate 1) supported visible zones typical of semi-exposed, stable, rocky intertidal substrates as described by Ricketts, et al. (1968).

In June, 1968 four transects were established. In order to investigate possible effects of wave action on zonation and redevelopment, two seaward transects, a control and a test, were established on the west side of the rock where they were more exposed to wave fronts than the two landward transects, also a control and a test, on the protected east side. Each transect extended from the top to the bottom of the rock (Fig. 2) and was divided into 20 contiguous quadrats, 10 cm wide and 20 cm long. For each of the 40 test quadrats there was an adjacent control quadrat with the same tidal height and wave exposure. The seaward and landward transects had similar profiles except for a 60 cm long horizontal ledge between samples S7 and S8 (Fig. 2).

Two methods were used to determine zones. One method established zones by grouping those contiguous quadrats, along the

test transects, that were visually dominated by the same species or group of species. The other method established zones by cluster analysis of all organisms collected along both test transects. Collections were made during the summer of 1968, by scraping each quadrat (also referred to as site or sample) along the seaward and landward test transects with a hammer and chisel. Organisms within or touching the inside edge of a 20 cm by 10 cm metal quadrat were removed from the rock, placed in plastic bags, and fixed with 10 per cent formalin in sea water. These specimens later were sorted into major taxa under 10x magnification, identified, and counted.

A study of the redevelopment of each zone was not started until October 3, 1968 when organisms on the two test transects again were removed with a hammer, chisel, and metal brushes so that recolonization of the denuded quadrats could be monitored periodically during the ensuing 39 months. Only the macroscopically visible and sessile or sedentary forms were recorded. A study of the obscure and errant forms would have provided more information but would have involved considerably more sampling time. For the first 12 surveys, each test quadrat was checked qualitatively and quantitatively in the field. Invertebrates were counted directly, except for barnacles which were estimated by taking ten arbitrary subsamples (all barnacles within the 3.3 cm^2 field of a 3x hand lens) per quadrat. For each barnacle species, the sum of the ten subsamples was

multiplied by six to give barnacle density per 200 cm^2 , the area of each quadrat. Percentage cover of algal species was estimated in each quadrat.

By the 12th visit heavy growth of organisms on the transects made direct counting of organisms difficult. Therefore, on January 21, 1972, during the 13th and final survey, photographs were taken of all test quadrats. Organisms were recorded qualitatively in the field and later quantitatively with a method similar to that of Connell (1970) and Dayton (1971). The procedure consisted of marking 200 random points (of a possible 1000 points) on a plastic sheet with a rapidograph pen and placing the sheet over a two-inch by four-inch photograph of each quadrat. Percentage cover was calculated by dividing the number of points lying over each species by the total number of possible points (200) per quadrat and then multiplying this fraction by 100. Dayton (1971) found 1 - 4 per cent differences on repeated measurements of large organisms with 100 random dots on the same photograph.

The control (unscraped) transects were sampled during the final survey qualitatively and quantitatively in the manner described above for the test transects. An index of redevelopment was calculated at the end of the study by comparing the biota of each test quadrat to the corresponding control or unscraped quadrat.

The relationship between measured elevations on the rock and certain levels of the tides was studied to investigate possible factors

controlling zonation. Tidal levels between quadrats were measured by taking a series of readings with a surveyor's level and stadia rod from a U. S. Geological Survey bench mark, number 76 (Fig. 1). The elevation of this bench mark was based on tidal readings in Trinidad Bay, a small protected harbor two miles north of the study site. Since wave activity on the protected east side of the rock is comparable to Trinidad Bay, measured elevations along the landward transect should be accurate. In contrast, measured elevations for the wave-exposed seaward quadrats are not accurate unless a wave factor is included.

Trinidad, like most of the west coast of North America, is exposed to a mixed tidal cycle (Doty, 1957) in which two unequal low tides alternate daily with two unequal high tides. Mean yearly levels of these four daily tidal levels (higher high, lower high, higher low, and lower low) were calculated from predicted tidal levels in Trinidad Bay (U. S. Department of Commerce, 1971) and compared to actual measured tidal elevations on the rock. This comparison was made only on the landward transect, which was comparable in terms of wave action to the site, Trinidad Harbor, where both the elevation for the bench mark and the predicted tidal levels were derived.

ANALYSIS OF DATA

The procedure for cluster analysis applied in this paper is similar to the method used by Field and McFarlane (1968) in their study of rocky intertidal areas in South Africa and involved three steps (Fig. 3). Cluster analysis was applied separately to two forms of the data, presence-absence (algae and invertebrates) and densities (invertebrates) per quadrat.

Step 1. Sample information, species lists and quantitative data, were gathered in the formation of a species-sample matrix.

Step 2. A coefficient of similarity for every combination of two samples was calculated. For presence-absence data, Czekanowski's coefficient of similarity (1913), designated here as S_{CZ} , was determined using the notation of Stephenson (1972) in which:

$$S_{CZ} = \frac{2a}{2a+b+c} \quad (\text{formula 1})$$

where:

a = number of co-occurrences
(each species in both
samples),

b = presence of species in site
one but not site two, and

c = presence of species in site
two but not site one.

This index is mathematically equivalent to the coefficient of Dice (1945) according to Hall (1969).

Similarly, coefficients for numerical data were calculated using the formula cited by Bray and Curtis (1957), designated here as S_{bc} , in which:

$$S_{bc} = \frac{2w}{a+b} \quad (\text{formula 2})$$

where:

a = the sume of the quantitative measures of plants (and/or animals) in one stand (sample),

b = the similar sum for a second stand,

w = the sum of the lesser value for only those species which are in common between the two stands.

Formula (2), according to Bray and Curtis (1957) who cited Osting (1956), was derived by Motyka, et al. (1950), and Kulczynski (1927). The same index (S_{bc}) has been also termed a "Czekanowski coefficient" (Field and McFarlane, 1968; Day, et al., 1971; Cimberg, et al., 1973; and Stephenson and Williams, 1971) since the formula (2) is a quantitative extension of the original Czakanowski coefficient (1913) according to Stephenson (1972). Finally, Smith (1973) used what he termed a Bray-Curtis index, which is a reciprocal of the

similarity index used in this paper and is therefore a "dissimilarity" measure.

When raw density values are used in formula (2), numerous but small organisms, such as barnacles, can overwhelm the presence of seastars and other larger but less numerous animals. Therefore, density values were transformed by taking the logarithm of each number plus one ($\log(n+1)$) in formula (2). Values of both S_{CZ} and S_{bc} can range from zero, indicating no similarity, to one indicating perfect similarity.

Step 3. Samples were clustered into groupings by the pair group method of group average linkage (Sokal and Sneath, 1963) in the formation of a dendrogram, a hierarchy of coefficients between sites using the following series of operations: (a) Similarity coefficients are arranged in an original sample-sample ("Q") matrix; (b) the two quadrats with the highest coefficient in the original Q matrix were joined to form the first cluster; (c) the original matrix was then recalculated by replacing all coefficients involving the clustered samples with new values determined by averaging the coefficients between samples clustered and each of the other samples. Operations (b) and (c) were repeated consecutively until all samples were linked in the dendrogram.

An index of species diversity for invertebrates was computed for each quadrat scraped in June, 1968. The index of Brillouin "H" (Brillouin, 1960) was applied since all invertebrates collected along both test transects were considered (Pielou, 1966a). This value was determined by:

$$H = \frac{1}{N} \log \left(\frac{n}{n_1! + n_2! + n_3! \dots n_s!} \right) \quad (\text{formula 3})$$

where: N = the total number of specimens in the sample,

 n = the number of specimens per species, and

 s = the number of species.

A mean species diversity index per quadrat was determined for each numerically determined zone and a simple regression analysis was run between diversity and tidal elevation of each quadrat.

An index for estimating redevelopment of each quadrat was calculated, similar to the procedure used by Huhta (1971) in a study of spider succession. The method used was based on the idea that a coefficient of similarity between the scraped test quadrat and its corresponding control site would indicate the extent of redevelopment. In the present study the index of redevelopment was the Bray-Curtis similarity coefficient S_{bc} (formula 2) using percentage cover of species from the January, 1972 photographs.

A test quadrat with a S_{bc} of 1.00 or 100 per cent similarity to its respective control site would be considered completely

redeveloped. A mean index of redevelopment for each zone was calculated by averaging the indices of all test quadrats in that zone.

Computer programs for similarity analysis (CLASS) and the species diversity index of Brillouin (SPDIV) were written in PL-1 computer language. Regression analysis for diversity was written in Fortran Four. All programs were run on an IBM (155) computer at the University Computer Center, University of Southern California.

RESULTS

Visual Zones

Zones_v* of visually dominant species or groups of species were determined before the transects were scraped (Fig. 4). The following four zones (I - IV) were recognized on the seaward transect and were named after the visibly dominant species: Zone_v I - Collisella (Acmaea) digitalis; Zone_v II - Balanus glandula; Zone_v III - Mytilus californianus; and Zone_v IV - Chthamalus dalli. The following three zones were likewise identified on the landward transect: Zone_v I - Collisella digitalis; Zone_v II - Balanus glandula; and Zone_v III - Balanus cariosus.

Zones_v I on the seaward and landward transects (Fig. 4) were visibly similar, both dominated by Collisella digitalis. Zones_v II on the seaward and landward transects, both dominated by Balanus glandula, differed in their dominant alga (Endocladia muricata versus Pelvetiopsis limitata, respectively). Zone_v III on the seaward transect, dominated by Mytilus californianus, was not visibly

* "v" refers to visually determined zones as opposed to numerically determined Zones_n (subscript "n") and visibly-numerically determined Zones_{vn} (subscript "vn") which are discussed later.

like Zone_v III on the landward transect, dominated by Balanus cariosus. Zone_v IV, dominated by Chthamalus dalli, was found only on the seaward transect; Balanus cariosus had extended down to the sand on the landward side.

Numerically Determined Zones

Zones were determined by similarity analysis of all organisms collected from the scraped test quadrats. These organisms (including 47,999 invertebrate specimens) were identified (65 invertebrate and 12 algal species) and placed in a species-sample matrix (Tables 1, 2). Two separate dendrograms (Figs. 5, 6), one from presence-absence data and the other using logarithmically transformed densities, were generated from their respective original Q matrices.

The two dendrograms provided similar results. Groupings of quadrats which occupied tidal intervals one below the other were recognized as zones. In each dendrogram four zones were identified. Each zone from the presence-absence dendrogram was composed of the same quadrats and occupied the same tidal intervals as the respective zone from the abundance dendrogram.

Quadrats within numerically determined Zones_n II, III, and IV were linked at similarity levels greater than 0.50 (Fig. 5). Some quadrats in Zone_n I located in the highest portion of each transect

were linked below the 0.50 level, probably due to the high variability in barnacle abundance.

The dendrogram from logarithmically transformed densities (Fig. 5) separated seaward from landward quadrats within Zone_n III. Analysis of presence-absence data (Fig. 6) did not segregate these quadrats, indicating that seaward and landward Zone_v III quadrats had similar species present although their abundances differed.

Stratification

In the process of collecting the samples, a stratification of organisms was observed in seaward quadrats S17 and S18 of Zone_v III (Fig. 4). The canopy layer consisted of large Mytilus californianus (2.5 cm or greater in length) on which Balanus glandula, B. cariosus, Chthamalus dalli, Pollicipes polymerus, and Anthopleura elegantissima were attached. The three understory strata, from outside to inside, were composed of: 1) small M. californianus (less than 2.5 cm); 2) byssal threads of Mytilus californianus and tubicolous polychaetes (Schizobranchia sp. and Pseudopotomilla intermedia) which provided a habitat for many errant invertebrates; and 3) the large barnacle, Balanus cariosus, that was attached to the surface of the rock and whose mural (outer) plates had fused with adjacent specimens.

Such stratification was not found in Zone_n III along the landward transect. Instead, small Mytilus californianus and the other

invertebrates species found in Zone_v III on the seaward transect were located between the specimens of Balanus cariosus in Zone_v III on the landward transect.

Breaks Between Zones

The tidal heights at the breaks between visual zones and numerical clusters on the landward transect were measured and were found to correspond closely to the mean daily tidal elevations calculated from predicted tides at Trinidad Bay (Fig. 7).

Species Diversity

The diversity index of each quadrat (Table 3) was plotted as a function of tidal elevation and a regression line was computed (Fig. 8). The slope of this line ($b = -7.7$) indicates a significant inverse correlation of diversity with tidal height ($p > 95$, one-tailed t Test) when compared to a slope of no correlation ($b = 0$). This analysis indicates that diversity increased as tidal elevation decreased. The lowest quadrat, however, indicated the opposite trend; diversity decreased as tidal elevation decreased.

Pisaster Predation

By the end of the redevelopment study in January, 1972, Zone_v III (Mytilus californianus) on the control seaward transect and Zone_v III (Balanus cariosus) on the landward control transect

were no longer present and both were replaced by zones visually dominated by Chthamalus dalli (Fig. 4).

Field observations and photographs (Plates, 1, 2, 3) indicated the following events had occurred. Heavy predation by the seastars, Pisaster ochraceus, increased after July, 1969 beginning at the lowest tidal levels at which B. cariosus and M. californianus occurred. Pisaster, as it moved to progressively higher elevations on the seaward side, fed on the canopy M. californianus leaving the understory B. cariosus. These seastars then returned to the lowest tidal level of the B. cariosus and consumed these barnacles at progressively higher elevations exposing bare rock. On the landward transects with less stratified quadrats, B. cariosus and M. californianus were consumed at the same time. By the final survey the majority of the B. cariosus and M. californianus on the transects were found only in the Balanus glandula Zones_v.

The areas denuded by Pisaster were recolonized by Collisella sp. from adjacent areas of the rock and later by C. dalli and B. glandula from planktonic larvae.

Redevelopment of Zones

The results of the 13 surveys of the redevelopment study are presented diagrammatically for each quadrat on the seaward transect (Table 5) and landward transect (Table 6) and are summarized for each visible zone. The first organisms observed in the

redevelopment of Zone_v I on both transects were the periwinkle, Littorina scutulata, and the limpet, Collisella digitalis, recorded at relatively higher and lower elevations, respectively, during all surveys. By the second month, the barnacles, Chthamalus dalli and Balanus glandula, had settled. At the same time the alga, Pelvetiopsis limitata, was first found on the landward transect. This species grew slowly and continuously throughout the remainder of the study.

With the exception of motile mites and the lined shore crab, Pachygrapsus crassipes, no other species was observed during the redevelopment study of this zone. There were no visible differences between test and control transects, indicating that this zone_v had redeveloped completely.

In redevelopment of Zone_v II on both transects, Collisella digitalis and Collisella sp. were noted at high and low levels, respectively, throughout the study. Chthamalus dalli, observed during the second week, was initially the most abundant barnacle on both transects. Balanus glandula settled by the fourth week and subsequently became more numerous than Chthamalus on the landward side. This change in dominance (density) occurred first at the lowest quadrats within the zone (L16) in January, 1969 and in time progressed to higher elevations. In January, 1972, B. glandula was more abundant than C. dalli in all quadrats of Zone_v II on the landward test transect.

The first macroscopic alga observed was Ulva sp., recorded during the second week on both transects. With additional settlement and growth, Ulva cover in the lowest landward quadrat (L16) increased to 100 per cent by November, 1968 and remained greater than 25 per cent until March, 1969, at which time thalli began to bleach and die presumably because the low tides now occurred in the morning and exposed the eastward (landward) transect to the sun. Percentage cover of Ulva decreased even though some of the remaining thalli continued to grow until July, 1969.

The red alga, Porphyra perforata, was first observed on the landward side in February, 1969 and on the seaward transect in April, 1969 and grew rapidly after settlement. Following the period of Ulva bleaching Porphyra was the most abundant alga (percentage of cover) from May to June, 1969 on the landward quadrats. Neither Ulva nor Porphyra was observed on the test transect during the final survey. Two other species of red algae, Gigartina agardhii and Endocladia muricata, were recorded initially during the first winter (November, 1968 - January, 1969). These species grew at a slower rate than Ulva and Porphyra but were present throughout the remainder of the study.

Balanus glandula was extremely dense in the lowest landward quadrats (L15, L16). Crowding resulted in one or both of the following phenomena: 1) elongated specimens, tapered at their

bases and 2) mutual crushing of adjacent organisms. Most of these crowded specimens were not present by the next survey; only their basal plates remained.

A small number of Mytilus californianus and Pollicipes polymerus were initially observed in rock crevices in January and March, 1969, respectively. Balanus cariosus was first noted in March, 1970. By the last survey portions of the lowest seaward quadrat (S14) consisted of B. cariosus, attached on the rock, covered by Endocladia muricata with M. californianus growing amongst the basal portions of the thalli. The mean index of redevelopment for all quadrats of Zone_v II (seaward and landward) was 0.68 (Table 3).

Zones_v III on both control transects were destroyed by Pisaster predation, which also affected redevelopment of the test quadrats. The results of the redevelopment of these zones are presented below, followed by a hypothetical sequence of events predicting the development of Zones_v III (seaward and landward) which is proposed on the basis of quadrats not preyed upon by seastars.

Both Collisella digitalis and Collisella sp. were observed in Zone_v III during the first survey. By the second week Chthamalus dalli had settled and was the most abundant species on both transects. Balanus glandula was the most abundant organism on the landward quadrats in November, 1968 and on the seaward side in June, 1969. Ulva sp., the initially dominant alga (percentage cover), was first

observed in November, 1968. Porphyra perforata, first recorded in February, 1969, was the most abundant seaweed (percentage cover) one month later. Gigartina agardhii and Endocladia muricata first were noted in January, 1969 and March, 1970, respectively. These algae grew more slowly than either Ulva or Porphyra, but were more abundant than the faster growing species after the first year.

Between June, 1969 and the end of the study, January, 1972, changes in redevelopment occurred in the test quadrats due to Pisaster predation. Seastar predation on Balanus glandula and the subsequent larval settlement of Chthamalus dalli reversed the relative abundance of barnacles in favor of C. dalli in the test quadrats. These changes occurred in the lower quadrats initially and progressed to higher elevations.

A proposed scheme of redevelopment of Zone_v III without the heavy predation factor is presented from observations of quadrat S14, the sample on both transects in which M. californianus and B. cariosus were still present at the end of the redevelopment study. The first organisms to colonize the zone were Collisella digitalis and Collisella sp., which moved in from undisturbed areas of the rock, followed by the settlements of C. dalli and later of B. glandula. B. cariosus was observed initially in March, 1970 and was dominant (percentage cover) over B. glandula in January, 1972. Mussels were found among the tufts of Endocladia at the end of the

redevelopment study. The coefficient of redevelopment (0.35) for this quadrat (S14) (Table 3) represents the index of redevelopment for all the quadrats of Zone_v III (seaward and landward).

The first organisms observed in the redevelopment of Zone_v IV were Collisella sp. and Chthamalus dalli, initially recorded during the first and second surveys, respectively. B. glandula juveniles were not observed until the fourth visit, one month after juveniles were noted in higher zones. C. dalli was the most abundant organism during the remainder of the study. The mean coefficient of redevelopment for the two quadrats of Zone_v IV was 0.95 (Table 3), with no visible differences between the control and test quadrats.

DISCUSSION

Visible Zones

The zones of visually dominant species (Fig. 4) are similar, in respect to dominants and relative vertical tidal position, to zones described at other localities along the west coast of North America (Table 4). These same visually determined zones occur on physically stable rocky substrates from Alaska to Point Conception due to the wide latitudinal distribution of the component species (Dayton, 1971). Similar zones are also found from Point Conception south to San Diego even though some organisms are replaced by ecologically similar species, for instance, Chthamalus dalli by C. fissus (Ricketts, et al., 1968).

Numerical Zones

Numerical analysis in general gave similar results to visually determined zones (Fig. 4). Quadrats comprising each of the four numerically determined zones are the same quadrats which formed each of the four visually distinguished zones. The quadrats of visibly similar Zone_v I on the landward transects and Zone_v I on the seaward transects together comprise Zone_n I and are now referred to as Zone_{vn} I, the Collisella digitalis Zone. The "vn" refers to

visually and numerically determined zones. Ligia occidentalis and Littorina planaxis, often found in the highest zone (Ricketts, et al., 1968), were not observed in Zone_{vn} I. The rock probably did not extend high enough to provide these species with the needed refuge from waves during very high tides and/or storms. Additionally, since the study site was isolated from other rocky areas by sand, colonization by adult migration appears difficult.

Sites comprising seaward and landward Zones_v II, which differed in their respective dominant algae, were all grouped together by numerical analysis into Zone_n II, indicating similar species compositions (presence and abundance). These quadrats together now are referred to as Zone_{vn} II, the Balanus glandula Zone.

The degree of similarity between seaward and landward Zones_v III is dependent on the method of analysis used. First, seaward Zone_v III, dominated by Mytilus californianus, was distinctly different visually from landward Zone_v III, the Balanus cariosus Zone_v. Second, cluster analysis using presence-absence of species indicated that seaward and landward Zones_v III had the same species present although the third method, cluster analysis using densities, demonstrated that abundances of these species differed on the two transects.

The resulting discrepancies in the analysis of Zones_v III (seaward and landward) apparently are due to the size of Mytilus

californianus, which in turn modified the abundance and stratification of other organisms within these visible zones. The four quadrats of landward Zone_v III contained more but smaller mussels (only one of the 215 specimens was greater than 2.5 cm in length, Table 2) than the four seaward Zone_v III samples (58 of 201, Table 1). The smaller mussels on the landward side (along with the other invertebrates) were found between specimens of Balanus cariosus and, therefore, were not obvious before the quadrats were scraped. Large mussels on the seaward sites covered B. cariosus and were conspicuous. Beneath and because of the large mussels, water motion is reduced. Therefore, an enlarged crevice area (Connell, 1972) was available for larger and more infauna which are otherwise restricted to the spaces between B. cariosus on the landward transect. Additionally, the large mussel shells on the seaward side provided a substrate for the attachment and growth of barnacles and anemones. Despite the differences in abundance and stratification of organisms on the two transects, the quadrats of both seaward Zone_v III and landward Zone_v III are considered together as Zone_{vn} III, the Mytilus californianus - Balanus cariosus Zone, since the same species were present.

The presence of understory organisms beneath Mytilus californianus was noted also on Turn Island in Washington Sound, Washington by Paris (1960). Stratification of intertidal organisms within a zone also has been observed in Matsushima Bay, Japan by

Hoshiai (1961) and termed a "covering phenomenon." He found dead Chthamalus challengerii and Balanus amphitrite albicostatus covered by Mytilus edulis, Crassostrea gigas, or Septifer virgatus. In contrast, the barnacles at the lowest stratum on the Trinidad transect, B. cariosus, remained alive. Hoshiai's observation, that the same species of barnacles covered by bivalves later resettled on the shells of the canopy species, was also noted in Trinidad. In the New Zealand rocky intertidal, the mussel, Perna canaliculus, similarly served as a canopy cover for understory organisms (Paine, 1971).

A hypothesis, which might explain why Mytilus californianus is larger on the seaward than landward transect, involves the effect of surge (local water movements) on the amount of food available to the mussels. More water movement on the seaward side, generated by greater wave action, could provide a greater amount of food per unit time for the seaward than landward mussels to feed on. Coe and Fox (1944) also discuss the growth of M. californianus due to the abundance of food. They indicate that the amount of food changes with time (days, weeks, and even hours) due to water movement, and results in corresponding changes in mussel growth. Somewhat similarly, the proposed theory states that 1) even though the amount of food per volume of water might be the same on both sides of the rock, 2) the volume of water and hence the total amount of food per unit time which passes over the seaward side is greater than on the

landward side which 3) permits increased mussel growth on the seaward side.

The lowest strata of Zone_{vn} III on the seaward side consisted of B. cariosus which formed a solid phalanx on the rock, composed of fused mural plates of adjacent specimens. Fusion of plates also has been observed by the author among specimens of Chthamalus fissus in crowded regions of the high intertidal in Southern California. Similar intraspecific fusion of outer shells or tubes has been observed among the tubicolous polychaete, Phragmatopoma californica, and the vermetid gastropod, Serpulorbis squamigerus.

A number of infrequently recorded juvenile stages of some species (Pisaster ochraceus, Pachygrapsus crassipes, and insects) were cryptic in the understory of Zone_{vn} III. Conrad Limbaugh (Feder, 1970) reported finding P. ochraceus juveniles in Southern California only in mussel pilings at La Jolla, California. Juvenile abalones also are more cryptic than their adult stages (Ted Tutschulte and James Young, personal communications).

Numerical Zone_n IV consisted of the same quadrats (S19, S20, Figs. 5, 6) as did visible Zone_v IV on the seaward transect (Fig. 4) and is now referred to as Zone_{vn} IV, the Chthamalus Zone.

The fact that the same general pattern of zones is generated using either numerical analysis of all species collected or observations of the visual dominant species supports Ricketts, et al. (1968) who stated that "zones are not only bands of organisms along the

shore; they are also groups of biotic aggregations..." Stephenson, et al. (1972) reported similar conclusions from a benthic study; the results of their cluster analyses of all species present from Peterson's (1914) original data were similar to Peterson's own results, based on analysis of only the dominants.

Distributional Records

Three new distributional records of species on the transect were noted. The northern range of the erycinid bivalve, Lasaea subviridis, was recorded previously at Shetler Cove (Dr. James McLean, personal communication), 70 miles south of Trinidad in Humboldt County. The single specimen of the sabellariid polychaete, Phragmatopoma californica, is a northern extension from Sonoma County (Ricketts, et al., 1968). This tube-dwelling polychaete normally lives in dense clusters further south and the occurrence of a single specimen indicates that this species is near its northern limit (Olga Hartman, personal communication). The presence at the study site of Crucigera irregularis, an intertidal and benthic serpulid polychaete, is a southern range extension from Vancouver Island, British Columbia as previously reported by Berkeley and Berkeley (1952).

Breaks Between Zones

The distribution of Zones_{vn} on the landward transect corresponds closely to the mean heights of the daily mixed tidal levels

(Fig. 7). Zone_{vn} I, the Collisella digitalis Zone, was located above mean higher high water (MHHW) and, therefore, on an average day is not submerged by the higher high tides and received only spray from waves. Rigg and Miller (1949) also described a similar visually determined zone above MHHW.

Zone_{vn} II, the Balanus glandula Zone, was distributed between MHHW and mean lower high water (MLHW) and, therefore, is immersed on the average once daily. Glynn (1966) reported that the Encocladia muricata - Balanus glandula association in Monterey Bay was submerged once during each of the eight days observations were made. Zone_{vn} III, the Mytilus californianus - Balanus cariosus Zone, located below MLHW, is immersed on the average twice per day.

Small discrepancies between the measured tidal levels separating the landward zones and the mean predicted tidal levels from Trinidad Bay (Fig. 7) could be attributed to one or a combination of factors. First, a finite rather than an infinite number of quadrats were employed; the use of smaller quadrats would have provided a more precise localization of boundaries between zones. Second, the actual tidal elevation of the bench mark could have changed due to variation in sea level since the time of its establishment in 1937 (U. S. Geological Survey, Palo Alto, California, personal communication). Nomias and Huang (1972) reported that mean sea level in La Jolla changed 5.6 cm between the periods

1948 - 1957 and 1958 - 1969. Third, differences in wave forces and other hydrographic factors between Trinidad Bay and the landward side of the rock would cause differences between measured elevations of breaks between zones and calculated heights of mean elevations of the daily tidal cycle. Finally, possible error in determining tidal elevations on the rock could be attributed to the necessary number of readings made from the bench mark to the study site, a distance of one-quarter of a mile and a difference in elevation of 75 feet.

Perhaps these were not sources of significant error and another aspect of the mixed tidal cycle (mean height of maximum spring or neap tides, for example) would correspond more closely to the actual breaks between zones than the boundaries proposed.

Although the break between Zone_{vn} IV, the Chthamalus Zone, corresponds closely to MHLW, sand activity is thought to be the controlling factor. Sand not only abraded the lower portion of the transect daily but, more importantly, covered and smothered species for long periods. Sand burial denuded portions of the rock and physically served as a lower limit for the survival of Mytilus cali-fornianus. Subsequent removal of sand exposed the bare rock to re-colonization and favored the formation of a Chthamalus Zone_{vn}. This process of sand deposition and cut appeared to occur as often as once a month.

The distribution of the Chthamalus Zone (Zone_{vn} IV) is thereby a function of the extent of sand interference with Zone_{vn} III. The

greater the deposition and cut of sand at the base of the transects, the greater the width of Zone_{vn} IV and the narrower the width of Zone_{vn} III. Zone_{vn} IV was not observed on the landward side since sand was still deposited at the base of the transect. Successive periods of sand deposition and removal with decreasing amplitudes would cause the formation of additional zones at the base of the rock, due to differential times available for recolonization at each level.

Zones on the seaward transect occupied higher and wider tidal intervals than zones on the landward side (Fig. 4), apparently due to greater wave activity and a higher effective tidal height (wave action plus tidal level). Zones at higher tidal levels on the seaward transect were elevated more than lower zones, indicating that waves apparently had a greater effect at higher elevations. Similar observations were reported by Hewatt (1937), Lewis (1964), and Ricketts, et al. (1968).

The difference in elevations between breaks in zones on the seaward and landward transects is due primarily to wave action. At the level of the Zone_{vn} I - Zone_{vn} II break, the wave factor would be 2.5 ft (9.1 ft - 6.6 ft), which is comparable to the 2 ft correction figure that Johnson and Skutch (1928), Orton (1929), Colman (1933), and Moore and Kitching (1939) suggested for comparisons of wave-exposed and protected shores (Doty, 1957).

Species Diversity

Regression analysis indicates that species diversity in general increased with decreasing tidal elevation (Fig. 8). The highest intertidal area (Zone_{vn} I) is exposed for the longest time to the aerial environment and the shortest time to sea water. With less sea water immersion, less energy was available to the organisms. Additionally, greater exposure to air probably requires more energy to prevent desiccation. Under such conditions only a relatively small number of species survive, an explanation for the low values of species diversity at high elevations. Such areas would be described as physically controlled by Sanders (1969). At lower elevations (such as Zone_{vn} III) the problem of desiccation is lessened and more time was available for feeding, thus providing more energy. This region, therefore, was physiologically less harsh, allowing more species to survive and resulting in high indices of species diversity. This area would be termed biologically accommodated according to Sanders (1969).

There are some exceptions to the above generalizations. First, diversity of the lowest seaward quadrat decreased, probably due to the severe conditions created by sand abrasion and burial. This quadrat, therefore, is considered physically controlled. Second, diversity decreased with increasing stratification. The most stratified quadrats of Zone_{vn} III (S17, S18), which were the thickest part of the mussel bed, had lower diversities than

the higher quadrats (S15, S16). Although richness (number of species) was greater in the well stratified quadrats (Table 3), equitability (evenness in abundance among species) was much lower resulting in lower values of species diversity. Equitability decreased since the space afforded beneath large mussels benefited only a few species, which increased in abundance. The highest diversities on the seaward transect were not found in the most biologically accommodated areas but at the transition between biologically accommodated and physically controlled regions, at the highest quadrat of the Mytilus bed (S15) and just below the mussel zone (S19).

Pisaster Predation

Zones are not static entities. Changes in species abundance occur daily, weekly, seasonally, and at longer time intervals in a given area. Glynn (1966) described daily migrations of certain motile species in and out of the Endocladia muricata - Balanus glandula association with the ebb and flood of tides.

In the present study an extreme example of a natural fluctuation was the destruction of the Mytilus californianus - Balanus cariosus Zone_{vn} by Pisaster ochraceus predation between July, 1969 and January, 1972. This disturbance was unexpected since there were few seastars observed on the rock when the study began.

One explanation for the increase in Pisaster predation is the transfer of seastars to the rock during high tides on subtidal algal

mats carried by surge and tidal currents. This method of seastar movement across apparent sand barriers was suggested by Fager (1972) in a subtidal investigation. If such movement did take place in the present investigation, then Pisaster ochraceus should have been observed stranded in the sand at low tides more frequently, unless there was a very high rate of seastar success to either attach to the rock during flood tides or retreat back into the sea with the tidal ebb.

An alternate explanation for the heavy seastar predation is the maturation of Pisaster specimens within the Mytilus californianus Zone_v. The dense mussel zone on the seaward side is a habitat in which juvenile Pisaster occur and which also supports small bivalves serving as food for the maturing seastars. When large enough, Pisaster would move from its cryptic juvenile habitat and consume the larger M. californianus and B. cariosus. With food resources gone, the seastars would move from the area enabling the redevelopment of another mussel zone.

The preferential predation of P. ochraceus on M. californianus (see Paine, 1969; Landenberger, 1968; and Feder, 1959) and the foraging movement of the seastar to progressively higher elevations resulted in the following zonation scheme of visual dominants observed on the seaward transect in January, 1972 and noted by Paris (1960) in Washington Sound: M. californianus covered B. cariosus

at mid-intertidal elevations with B. cariosus exposed at lower tidal levels.

Damage to M. californianus populations also has been attributed to floating logs (Dayton, 1971) and storms (Hewatt, 1937; MacGinitie, 1938; Feder, 1959; Paine, 1966; Dayton, 1971; and Harger, 1967). At the study site, log damage was probably of minor importance since the pattern of mussel bed destruction was systematic, moving from lower to higher tidal elevations; log damage would have been a more random process. Storms could have assisted in ripping off clumps of mussels after Pisaster initially disturbed the byssal connections of the mussel bed (Landenberger, 1967), but wave action probably did not remove B. cariosus from the surface of the rock.

The upper limit of Pisaster predation, as noted in January, 1972, was the lowest quadrats (S14, L16) of the Balanus glandula Zone_{vn}. Exposure to desiccation is a factor limiting the upper extent of Pisaster predation (Dayton, 1971 and Mauzey, 1966) and contributes to Pisaster's time-energy budget in pursuit and consumption of prey items. This predation line also serves as the lower boundary of a refuge zone for Mytilus from Pisaster as Connell (1970) observed with B. glandula and the carnivorous snail Thais.

Redevelopment

Redevelopment of each zone involved the appearance with time

of different visibly dominant species or groups of species which compose different stages of development (Fig. 9). A presentation of these stages in redevelopment is made below, followed by a discussion of the factors determining the appearance of these stages. Finally, whether succession occurs in the redevelopment of rocky intertidal zones is discussed.

Diatoms, which formed stage one, are usually the first organisms to recolonize denuded or new surfaces in the intertidal (Hewatt, 1935; Scheer, 1945; Cirino, 1955; and Castenholz, 1967) by settling from the plankton within a few hours after the substrate is immersed (Redfield and Deevy, 1952). Diatoms probably were present in all zones, although a heavy growth was not observed since adult herbivorous gastropods, species comprising stage two, encroached from adjacent unscraped areas during the first week of the study.

Chthamalus dalli, which composed stage three, was the first sessile species to recolonize the transects. The presence of juveniles during most surveys indicated that this organism settled throughout the year at the study site. An ecologically similar species, C. fissus, was observed carrying fertilized eggs during all months of the year near Santa Barbara (Straughan, 1971). C. dalli inhabited all four zones early in development, indicating a wide vertical tolerance range. This barnacle was the smallest and

poorest competitor for primary space (physical substratum on which they attach, Dayton, 1971) of the three species of acorn barnacles studied.

The next sessile species observed, Balanus glandula, constituted stage four, and apparently did not settle throughout the year at the study site. During the first ten months of the study (October, 1968 - July, 1969) heavy spatfalls were noted only in December, 1968 and May, 1969. B. glandula was reproductive during limited portions of the year in Vancouver and La Jolla (Barnes and Barnes, 1956), in Washington and Santa Barbara (Connell, 1970), and Santa Barbara (Straughan, 1971). This species was found in all four zones, but was not as abundant as C. dalli in the lowest two zones. B. glandula was the second largest species and the second best competitor for primary space of the three acorn barnacles studied.

During redevelopment, small acorn barnacles, Balanus glandula and Chthamalus dalli, were found in all four zones. However, initial settlement of both species was heaviest within Zone_{vn}III, where diversity was the highest and conditions considered least harsh. These barnacles apparently "preferred" this level of the intertidal.

A heavy spatfall of B. glandula occurred in December, 1968 within Zone_{vn}III. The density of settled juveniles did not leave enough space for normal adult growth. These barnacles were of the same age and size and, therefore, possessed equivalent competitive

abilities. Usually intraspecific populations are of mixed sizes; the larger specimens are better competitors and as their basal diameter increased they removed smaller specimens by undercutting or crushing them. Due to the lack of space on the rock and the equivalent competitive abilities of specimens of the same size, barnacle growth was mostly vertical. These specimens were both elongate and tapered toward their attachment site to the rock. Subsequent growth caused mutual crushing and destruction of adjacent specimens. Such growth of Balanus glandula under crowded conditions also was reported by Hewatt (1937) and Paine (as cited by Dayton, 1971) and termed "hummocks" for B. balanoides, an ecologically similar species (Barnes and Barnes, 1956) by Lewis (1964). The species discussed so far constitute the major visible stages in the recolonization Zones_{vn} I and Iv.

Ulva sp. and Porphyra sp., recorded in the lowest three zones, were the initial dominant algae in this and other redevelopment studies (Bokenham, 1938; Northcraft, 1948; and Castenholz, 1967). Endocladia muricata and Gigartina agardhii grew at a slower rate than Ulva and Porphyra (also Northcraft, 1948 and Knight and Parker, 1950) but were more abundant in Zones_{vn} II and III than the latter two species after the first year. Pelvetiopsis limitata, a slow-growing brown alga, was observed initially on the landward quadrats of Zone_{vn} II in March, 1969. All the species discussed

thus far complete redevelopment of the visible dominants in Zone_{vn} II.

Stage five, consisting of Balanus cariosus, was not recorded in this study until eighteen months after the transects were scraped. This species probably has a narrow vertical tolerance range and was recorded only in Zones_{vn} II, III, and IV. Dayton (1971) also considered settlement of this barnacle to be "very patchy in time (settled only in late summer and autumn) and space." This species was the largest and the best competitor for primary space of the three species of acorn barnacles studied.

Mytilus californianus, which dominated stage six, was recorded during the second month of the study (October, 1968). The period of settlement during the year could not be determined because of the cryptic nature of the juveniles. M. californianus was found to settle throughout the year in studies conducted in the San Francisco area (Whedon, 1936), near Tomales Bay (Bartlett, 1972), and at Santa Catalina Island (Bill Jessee, personal communication). This species probably has a narrow vertical intertidal range and was found only in Zones_{vn} II and III. Mytilus is a poor competitor for primary space and usually occupies secondary space (above other organisms, Dayton, 1971).

A description of the completion of Zone_{vn} III redevelopment is based on observations of 1) the mussel zone in 1968, 2) redevelopment before Pisaster predation, and 3) redevelopment at elevations

where Mytilus was not consumed. On landward quadrats, M. californianus and other invertebrates settled and resided between B. cariosus. On the seaward transects, this mussel grew on top of Endocladia thereby shading and killing the alga. The increased growth of Mytilus on top of B. cariosus enables the completion of redevelopment on the seaward side, which includes the following processes in strata formation: 1) enlargement and fusion of adjacent B. cariosus attached to the rock; 2) establishment of a stratum of tubiculous polychaetes and byssal threads of Mytilus attached to and covering B. cariosus; 3) formation of a layer of small mussels between the byssus-polychaete level below and the Mytilus canopy above; and 4) settlement of barnacles (Chthamalus dalli, Balanus glandula, B. cariosus, and Pollicipes polymerus) and anemones on the mussel canopy.

Appearance of species comprising stages in the redevelopment of rocky intertidal zones appears to be a function of their 1) time of settlement, 2) speed of growth, and 3) ability to compete for space. The species that settle earlier are usually in the plankton during most of the year. These organisms are displaced by later forms which are larger and better competitors for space. Among the barnacles, Chthamalus dalli was the first species to settle and later was outcompeted for space by B. glandula, which settled next and then in turn was outcompeted by B. cariosus. This hierarchy of competitors among these three cirripedes was demonstrated

experimentally by Dayton (1971). The superior barnacle competitors are larger species which either undercut or crush adjacent specimens as shown by Connell (1961) with B. balanoides and C. stellatus.

Other authors have indicated also that the stages of redevelopment are determined by the time of settlement, speed of growth, and ability to compete for space. Kitching (1937) stated "that the sequence of stages is largely determined by the order of arrival of larvae or spores and the growth rate of these species... . Sessile organisms which finally became established eliminate their predecessors by smothering them and occupying all the space available; the slower growing but persistently spreading perennial algal species eventually triumph." Bokenham (1938) and Northcraft (1948) reported that the order in algal recolonization was primarily a function of the speed of growth; the earlier species were relatively faster growers than the later forms. Fahey and Doty (1949), who considered growth rate, reproduction, and life cycle to be important, described initial colonizers as rapidly growing forms and later stages as long lived or slower growing species. Connell (1972) stated that development is a result of: 1) differences in length of breeding season; 2) motility of plankton stages [which with 1) affect time of settlement]; 3) rates of growth after settlement; and 4) eventual size reached by the species (which affect the ability to compete for space).

The occurrence of the specific phenomenon of succession during the general process of redevelopment depends upon the third

factor discussed earlier, environmental modifications by earlier stages being necessary for the appearance of succeeding forms (Shelford, 1930 and Odum, 1969). Early investigators (Wilson, 1925, Pierron and Huang, 1926, and Hewatt, 1935) applied the term "succession" without providing evidence for environmental modifications by colonizing species. Other researchers discussed the relationship between changes in the substrate by earlier forms on the appearance of subsequent stages. Moore (1939) and Dayton (1971) found that a certain amount of weathering of rocky substrates, with the loss and/or gain of certain chemicals, was necessary for colonization to occur. According to Cirino (1955), Hilen (1923), and Miller, et al. (1948) believed that a slime film facilitated, but was not essential for, the settlement of later forms. Miller (1946) found that the larvae of the bryozoan, Bugula neritana, preferred slime-coated surfaces, although attachment would occur if the slime were not present. Zobell (1939) presented seven mechanisms by which slime films enhanced subsequent settlement. Hatton (1932) found that the initial growth of Enteromorpha promoted, but was not necessary for, the settlement of Fucus (Cirino, 1955).

Some researchers have noted a substrate preference for M. californianus settlement. Like M. edulis (Bayne, 1964), M. californianus settles on algal thalli, such as Endocladia muricata (Glynn, 1966 and Dayton, 1971) and Ptilota filicina (Bartlett, 1972). In the work by Dayton (1971), Endocladia was the most important

settling resource of M. californianus larvae. Clarke (1967) stated that a barnacle stage was necessary for mussel settlement, since seating did not occur on smooth rock, although Rasmussen in Shelford, et al., (1935) indicated that the presence of cirripedes was not necessary for mussel settlement. In the present study M. californianus was found on bare rock in crevices during the second month of redevelopment study. From the preceding reports settling M. californianus larvae appear, in decreasing order, to have the following substrate preferences: bushy algae; barnacles; rough rock surfaces; and finally, smooth rock.

The enlargement of M. californianus might be considered essential for the settlement of understory organisms. However, as seen in Zone_{vii} III at the study site, the same species present under the thick Mytilus canopy on the seaward side also were found between B. cariosus in the landward quadrats, although species number, size, and stratification were less. The larger mussels, therefore, were not necessary for the presence of other species but rather increased their size, numbers, and stratification.

These examples of the relationship between substrate and larval settlement indicate that the presence of certain species facilitates the seating of later organisms. Apparently no evidence has been presented to demonstrate that an earlier stage is essential for the settlement of a later stage, an important criterion Shelford (1930) and Odum (1969) set up to determine if succession occurs.

Therefore, the presence of earlier forms is a factor in redevelopment but not as important as the time of settlement, speed of growth, or ability to compete for space. Since earlier stages are not essential for the appearance of later colonizers, succession, as defined by Shelford (1930) and Odum (1969), has not been demonstrated to occur in the rocky intertidal. Therefore, another term should be used to describe this type of redevelopment. Perhaps "sequential non-successional development" could be used to describe the formation of rocky intertidal zones in which there is a sequence of stages leading to a climax but where earlier stages are not necessary for the settlement of subsequent forms.

An index of redevelopment was determined for Zones_{vn} II (0.68), III (0.35), and IV (0.95) after three years and three months. The time needed for complete redevelopment (an index of 1.0), assuming no changes in present rates, was calculated using the ratio:

$$\frac{\text{present index}}{3.25 \text{ years}} = \frac{1.0 \text{ index}}{X \text{ years}}$$

The estimate for Zone_{vn} II was 4.8 years, for Zone_{vn} III 9.3 years, and for Zone_{vn} IV 3.4 years.

The 3.4 year estimate for Zone_{vn} IV redevelopment is misleading since both the control and test quadrats were disturbed periodically by sand burial. This zone had redeveloped a number of times, following each disturbance (burial) by sand, since the scraping of the transect in October, 1968. Due to periodic sand

burial, this area developed as far as a stage dominated by Chthamalus. Field observations indicate that this zone took approximately two months to redevelop, after which another sand burial and cut initiates redevelopment once again.

In comparison to the 9.3 year period predicted for redevelopment of a M. californianus Zone, Hewatt (1935) stated that his scraped M. californianus Zone in Monterey would take at least two and one-half years to redevelop. Clark (1967) reported from his study in La Jolla that it was "four years before Mytilus established again, and it was not full grown at that time." Castenholz (1967) saw little replacement of Mytilus californianus in Oregon after six years. MacGinitie (1938) stated that there is a nine- to ten-year cycle between predation by Pisaster and redevelopment of a mussel zone.

Interrelationships

Differentiation along the transects, as noted by the distribution of sessile species competing for primary space, occurs with time (redevelopment) and vertical space (zonation) (Fig. 9). The first organisms to settle tolerate a wide vertical tidal range and as a result are initially present in all four zones. In the earlier portions of redevelopment the transects are more homogenous than later on; there is little differentiation.

Species comprising later stages have a more limited period of settlement, a narrower vertical tolerance range, and a superior

ability to compete. The differences between time of settlement and ability to compete cause stages in redevelopment, whereas the differences between vertical tolerance range and ability to compete result in the formation of zones. Since the later colonizing forms are more specialized in their habitat requirements (time and space) and are better competitors, the formation of zones and stages of redevelopment occurs simultaneously. Zones, like organisms, undergo greater differentiation with time due to the development of more specialized components.

Although species diversity as related to time was not calculated during the redevelopment study, models of this relationship can be developed from similarities with other investigations (Fig. 10). In the case of developing forests which occur in the extreme portion of an environmental gradient, diversity increases with time (Auclair and Geoff, 1971). Similarly, in rocky intertidal zones located in extreme portions of an environmental gradient, notably Zones_{vn} I and II (aerial exposure) and Zone_{vn} IV (sand burial), diversity probably increased throughout redevelopment. Characteristic of these zones and other high-stress environments, such as deserts (Schrere, 1942) and boreal spruce forests (Curtis, 1959), is the entrance of climax dominants early in development (Auclair and Geoff, 1971).

In redevelopment of low-stress environments, species diversity initially increases with time but decreases in later stages

as reported in boreal rain forests (Maycock and Curtis, 1960), tropical rain forests (Grant, 1963), coral reefs (Grigg, et al., 1970), and upland Wisconsin forests (Auclair and Geoff, 1971). This decrease in species diversity probably occurred in Zone_{vn} III on the seaward transect, the quadrats visibly dominated by Mytilus californianus.

A decrease in equitability rather than richness is the probable cause for such a reduction in species diversity with time. This prediction is based on the same rationale as that for the reduction in diversity with space. As the climax species (M. californianus) enlarges within Zone_{vn} III, as demonstrated by moving from higher to lower elevations, stratification increases and so does the number of species (richness). However, since only a few organisms increase in abundance due to environmental modifications caused by the enlarging mussels, equitability decreases. In summary, as the climax species increases in size, the equitability component decreases more than richness increases and a net reduction in species diversity results with space. A similar reduction in species diversity probably would occur with time for the same reason as it decreased with space, a reduction in equitability with increasing mussel size.

The point of maximum species diversity during redevelopment of biologically accommodated areas probably occurred at an intermediate point in time. Looking at time as an environmental factor, the extreme or early portions of redevelopment can be considered as

occurring in a physically controlled or new environment which later changes to a biologically accommodated region. The same change in diversity with space would be expected to occur with time; that is, diversity would increase as one moves from the extreme physically controlled areas, then reach a maximum, and decrease in the more biologically accommodated regions (older and/or less stressful).

The point of maximal diversity in time, as observed in space, would be at the transition between the physically controlled and biologically accommodated regions. In time maximum diversity would occur at the beginning of the climax stage or when Mytilus starts to be dominant on top of Balanus cariosus. This event in the present study occurred sometime between the July, 1971 and January, 1972 surveys or approximately three years after the beginning of redevelopment.

Disturbances (perturbations) in advanced climax stages of developing areas of low physiological stress, such as areas dominated by mussels, could function in increasing diversity once again (Fig. 10). Paine (1966) indicated that removal of the dominant organism (in this case Mytilus californianus by Pisaster) increased diversity. In effect, redevelopment is "pushed back" in time closer to the point of maximum diversity, the early portion of the climax stage when Mytilus first became dominant (Fig. 10).

Pisaster, as a preferential consumer of M. californianus, is benefited by the relatively short time needed for mussels to

redevelop. Selective predation on mussels, leaving B. cariosus on the rock, aids in driving development back to the point of maximum diversity, at approximately three years of redevelopment. A period of approximately six additional years would be needed for the mussels to reach maturity.

Unselective disturbances could overshoot the point of maximum diversity and remove all organisms. In this study Pisaster, after preferential feeding on M. californianus, was not able to migrate easily to another mussel-dominated site. The seastars, therefore, consumed the less preferred Balanus cariosus. In essence this method of feeding was non-preferential predation and development was pushed back to the initial point of redevelopment, bare rock. Under such circumstances mussels would take approximately nine years to reach maturity.

Disturbances also increase diversity in other systems. In tropical rain forests disease is a major factor maintaining high diversity levels (Grant, 1963). Auclair and Geoff (1971) considered fire, windthrow, disease, insect attacks, certain cutting procedures, and the use of some biocides as mechanisms which increase diversity of forests. Dayton and Hessler (1972) proposed that continued biological disturbances maintain high species diversity in the deep sea.

The older and larger (thicker) mussel beds probably are more likely to be disturbed (hence less stable) than a mussel zone earlier in development. This prediction is due to thicker mussel zones

providing: 1) a larger target for logs to hit; 2) greater resistance to crashing waves; and 3) greater weight for the mussels at the lowest level to support, than do young zones consisting of smaller mussels.

The alternation in time of periods of perturbations and periods of subsequent redevelopment of mussel zones produces oscillations in diversity (Fig. 11). The point at which development is pushed back and the subsequent period required for redevelopment is dependent on the severity of the previous disturbance. Loucks (1970) described a similar "wave form phenomenon" consisting of alternating periods of perturbations and redevelopment in 30- to 200-year cycles in southern Wisconsin forests.

The rate of development of each of the four zones appeared to be a function of the size of the largest sessile organism, which in turn was regulated by the severity and periodicity of harsh environmental factors on the organisms. Conditions which occur daily are considered "stresses;" those conditions which occur at longer time intervals are "disturbances" (Fig. 12).

Zone_{vn} IV, immersed on the average day for approximately 18 hours (Fig. 7) and exposed to air for only six hours, is under the least stressful physiological conditions (Fig. 12). At this tidal elevation organisms are exposed to both fewer and shorter periods of heat and wind, factors which cause drying out (Dayton, 1971). These physiological stresses are longer and more intense at higher

elevations. But disturbances do occur whenever sand denudes Zone_{vn} IV and in effect initiates redevelopment. Because of periodic sand disturbances this zone does not develop beyond the stage dominated by Chthamalus. Since this small species is a quick colonizer, Zone_{vn} IV redevelops the fastest, approximately two months.

Zone_{vn} I, on the average day, is not immersed and is under the most stressful physiological conditions. The little food that is present comes from the splash and spray of waves. The low quantity of food and the energy presumed to be required to prevent desiccation results in little energy available for growth. The only sessile species present are small barnacles which live in crevices. The rate of development, estimated from visual comparisons of test and control transects, was slower than Zone_{vn} IV (dominated by Chthamalus) but faster than Zone_{vn} II (dominated by Balanus glandula). This intermediate rate of development is a reflection of the presence of nearly equal numbers of both these barnacle species in Zone_{vn} I.

Zone_{vn} II, immersed on the average for one six-hour period per day, is under less stressful conditions from exposure to air. With more time to feed and less energy needed to avoid drying out, more energy is available to support a larger dominant organism (Balanus glandula). This species, due to its time of settlement and enlarged size, takes more time to reestablish than Chthamalus.

Consequently, this zone requires more time to redevelop than Zone_{vn} I.

Zone_{vn} III on the average is immersed daily for two six-hour periods, and is under less stressful conditions than Zones_{vn} I and II. Since more time is available for feeding, less energy is required to prevent desiccation, and disturbances (Pisaster predation, logs, and waves) occur infrequently. This zone is able to support the largest sessile species (M. californianus and B. cariosus). These two species take the longest period to reach full size of all the dominant sessile species studied, which is the reason why this zone takes the longest time to redevelop.

CONCLUSIONS

1. A three-year, seven-month field study in the rocky intertidal was made on the interrelationships among ecological factors, species diversity, zonation, and redevelopment along stable seaward and landward transects near Trinidad, northern California.
2. Four zones of visually dominant species were distinguished along the transects and are similar to zones described at other localities along the protected outer coast of North America from Alaska to Point Conception, and possibly further south.
3. Zones determined from numerical analysis of all organisms collected were very similar to the visibly distinguished zones of dominant species. One discrepancy between the two methods was due to the enlarged size of Mytilus californianus on the seaward transect, which permitted greater stratification, abundance, and size of the understory fauna. There also was a mussel zone on the landward transect which consisted of the same species although the stratification, mussel size, and size and abundance of other species were less. The larger size of M. californianus on the seaward transect might be a function

of the greater surge providing more food for growth in the same amount of time than on the landward side.

4. Tidal elevations at breaks among the three high zones corresponded closely to the mean levels of the daily tidal cycle. The break between the two lowest zones is controlled by sand burial serving as a physical factor limiting the lower distribution of the mussel zone.
5. Species diversity of invertebrates was lowest in the extremely physically-controlled areas, such as the top of the transect exposed to the stresses of aerial exposure and at the base of the rock exposed to disturbances by sand. Moving away from these areas toward the biologically accommodated regions, diversity increased. But the highest diversities were found at the transition between the physically controlled and biologically accommodated areas, where mussels first began to dominate. The area of the thick, stratified mussel bed (most biologically accommodated region) is richer (number of species) but lower in species diversity due to decreased equitability, than the less stratified quadrats of the mussel zone on the seaward transect.
6. The appearance with time of recolonizing species, serving stages in the redevelopment of each zone, was a function of the time of settlement, speed of growth, and the ability to compete for space. Since environmental modifications by earlier stages

did not appear to be necessary for the appearance of later forms in this study or in similar investigations, succession as defined by Odum and Shelford has not been demonstrated to occur in the rocky intertidal; instead, there is "sequential non-successional redevelopment."

7. A model for changes in diversity with time and space is proposed. In development of all four zones richness increases with time. Diversity also increases with time in the physically controlled environments. In biologically accommodated regions diversity initially increases then reaches a maximum point when one species (Mytilus californianus) begins to be dominant, and decreases as the mussels enlarge. Disturbances, such as abrasion by logs, Pisaster predation, and the impact of waves, push redevelopment back in time closer to the point of maximum diversity by preventing dominance by Mytilus.
8. Preferential predation by Pisaster on M. californianus probably decreases the time needed for the regrowth of large mussels, the preferred resource of Pisaster. A refuge area for M. californianus is provided above the upper limit of Pisaster predation.
9. The rate of development for each zone appears to be a function of the size of the largest sessile invertebrate which in turn is regulated by the severity and periodicity of stresses and disturbances. The M. californianus - B. cariosus Zone_{vn}, which

is under less stress than the two zones above and less frequent disturbances than the zone below, supported the largest sessile species and takes the longest time to redevelop.

Plate 1 Photograph of the seaward side of the rock in June,
1968 before sampling. The white string indicates the
location of the seaward test transect.

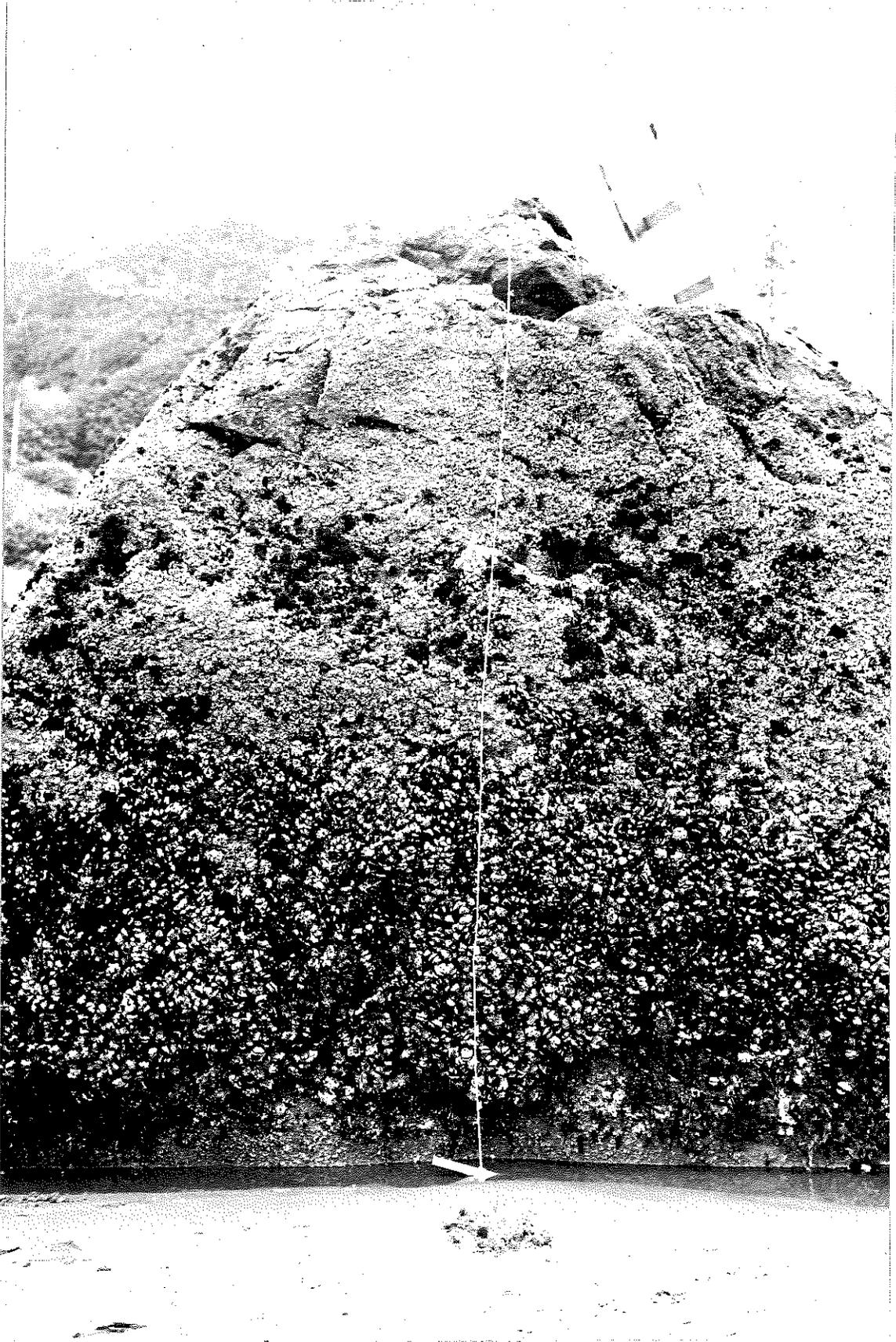


Plate 2 Photograph of the seaward transect in November, 1969 showing effect of Pisaster predation on Mytilus, thereby exposing Balanus cariosus.



Plate 3 Photograph of the seaward side of the rock in January, 1972, 39 months after the test transects were scraped to study redevelopment. Most of the Mytilus present in 1968 were preyed upon by Pisaster, seen at the base of the rock.

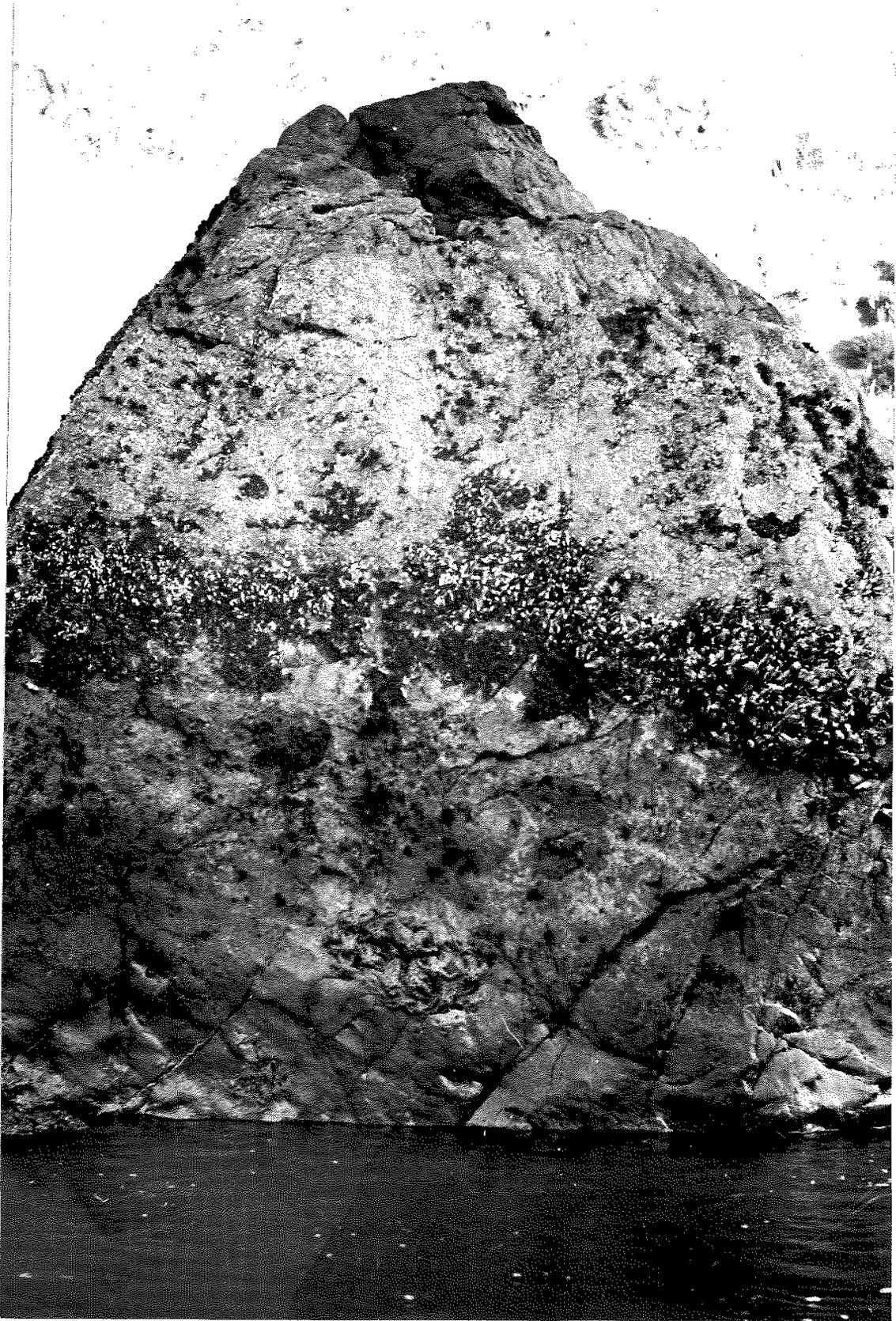


Figure 1 Map of the study site in relation to sandy beaches (stipple) and sites near Trinidad, northern California.

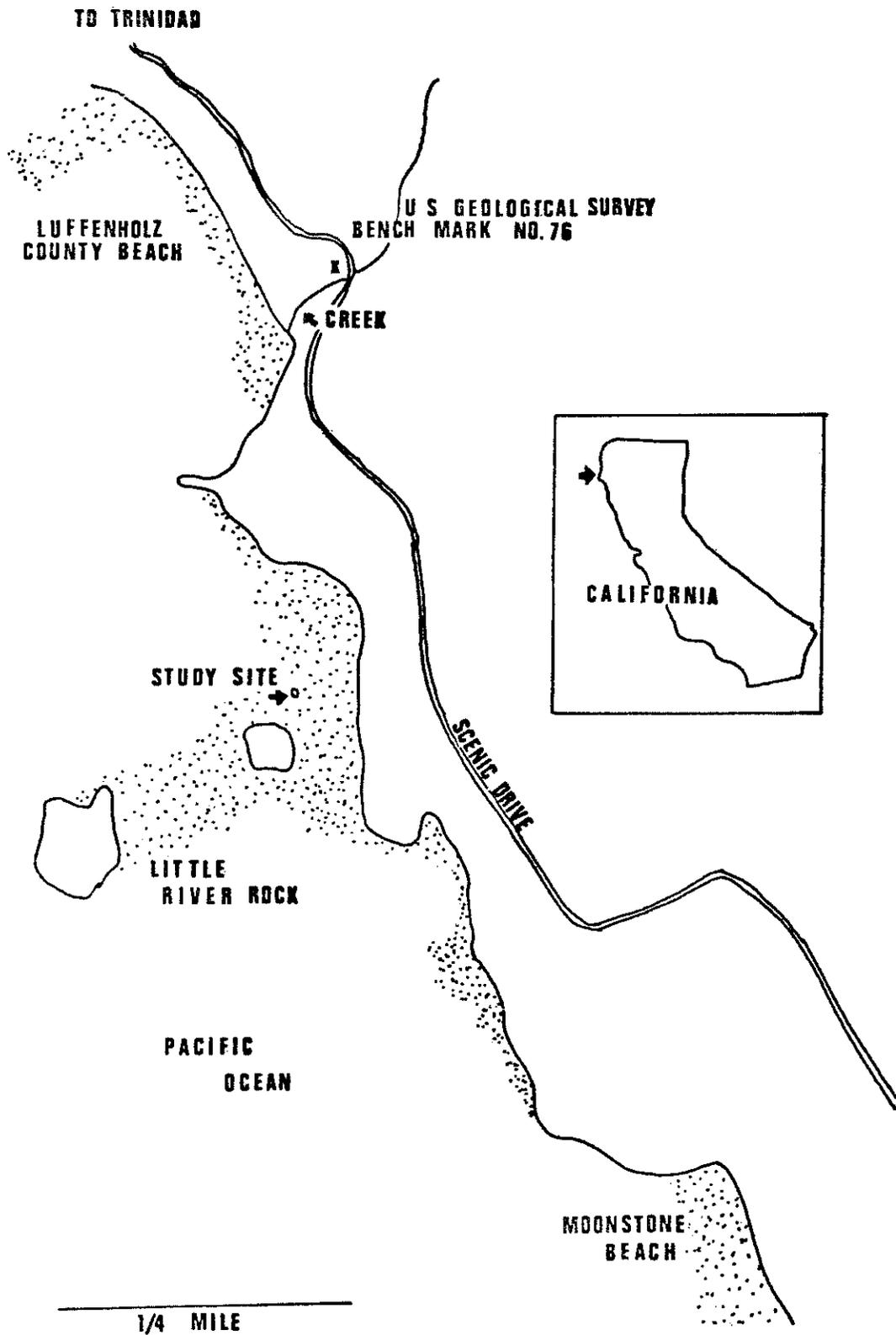
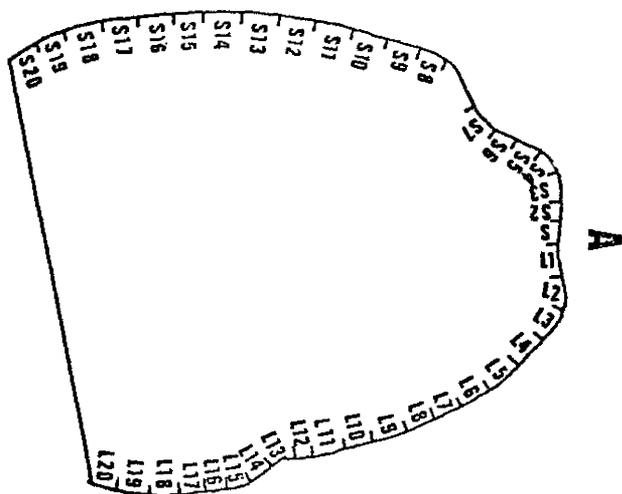


Figure 2 Schematic diagrams of the four transects investigated as observed from the south (A), west (B), and east (C) sides of the rock. Each quadrat was 10 cm wide and 20 cm long.

SEAWARD TRANSECT



LANDWARD TRANSECT

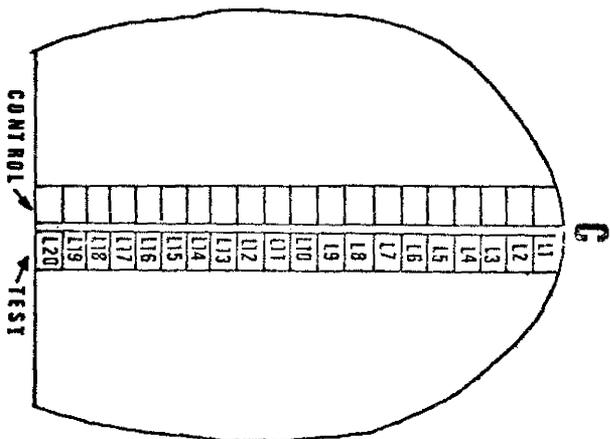
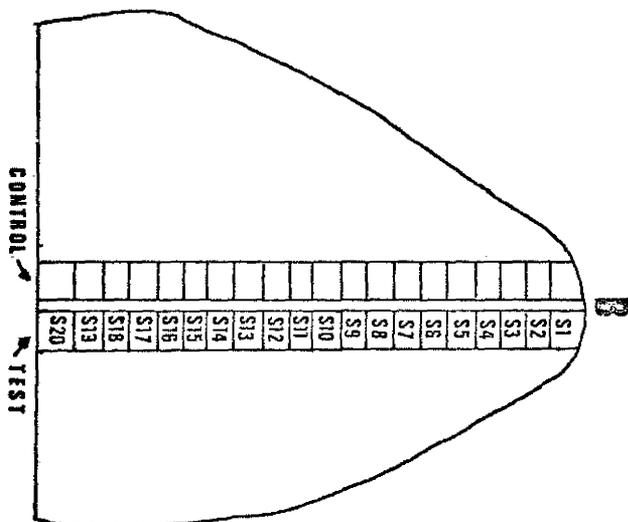


Figure 3 Procedure for determining zones using cluster analysis of sites. Hypothetical data was used to demonstrate the steps involved.

Step 1. Construct a species-sample matrix.

		Samples			
Species		1	2	3	4
<u>Lacuna sp.</u>		10	10	0	25
<u>Balanus sp.</u>		20	20	25	0
<u>Mytilus sp.</u>		20	20	25	25
Summation		50	50	50	50

Step 2. Determine an index of affinity between all possible pairs of samples. The Bray-Curtis coefficient, (S_{bc}) is calculated below for samples one and three.

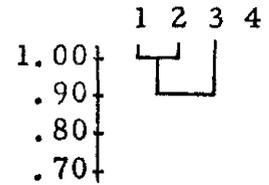
$$S_{bc} = \frac{2W}{A+B} = \frac{2(40)}{100} = 0.80$$

Step 3a. Construct a sample-sample or "Q" matrix of coefficients between all samples.

		Samples			
		1	2	3	4
Samples	1	1.00	.80	.60	
	2		.80	.60	
	3			.50	
	4				

Step 3b. Join samples with the highest coefficient in the Q matrix.

		Samples		
		1+2	3	4
1+2		$1.00 + .90 / 2 = .90$	$1.00 + .60 / 2 = .80$	
3			.50	
4				



Step 3c. Reconstruct the Q matrix by replacing individual values of linked samples with average values.

Figure 4 Diagram of the transects as viewed from the south in June, 1968 and January, 1972. Both visibly determined zones (subscript "v") as well as visibly and numerically determined zones (subscript "vn") are shown as they appeared in 1968. The 1972 diagram shows the zones after predation by Pisaster.

◻ CHTHAMALUS DALLI
 ◻ BALANUS GLANDULA
 ◻ BALANUS CARIOSUS
 ○ MYTILUS CALIFORNIANUS

D ACMAEA DIGITALIS
 C ACMAEA SP.
 S1 LITTORINA SCUTULATA
 S1 TUBICULOUS POLYCHAETES

EF ENDOCLADIA MURICATA
 EF PELVETIOPSIS LIMITATA

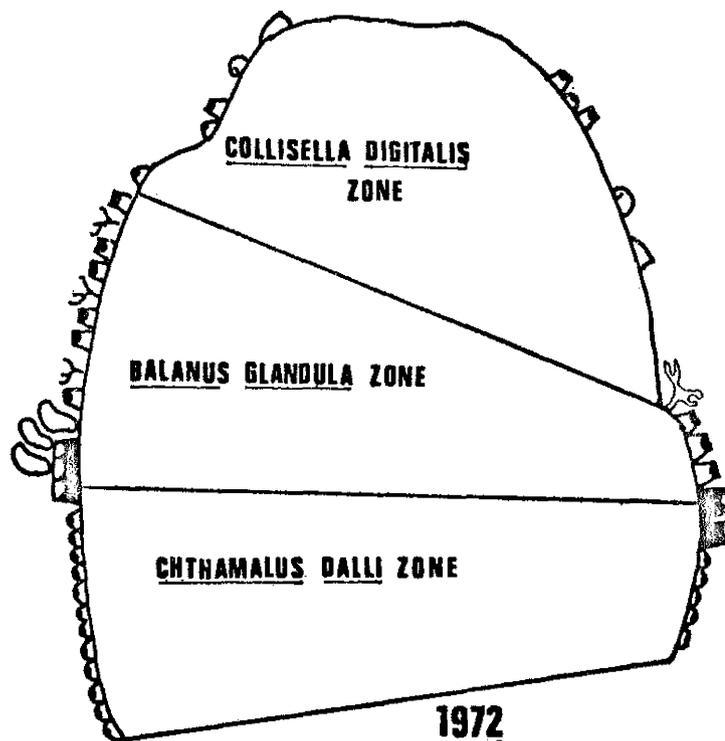
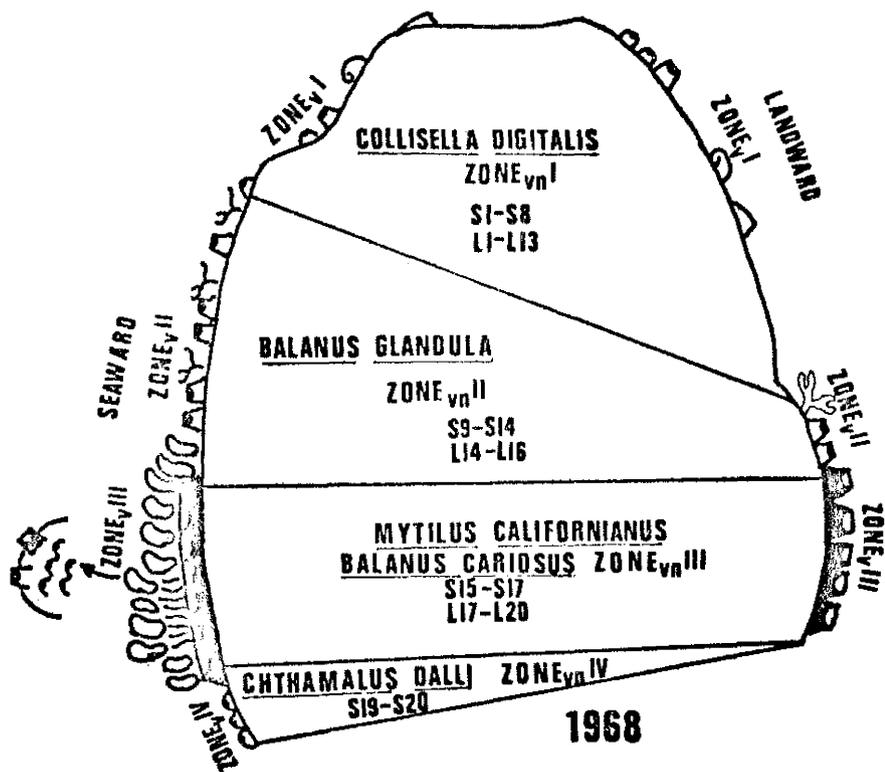


Figure 5 Dendrogram showing relationships between quadrats based on the Bray-Curtis coefficient of similarity using logarithm-transformed densities with group average sorting. Roman numerals indicate groupings which are considered zones.

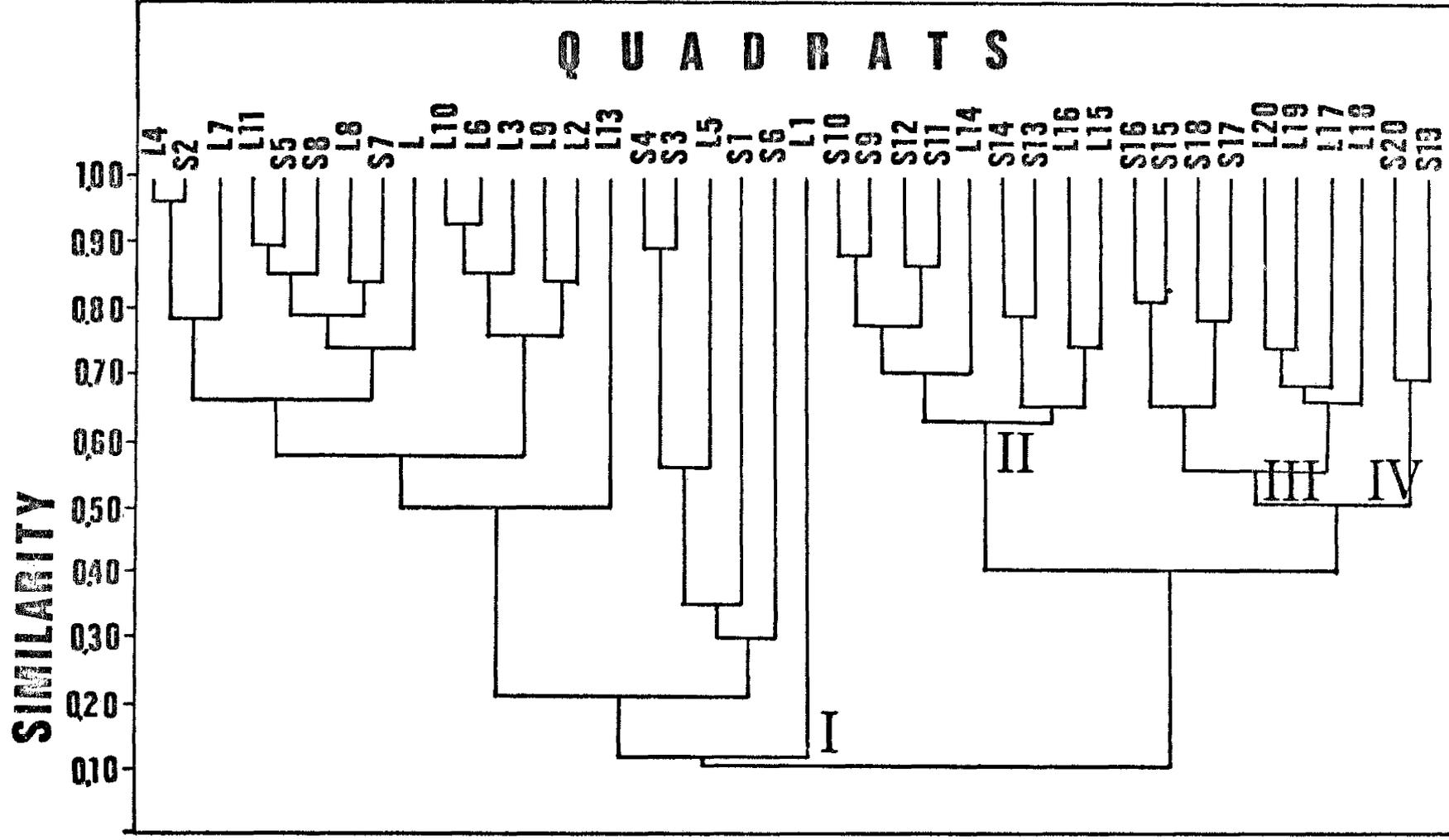


Figure 6 Dendrogram showing relationships between quadrats based on Czekanowski's coefficient of similarity using presence-absence of species with group average sorting. Roman numerals indicate groupings which are considered zones.

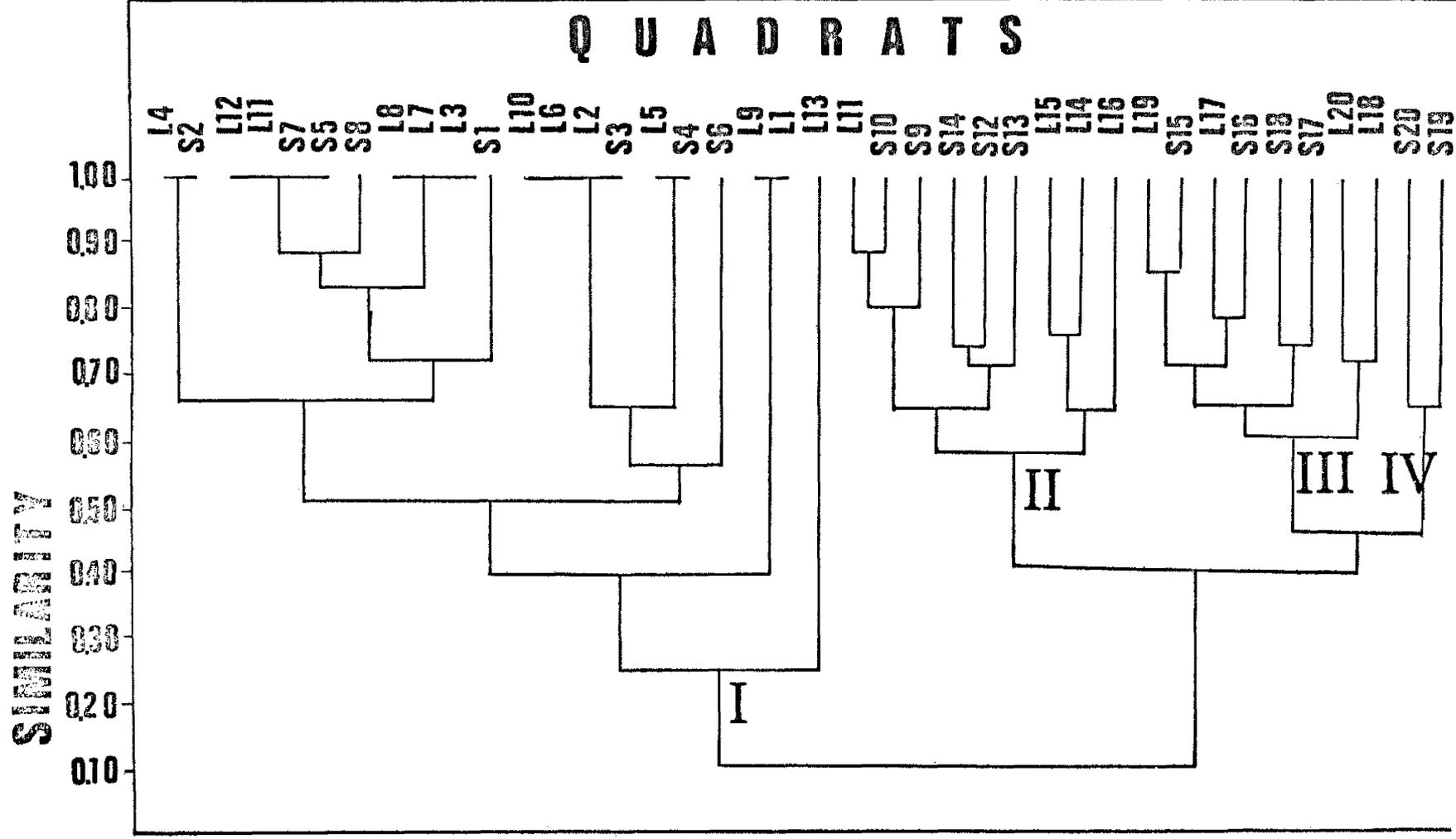


Figure 7 Comparison of the measured tidal elevations between zones_{vn} along the landward transect with the calculated mean elevations of the daily mixed tidal cycle at Trinidad.

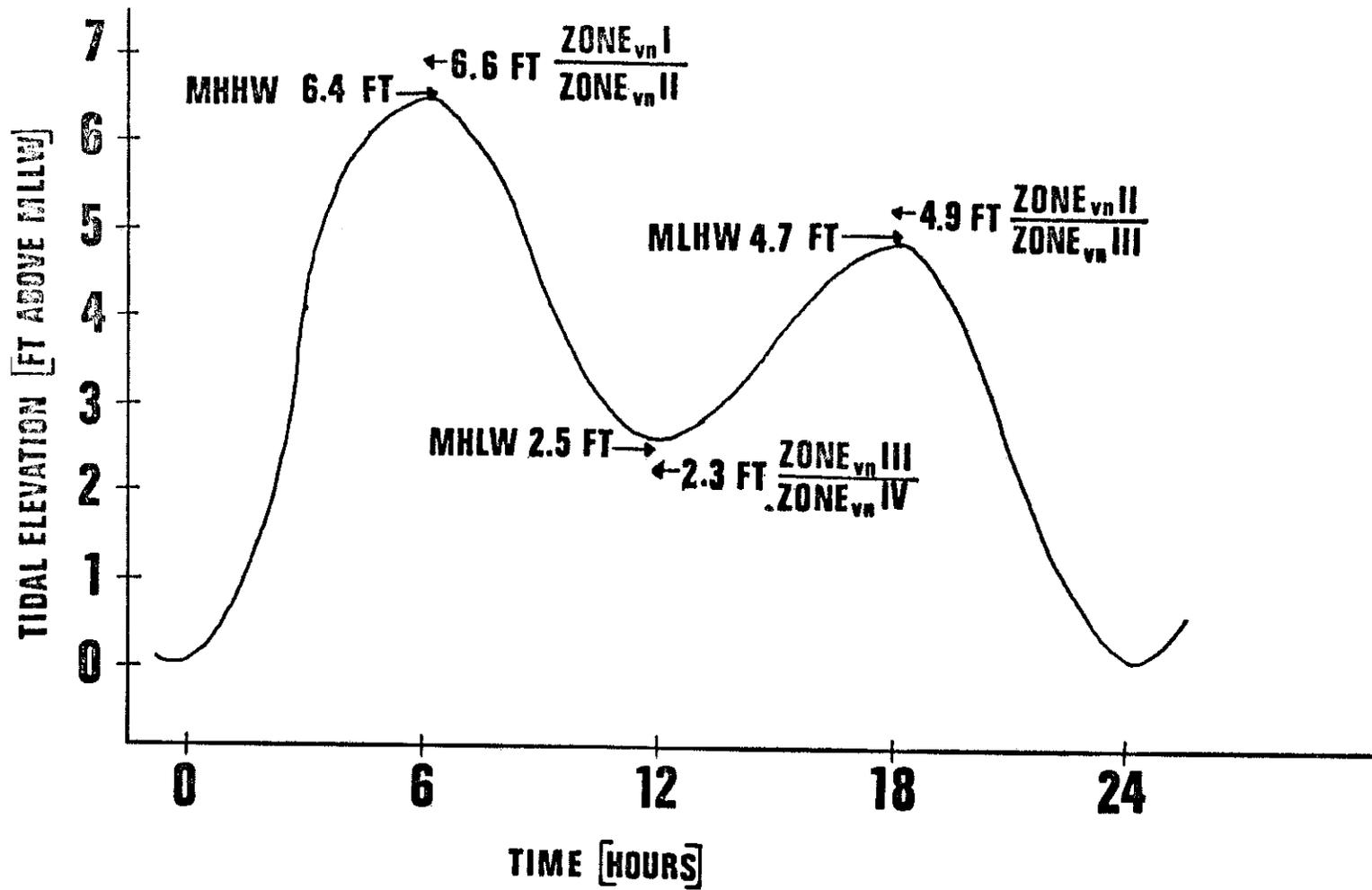


Figure 8 Correlation between the species diversity index of Brillouin and tidal elevation for each test quadrat in 1968 ($b = -7.7$; $p > 0.95$).

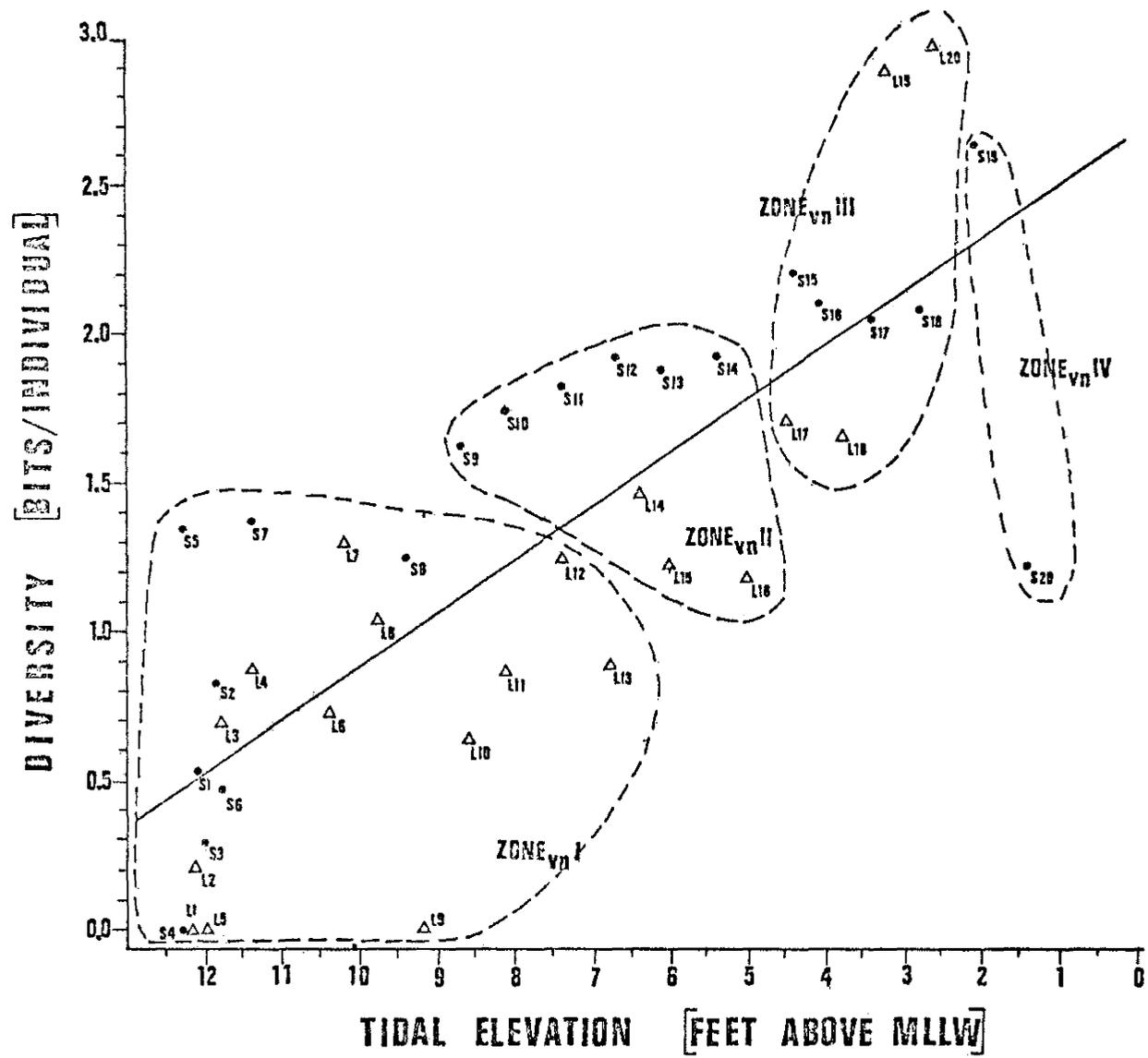
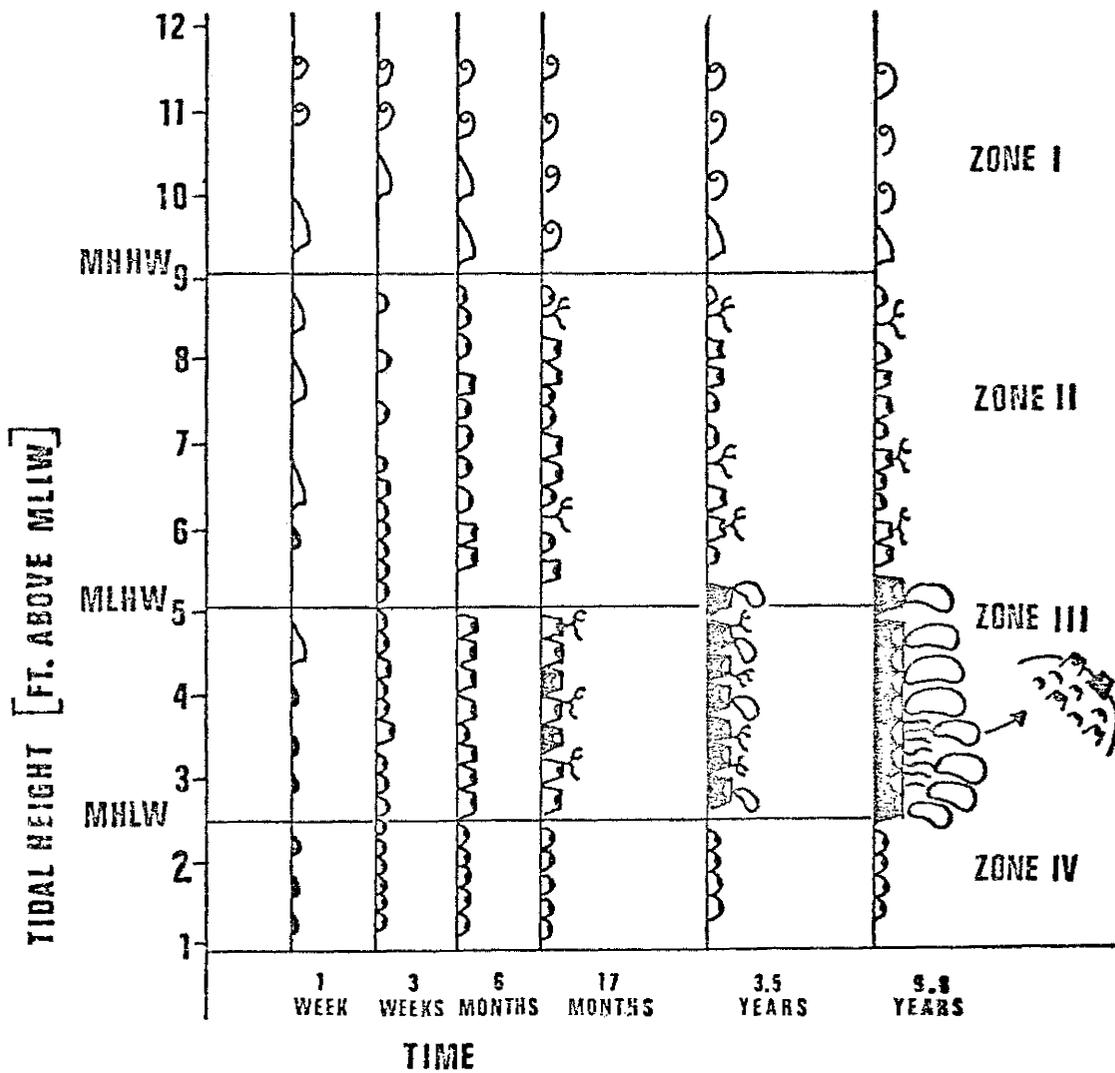


Figure 9 Schematic diagram of the major visible stages in the redevelopment of the four seaward zones. Redevelopment on the landward side was similar but did not change after the 17-month period.

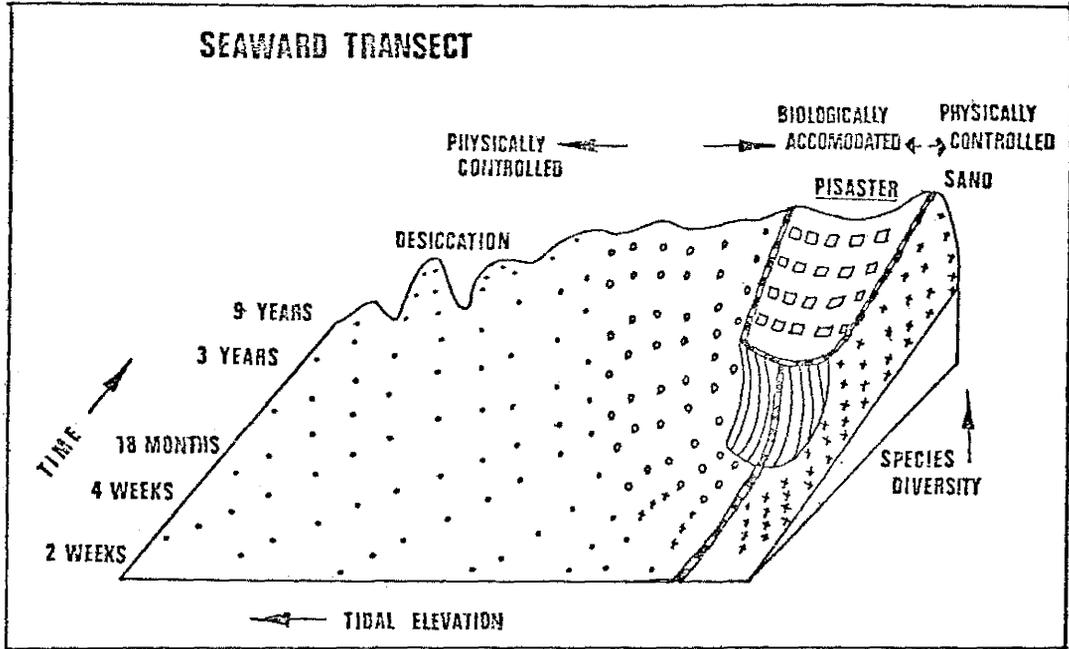


- CHTHAMALUS DALLI
- BALANUS GLANDULA
- BALANUS CARIOSUS
- MYTILUS CALIFORNIANUS

- COLLISELLA DIGITALIS
- COLLISELLA SP.
- LITTORINA SCUTULATA
- TUBICULOUS POLYCHAETES

- ENDOCLADIA MURICATA
- PELVETIOPSIS LIMITATA

Figure 10 Proposed model of invertebrate species diversity with time, space, and ecological factors on the seaward and landward transects. Symbols represent the visually dominant species.



- COLLISELLA DIGITALIS
- xxx CHTHAMALUS BALLI
- ooo BALANUS GLANDULA

- BALANUS CARIOSUS
- MYTILUS CALIFORNIANUS
- xxx HIGH DIVERSITY

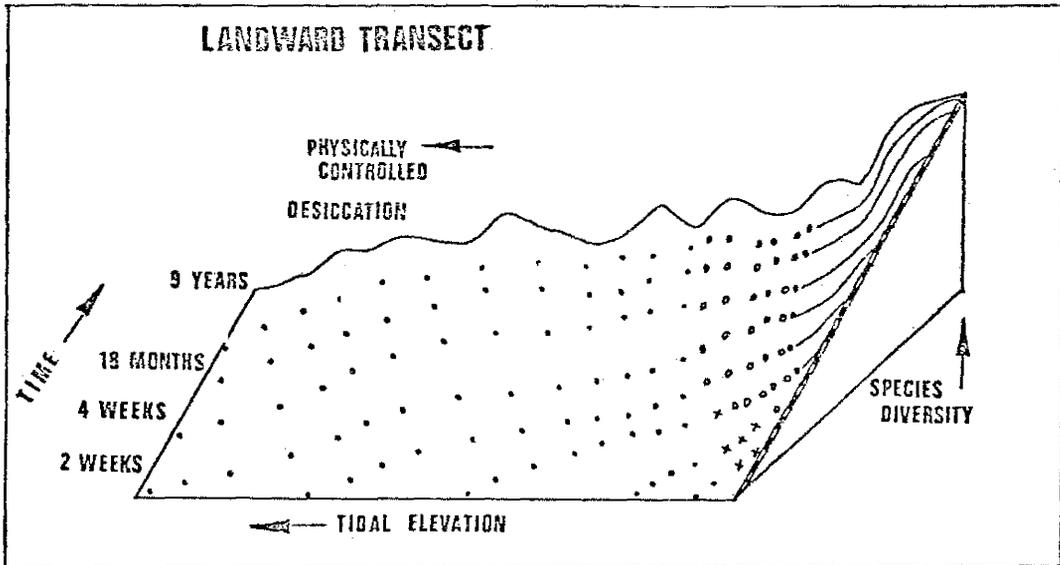
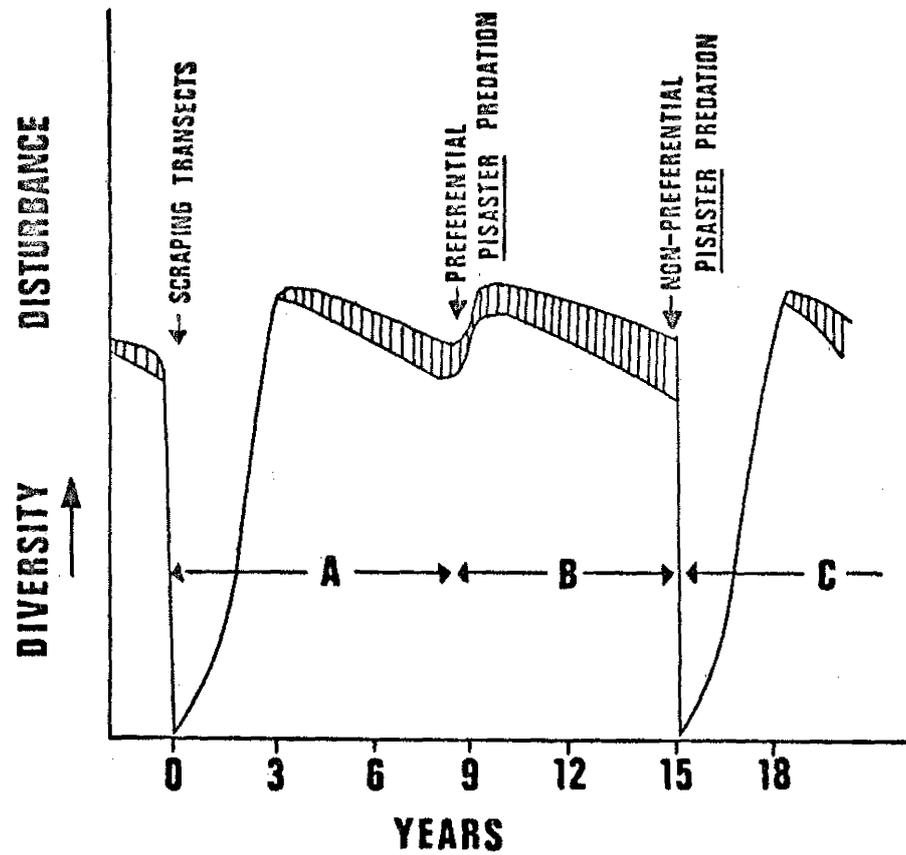


Figure 11 Proposed model of fluctuations in invertebrate species diversity and mussel size with time in the Mytilus californianus Zone, on the seaward transect following disturbances such as scraping the transects (A), preferential Pisaster predation (B), and non-preferential Pisaster predation (C).



▨ MUSSEL SIZE

Figure 12 Severity and periodicity of stresses and disturbances in each zone_{vn}.

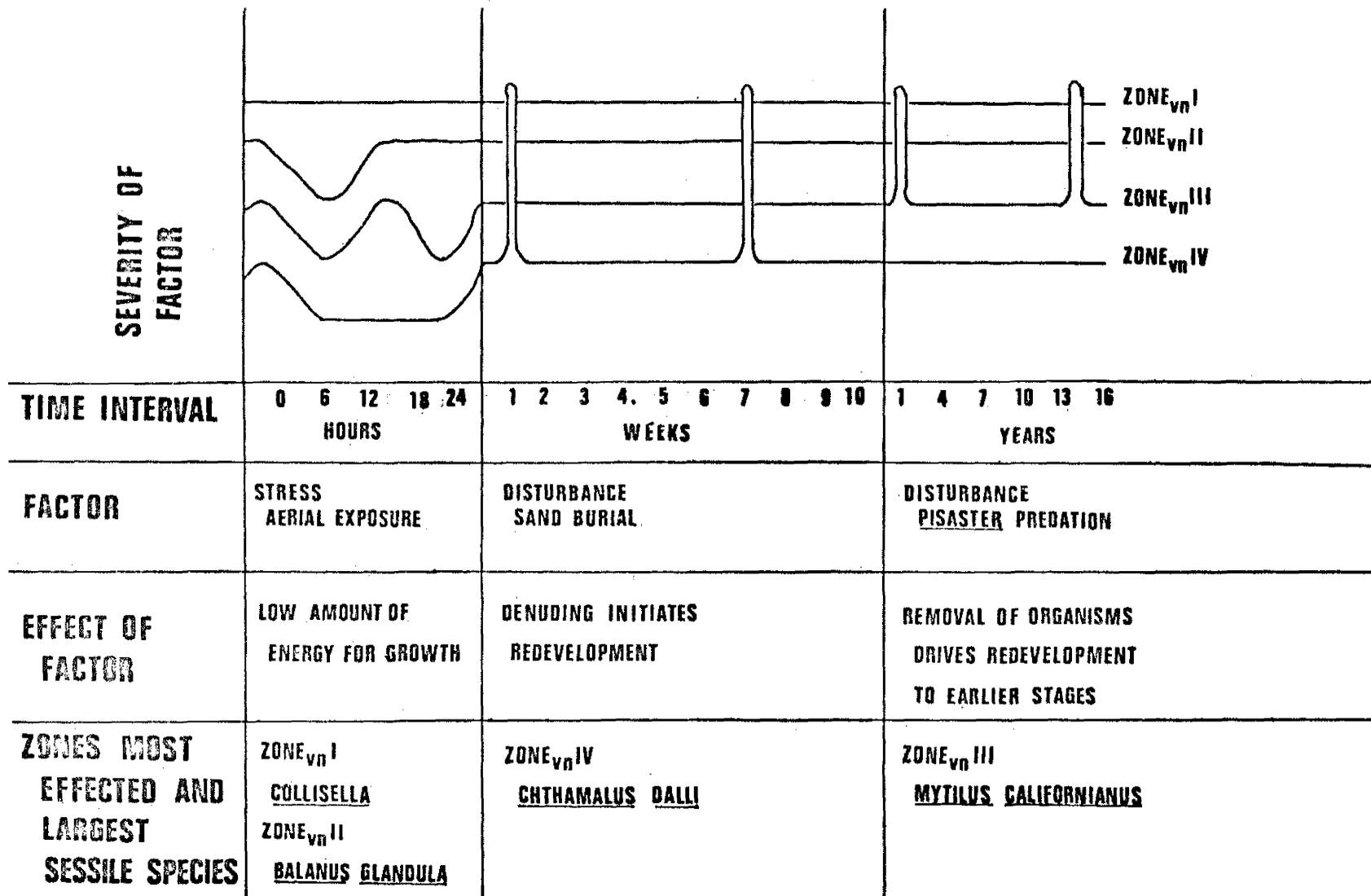


Table 1 Species-sample matrix representing organisms collected in the 20 seaward test quadrats in 1968.

	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	S18	S19	S20
CNIDARIA																				
Anthopleura elegantissima															16	16	20	21	2	9
NEMERTINA																				
Emplectonema gracile										1	2	5	17	8	11	1	3	6		
Paranemertes peregrina												1	3	1	2		1	2		
Unidentified nemerteans										1						3	4	9		
PLATYHELMINTHES																				
Unidentified turbularians															1		1	2		
SIPUNCULOIDEA																				
Phascolosoma agassizzi															1		3	8		
ARTHROPODA																				
AMPHIPODA																				
Corophiid															2	2	177	6		
Phodtid															4		2			
Podocerid																2				
Pontogeniid																		273		
CIRRIPIEDIA																				
Balanus cariosus												1	2	9	53	99	231	143	54	23
Balanus glandula		19	1		40		38	108	431	561	864	713	812	1199	2738	2817	931	1314	117	201
juveniles														283	1241	622	210	123		
adults		19	1		40		38	108	431	561	864	713	812	916	1497	2195	721	1191	117	201
Chthamalus dalli	2	10			38		40	120	57	60	113	13	70	223	823	3019	4986	3700	276	1014
juveniles														41	728	1850	3431	1737		
adults	2	10			38		40	120	57	60	113	13	70	182	95	1169	1555	1963	276	1014
Pollicipes polymerus									1				26	176	220	409	26	5	4	3
juveniles													13	173	216	401				
adults							1						13	3	4	8	26	5	4	3
DECAPODA																				
Pachygrapsus crassipes																2	1	10		
INSECTA																				
Acarina																		1		
Aphrosylus sp.															2	2	2	3	1	
pupae															1				1	
larvae															1	2	2	3		
Diaulota brevipes															1					
larvae																				
adults															1					
Halobisium sp.																				
Limonia marmorata																				

	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	S18	S19	S20
<i>Liparocephalus cordicollis</i>										2	2	4	1		3	2				
larvae																1				
adults										2	2	4	1		3	1				
ARTHROPODA																				
<i>Paraclunio</i> sp. larvae																18				
<i>Parydra</i> sp.									9	7	5	5	4	6						
pupae																				
larvae									9	7	5	4	4	6						
adults												1								
ISOPODA																				
<i>Cirolana harfordi</i>																	1	3		
<i>Dynamene sheareri</i>														12	27	29	31	17	13	
<i>Dynamene</i> sp.																	5			
<i>Exosphaeroma amplicauda</i>																	7			
<i>Gnorimosphaeroma oregonensis</i>																	61			
<i>Muna chromatoccephala</i>															4	4	11	6	1	
PYCNOGONIDA																				
<i>Achelia simplissima</i>															1		1	3		
<i>Halosoma viridintestinale</i>												1			2	1	4	4		
Unidentified pycnogonids																1			1	
TANAIDACEA																				
<i>Pancolus californiensis</i>												3		5		1				
Unidentified tanaid																			1	
MOLLUSCA																				
AMPHINEURA																				
<i>Cyanoplax dentiens</i>												2	1	11	3			1		
GASTROPODA																				
<i>Collisella digitalis</i>					8	4	1	10	57	62	49	18	23	11	8	1				
<i>Collisella scabra</i>																				
<i>Collisella</i> sp.									22	19	48	34	42	34	80	146	159	143	20	
<i>Littorina scutulata</i>	1		11	11	1	1	9	3	52	69	43	27		2			24	10		
<i>Odostomia</i> sp.															4	1	14	42	15	
<i>Oncidiella</i> sp.											5	26	45	12	28	10	4			
<i>Thais emarginata</i>														1	2	5	25	24	5	
PELECYPODA																				
<i>Adula diegensis</i>														2	65	51	48	47	10	
<i>Hiatella arctica</i>															5	2	8	13		
<i>Kellia laperousii</i>																		6		

	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	S18	S19	S20
<i>Lasaea subviridis</i>									1	43	69	184	10	1	37	7				
<i>Mytilus californianus</i>									2	5	70	48	52	177	1034	821	641	308	87	83
juveniles													3	13	63	67	56	46	10	
adults									2	5	70	48	49	164	971	754	585	262	77	83
ANNELIDA																				
<i>Crucigera irregularis</i>																		1		
<i>Eulalia aviculiseta</i>																1	5	6	3	
Fabroniid																		1		
<i>Lumbrinereis</i> sp.																				
Maldanid																		1		
<i>Nereis vexillosa</i>												1			5	3	2	1		
<i>Phragmatopoma californica</i>																		1		
Phyllodocid																		1	1	
<i>Polydora websteri</i>															2					
<i>Pseudopotomilla intermedia</i>																	12	56	29	8
<i>Sabellaria gracilis</i>																		2	3	
<i>Schizobranchia</i> sp.															1	13	93	172	23	3
<i>Scolopus armiger</i>																		3	26	1
Spionid																			1	
<i>Typosyllis adamanteus</i>									5	7	20	46	66	37					4	
<i>Typosyllis pulchra</i>												2	3	6	137	95	99	160	13	
Unidentified oligochaetes																	1			
ECHINODERMATA																				
<i>Pisaster ochraceus</i>																		7		1
CHLOROPHYTA																				
<i>Ulva</i> sp.													*	*	*	*	*	*	*	*
PHTAEOPHYTA																				
<i>Fucus distichus</i>													*							
<i>Pelvetiopsis limitata</i>																				
Unidentified ralfsioid													*	*						
RHODOPHYTA																				
<i>Callithamnion pikeanum</i>													*							
<i>Endocladia muricata</i>									*	*	*	*	*	*	*	*	*	*	*	*
<i>Gigartina agardhii</i>								*	*	*	*	*	*	*	*	*	*	*	*	*
<i>Glaciopeltis furcata</i>													*	*						
<i>Iridaea</i> sp.																				
<i>Microcladia</i> sp.														*						
<i>Plocamium violaceum</i>																				
<i>Polyshipponia</i> sp.																		*		
<i>Porphyra perforata</i>													*			*	*	*		

Table 2 Species-sample matrix representing organisms collected in the 20 landward quadrats in 1968.

	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10	L11	L12	L13	L14	L15	L16	L17	L18	L19	L20	
CNIDARIA																					
Anthopleura elegantissima																	6	2	10	4	
NEMERTINA																					
Emplectonema gracile														1	14	26	66	14	7	39	
Paranemertes peregrina																3	3	3	1	4	
Unidentified nemerteans																9	6			5	
PLATYHELMINTHES																					
Unidentified turbularians															2	2	11	7	2	18	
SIPUNCULOIDEA																					
Phascolosoma agassizzi																	1		1		
ARTHROPODA																					
AMPHIPODA																					
Corophiid																	114		206	71	
Phodtid																		4	20	8	
Podocerid																					
Pontogeniid																					
CIRRIPEDIA																					
Balanus cariosus														1			30	11	38	29	
Balanus glandula	1	20	17	14		13	8	27	32	22	83	26	11	426	1213	2669	2117	855	232	240	
juveniles																					
adults	1	20	17	14		13	8	27	32	22	83	26	11	426	1213	2669	2117	855	232	240	
Chthamalus dalli			1	10			8	31			15	4		54	53	120	36	18	25	150	
juveniles																					
adults			1	10			8	31			15	4		54	53	120	36	18	25	150	
Pollicipes polymerus																					
juveniles																			1	2	2
adults																			1	2	2
DECAPODA																					
Pachygrapsus crassipes																		13	1	1	1
INSECTA																					
Acarina																					
Aphrosylus sp.														1	2		5	1	4	11	
pupae																					
larvae														1	2		5	1	4	11	
Diaulota brevipes															4	6	4	2	1		
larvae															4	4	3	2	1		
adults																2	1				
Halobisium sp.																					
Limonia marmorata																3	1				

	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10	L11	L12	L13	L14	L15	L16	L17	L18	L19	L20
<i>Liparocephalus cordicollis</i>															1	4	1		2	6
larvae																	1		1	6
adults															1	4			1	
ARTHROPODA																				
<i>Paraclunio</i> sp. larvae														1		1	4			1
<i>Parydra</i> sp.														6	6	27	12	2	1	
pupae																				
larvae														6	6	27	12	2	1	
adults																				
ISOPODA																				
<i>Cirolana harfordi</i>															2	5	27	5	1	2
<i>Dynamene sheareri</i>																				
<i>Dynamene</i> sp.																				
<i>Exosphaeroma amplicauda</i>																				
<i>Gnorimosphaeroma oregonensis</i>																				
<i>Muna chromatoccephala</i>																	1	2	2	
PYCNOGONIDA																				
<i>Achelia simplissima</i>																			1	
<i>Halosoma viridintestinale</i>																			1	
Unidentified pycnogonids																				
TANAIDACEA																				
<i>Pancolus californiensis</i>															6		9			
Unidentified tanaid																				
MOLLUSCA																				
AMPHINEURA																				
<i>Cyanoplax dentiens</i>																				
GASTROPODA																				
<i>Collisella digitalis</i>										5	2	10	8	1	10	3				
<i>Collisella scabra</i>															1					
<i>Collisella</i> sp.														7	15	16	9		7	1
<i>Littorina scutulata</i>		1	3		2	4	4	1		5	1	8	4	3	12					
<i>Odostomia</i> sp.																				
<i>Oncidiella</i> sp.															13	27	41	12		1
<i>Thais emarginata</i>															1	1	5	2		
PELECYPODA																				
<i>Adula diegensis</i>																	34	13	59	29
<i>Hiatella arctica</i>															10		2		1	
<i>Kellia laperousii</i>																				
<i>Lasaea subviridis</i>														49	35	57	1		3	

	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10	L11	L12	L13	L14	L15	L16	L17	L18	L19	L20
<i>Mytilus californianus</i>														24	110	187	221	223	237	180
small (<2.5 cm)																	1		1	
large (≥2.5 cm)														24	110	187	220	223	236	180
ANNELIDA																				
<i>Crucigera irregularis</i>																				
<i>Eulalia aviculiseta</i>																	2			
Fabronid																				
<i>Lumbrineris</i> sp.																	1			
Maldanid																				
<i>Nereis vexillosa</i>														1	1	1	1		5	5
<i>Phragmatopoma</i>																				
Phyllodocid																				
<i>Polydora websteri</i>																	1			
<i>Pseudopotomilla intermedia</i>																				
<i>Sabellaria graciles</i>																				
<i>Schizobranchia</i> sp.																	1		1	1
<i>Scolopus armiger</i>																1	1			
Spionid																				1
<i>Typosyllis adamanteus</i>																34	32	5		1
<i>Typosyllis pulchra</i>																	35	77	104	22
Unidentified oligochaetes														1	2	4	1	1	4	
ECHINODERMATA																				
<i>Pisaster ochraceus</i>																				1
CHLOROPHYTA																				
<i>Ulva</i> sp.													*	*	*	*	*	*	*	*
PHAEOPHYTA																				
<i>Fucus distichus</i>																				
<i>Pelvetiopsis limitata</i>													*	*	*					*
Unidentified ralfsiod																				
RHODOPHYTA																				
<i>Callithamnion pikeanum</i>																*				
<i>Endocladia muricata</i>													*	*	*		*			
<i>Gigartina agardhii</i>													*	*	*		*	*		*
<i>Gloiopeltis furcata</i>																				
<i>Iridaea</i> sp.																				
<i>Microcladia</i> sp.																				
<i>Plocamium violaceum</i>																				
<i>Polysiphonia</i> sp.																				
<i>Porphyra perforata</i>																	*			

Table 3 Number of species, number of specimens, index of species diversity, index of redevelopment, and tidal elevation for each test quadrat and mean values per quadrat for each zone.

Sample or Zone	Tidal Height (ft.)	Number Species	Number Speci- mens	Brillouin Diversity (bits)	Index Development
S1	12.1	2	3	0.528	not recorded
S2	11.9	2	2	0.836	" "
S3	12.0	2	12	0.299	" "
S4	12.3	1	11	0.000	" "
S5	12.2	4	87	1.340	" "
S6	11.8	2	5	0.464	" "
S7	11.4	4	88	1.362	" "
S8	9.4	4	241	1.250	" "
S9	8.7	10	637	1.623	.95
S10	8.1	12	837	1.743	.78
S11	7.4	12	1290	1.823	.62
S12	6.7	17	1131	1.924	.73
S13	6.1	18	1180	1.860	.45
S14	5.4	20	1920	1.923	.35
S15	4.8	32	5330	2.198	control destroyed
S16	4.1	34	7583	2.100	" "
S17	3.4	43	7729	2.053	" "
S18	2.8	41	6267	2.082	" "
S19	2.1	19	654	2.637	.93
S20	1.4	10	1352	1.219	.97
L1	12.2	1	1	0.000	not recorded
L2	12.1	2	21	0.209	" "
L3	11.8	3	21	0.693	" "
L4	11.4	2	24	0.871	" "
L5	12.0	1	2	0.000	" "
L6	10.6	2	17	0.660	" "
L7	10.2	3	20	1.295	" "
L8	9.8	3	59	1.024	" "
L9	9.2	1	32	0.000	" "
L10	8.6	2	27	0.640	" "
L11	8.1	4	104	0.870	" "
L12	7.4	4	40	1.247	" "
L13	6.8	4	21	0.876	" "
L14	6.4	14	584	1.458	.97
L15	6.0	19	1493	1.202	.88
L16	5.2	24	3226	1.180	.84
L17	4.5	37	2843	1.700	control destroyed
L18	3.8	22	1264	1.652	" "
L19	3.2	30	980	2.897	" "
L20	2.6	27	834	2.970	" "
S1-8,L1-13(zone _{vn} I)		2.4	41	0.689	not recorded
S9-14,L14-16(zone _{vn} II)		16.2	1366	1.637	.68
S15-18,L17-20(zone _{vn} III)		33.3	4103	2.206	.35
S19-20 (zone _{vn} IV)		14.5	1003	1.928	.95

Table 4 List of the four zones investigated at Trinidad with similar zones reported at other localities.

Visible Zone at Trinidad	Other Site	Term	Source
Zone _v I - <u>Collisella digitalis</u>	Vancouver Island, British Columbia	Supra Littoral Fringe	Stephenson and Stephenson (1961a, 1961b, 1972)
	Neah Bay, Washington	Splash Zone	Rigg and Miller (1949)
	Barkley Sound, Washington	Littorina-glandula fasciation	Shelford, <u>et al.</u> (1935)
	Pacific Grove, California	Zone I	Hewatt (1937)
	Pacific Grove, California	Zone I - uppermost horizon	Ricketts, Calvin, and Hedgpeth (1968)
	Pacific Grove, California	Supra Littoral Fringe	Stephenson and Stephenson (1972)
Zone _v II - <u>Balanus Glandula</u>	Vancouver Island, British Columbia	Barnacle Zone in Midlittoral	Stephenson and Stephenson (1961a, 1961b, 1972)
	Neah Bay, Washington	High Part of Upper Intertidal	Rigg and Miller (1949)
	Pacific Grove, California	Zone II	Hewatt (1937)

Pacific Grove,
California

Pacific Grove,
California

Pacific Grove,
California

Point Lobos,
California

Zone_v III - Mytilus californianus Neah Bay,
Washington

Barkley Sound,
Washington

Pacific Grove,
California

Pacific Grove,
California

Pacific Grove,
California

Endocladia muricata - Balanus glandula association	Glynn (1965)
Zone II - High	Ricketts, Calvin and Hedgpeth (1968)
Upper Midlittoral	Stephenson and Stephenson (1972)
Moss Zone and Barnacles	Stephenson and Stephenson (1972)
Lower Part Upper Intertidal	Rigg and Miller (1949)
Mitella (Pollicipes) Mytilus fasciation	Shelford, <u>et al.</u> (1935)
Zone III	Hewatt (1937)
Zone III - Middle Intertidal	Ricketts, Calvin and Hedgpeth (1968)
Lower - Midlittoral	Stephenson and Stephenson (1972)

	Point Lobos, California	Mussel Zone	Stephenson and Stephenson (1972)
Zone IV - <u>Chthamalus dalli</u>	Barkley Sound, Washington	Anthopleura fasciation	Shelford, <u>et al.</u> (1935)
	Olympic Peninsula, Washington	Chthamalus area	Dayton (1971)

Table 5 Organisms recorded in the seaward quadrats during the redevelopment study. Number after each animal for the first twelve surveys represents densities; values for survey thirteen (test and control) are percentage cover. All algal values are percentage cover; a "P" means less than 10 per cent cover.

Table 6 Organisms recorded in landward quadrats during the redevelopment study. Number after each animal for the first twelve surveys in the test quadrats represents densities; values for survey thirteen (test and control) are percentage cover. All algal values are percentage cover; a "P" means less than 10 per cent cover.

LITERATURE CITED

- Auclair, A. and F. Geoff. 1971. Diversity relations of upland forests in the western great lakes area. *Amer. Nat.* 105 (946):499-528.
- Barnes, H. and M. Barnes. 1956. The general biology of Balanus glandula Darwin. *Pacific Sci.* X:415-421.
- Bartlett, B. 1972. Reproductive ecology of the California sea mussel Mytilus californianus Conrad. Masters thesis. University of the Pacific, Stockton, California. 67 p.
- Batham, E. 1958. Ecology of southern New Zealand rocky shore at Little Papanui, Otago Peninsula. *Trans. Roy. Soc. New Zealand* 85 (4):647-658.
- Bayne, B. 1964. Primary and secondary settlement in Mytilus edulis L. (Mollusca). *J. Anim. Ecol.*, 33:513-523.
- Berkeley, E. and C. Berkeley. 1952. Polychaeta sedentaria. *Can. Pac. Fauna* 9b (2):1-139.
- Bokenham, N. 1938. The colonization of denuded rock surfaces in the intertidal region of the Cape Peninsula. *Ann. Natal Mus.* 9:47-81.
- Bray, J. and J. Curtis, 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27: 325-349.
- Brillouin, L. 1962. *Science and Information Theory*. Academic Press, New York. 320 p.
- Castenholz, R. 1967. Stability and stresses in intertidal populations, p. 15-28. In T. Olson and F. Burgess (eds) *Pollution and marine ecology*. Interscience, New York.
- Chapman, V. 1946. Marine algal ecology. *Bot. Rev.* 12 (10): 628-672.

- Cimberg, R., S. Mann, and D. Straughan. 1973. A reinvestigation of Southern California rocky intertidal beaches three and one-half years after the 1969 Santa Barbara oil spill: a preliminary report, p. 697-702. In Proc. of Joint Conference on Prevention and Control on Oil Spill, March 13-15, 1973, Washington, D. C.
- Cirino, E. 1958. Evidence on true succession in marine littoral associations. Ph.D. Dissertation. Boston Univ., Boston, Mass. 251 p.
- Clarke, W. 1967. Discussion, dynamics of the littoral marine community, p. 43-50. In T. Olson and F. Burgess (eds) Pollution and marine ecology. Interscience, New York.
- Coe, W. and D. Fox. 1942. Biology of the California sea-mussel (Mytilus californianus). I. Influence of temperature, food supply and sex on the rate of growth. J. Exp. Zool. 90 (1): 1-30.
- Colman, J. 1933. The nature of the intertidal zonation of plants and animals. J. Mar. Biol. Assn. U.K. 18: 435-476.
- Connell, J. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle Chthamalus stellatus. Ecol. 42:710-723.
- Connell, J. 1970. A predatory-prey system in the marine intertidal region. I. Balanus glandula and several predatory species of Thais. Ecol. Monogr. 40:49-78.
- Connell, J. 1972. Community interactions on marine rocky intertidal shores. Ann. Rev. Ecol. and Syst. 3:169-191.
- Curtis, J. 1959. The vegetation of Wisconsin: an ordination of plant communities. Univ. of Wisconsin Press, Madison. 657 p.
- Czekanoski, J. 1913. Zarys metod statystycznyck. Warsaw.
- Day, J., J. Field and M. Montgomery. 1971. The use of numerical methods to determine the distribution of the benthic fauna across the continental shelf of North Carolina. J. Anim. Ecol. 40:93-123.

- Dayton, P. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41 (4):351-389.
- Dayton, P. and R. Hessler. 1972. Role of biological disturbance in maintaining diversity in the deep sea. *Deep-Sea Res.* 19:194-208.
- Dice, L. 1945. Measures of the amount of ecological association between species. *Ecol.* 26:297-302.
- Doty, M. 1946. Critical tide factors that are correlated with vertical distribution of marine algae and other organisms along the Pacific Coast. *Ecol.* 27:315-328.
- Doty, M. 1957. Rocky intertidal surfaces, p. 535-585. In J. Hedgpeth (ed) *Treatise on marine ecology and paleoecology*. *Memoir. Geol. Soc. Amer.* 67. Washington, D. C.
- Druehl, L. 1967. Vertical distributions of some benthic marine algae in a British Columbia Inlet, as related to some environmental factors. *J. Fish. Res. Bd. Canada* 24 (1):33-46.
- Fager, E. 1972. Pattern in the development of a marine community. *Limn. and Ocean.* 16 (2):241-253.
- Fahey, E. and M. Doty. 1949. Pioneer colonization on intertidal transects. *Biol. Bull.* 97:238-239.
- Feder, H. 1959. The food of the starfish, *Pisaster ochraceus*, along the California coast. *Ecol.* 40:721-724.
- Feder, H. 1970. Growth and predation by the ochre sea star, *Pisaster ochraceus* (Brandt), in Monterey Bay, California. *Ophelia* 8:161-185.
- Field, J. and G. McFarlane. 1968. Numerical methods in marine ecology. I. A quantitative "similarity" analysis of rocky shore samples in False Bay, South Africa. *Zool. Afr.* 3:119-137.
- Gislen, T. 1930. Epibioses of the Gullmar Fjord II. *Kristinebergs Zool. Stat. 1877-1927, Skr. Utg. av Svenska Vetenskapakad.* 4:1-123.

- Gislen, T. 1943. Physiographical and ecological investigations concerning the littoral of the northern Pacific, Sect. I. Lunds Univ. Arsskr. N. F. Adv. 2. 39 (5):1-63.
- Gislen, T. 1944. Physiographical and ecological investigations concerning the littoral of the northern Pacific. Sec. II-IV. Lunds Univ. Arsskr. N. F. Adv. 2. 40 (8):1-92.
- Glynn, P. 1966. Community composition, structure, and interrelationships in the marine intertidal Endocladia muricata-Balanus glandula association in Monterey Bay, California. Beaufortia 12 (148):1-198.
- Grant, V. 1963. The origin of adaptation. Columbia Univ. Press, New York. 606 p.
- Grigg, R., J. Maragus, and S. Townsley. 1970. Recolonization of hermatypic corals on submerged lava flows in Hawaii, p. 45. In Abstracts of Symposia and Contributed Papers, The Western Society of Naturalists, 51st Annual Meeting, Univ. Hawaii, Honolulu, Hawaii.
- Hall, A. 1969. Avoiding informational distortion in automatic grouping programs. Syst. Zool. 18:318-329.
- Harger, J. 1967. Population studies on Mytilus californianus, Ph. D. Dissertation. Univ. California, Santa Barbara. 318 p.
- Hatton, H. 1932. Quelques observations sur le repeuplement en Fucus vesiculosus des surfaces rocheuses denudees. Lab. Maritime Saint-Servan Bull. 9:1-6.
- Hewatt, W. 1935. Ecological succession in the Mytilus californianus habitat as observed in Monterey Bay, California. Ecol. 16:244-251.
- Hewatt, W. 1937. Ecological studies on selected marine intertidal communities of Monterey Bay, California. Amer. Midl. Nat. 18:161-206.
- Hilen, E. 1923. Report on a bacteriological study of ocean slime. Bur. Constr. and Repair U. S. Naval Dept. (unpublished)
- Hoshiai, T. 1961. Synecological study of intertidal communities IV. An ecological investigation on the zonation phenomenon. Bull. Mar. Biol. Stat. Anamushi 9:27-33.

- Huhta, V. 1971. Succession in the spider communities of the forest floor after clear-cutting and prescribed burning. *Ann. Zool. Fennici* 8:483-542.
- Hurlbert, S. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecol.* 52 (4):577-586.
- Johnson, D. and A. Skutch. 1928. Littoral vegetation on a headland of Mt. Desert Island, Maine. I. Submersible or strictly littoral vegetation. *Ecol.* 9:188-215.
- Kitching, J. 1937. Studies in sublittoral ecology. II. Recolonization at the upper margin of the sublittoral region: with a note on the denudation of *Laminaria* forests by storms. *J. Ecol.* 25:482-495.
- Kitching, J. 1945. An introduction to the ecology of intertidal rock surfaces on the coast of Argyll. *Trans. Roy. Soc. Edin.* 58:351-374.
- Knight, M. and M. Parker, 1950. A biological study of *Fucus vesiculosus* L. and *F. serratus* L. *J. Mar. Biol. Assn.* 29:439-514.
- Kulczynski, S. 1927. Zespoły roślin w Pieninach (Die Pflanzenassoziation der Pieninen). *Internat. Acad. Polon. Sci., Letter Bull., Clase Sci. Math at Nat., ser. B. Sci. Nat. Suppl.* 2: 57-203.
- Landenberger, D. 1967. Studies on predation and predatory behavior in Pacific starfish (*Pisaster*). Ph. D. Dissertation. Univ. California, Santa Barbara. 164 p.
- Landenberger, D. 1968. Studies on selective feeding on the Pacific starfish *Pisaster* in Southern California. *Ecol.* 49:1062-1075.
- Lewis, J. 1964. The ecology of rocky shores. English Universities Press, London. 323 p.
- Lloyd, M. and R. Ghelardi. 1964. A table for calculating the "equitability" component of species diversity. *J. Anim. Ecol.* 33:217-225.
- Loucks, O. 1970. Evolution of diversity, efficiency and community stability. *Am. Zool.* 10:17-25.

- MacGinitie, G. 1939. Littoral marine communities. Amer. Midl. Nat. 21:28-55.
- Margalef, D. 1958. Information theory in ecology. Gen. Syst. 3:36-71.
- Mauzey, K. 1966. Feeding behavior and reproductive cycles in Pisaster ochraceus. Biol. Bull. 131:127-144.
- Maycock, P. and J. Curtis. 1960. The phytosociology of boreal conifer-hardwood forests of the Great Lakes region. Ecol. Monogr. 30:1-35.
- Miller, M. 1946. Toxic effects of copper on attachment and growth of Bugula neritana. Biol. Bull. 90:12-14.
- Miller, M., J. Rapean, and W. Whedon. 1948. The role of slime film in the attachment of fouling organisms. Biol. Bull. 94 (134):157.
- Moore, H. 1939. The colonization of a new rocky shore at Plymouth. J. Anim. Ecol. 8:201-238.
- Moore, H. and J. Kitching. 1939. The biology of Chthamalus stellatus (Poli). J. Mar. Biol. Ass. U. K. 23:521-541.
- Motyka, J., B. Dobranski, and S. Zawadski. 1950. (Preliminary studies on meadows in the southeast of the province Lublin.) Univ. Mariae Curie-Sklodowska Ann., Sect. 1, 5:367-447.
- Muenscher, W. 1915. A study of the algal associations of San Juan Island, Pbl. Puget Snd. Biol. Sta. 1:59-84.
- Muenscher, W. 1916. Distribution of shore algae on Shaw Island. Pbl. Puget Snd. Biol. Sta. 1 (18):199-210.
- Nomias, J. and J. Huang. 1972. Sea level at southern California: A decadal fluctuation. Science 177:351-353.
- Northcraft, R. 1948. Marine algal colonization of the Monterey Peninsula, California. Amer. J. Bot. 35:396-404.
- Nybakken, J. 1969. Pre-earthquake intertidal ecology of Three Saints Bay, Kodiak Island, Alaska. Biol. Pap. Univ. Alaska, No. 9:1-117.

- Odum, E. 1963. Ecology. Holt, Rinehart and Winston, New York. 152 p.
- Odum, E. 1969. The strategy of ecosystem development. Science 164:262-270.
- Orton, J. 1929. Observations on Patella vulgata. Part III. Habitat and habits. J. Mar. Biol. Assn. U. K. 16:277-288.
- Osting, H. 1956. The study of plant communities. 2nd ed. Freeman, San Francisco.
- Paine, R. 1966. Food web complexity and species diversity. Amer. Nat. 100:65-75.
- Paine, R. 1969. The Pisaster-Tegula interaction: prey patches, predator food preferences and intertidal community structure. Ecol. 50:950-961.
- Paine, R. 1971. A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. Ecol. Monogr. 52 (6):1096-1106.
- Paris, O. 1960. Some quantitative aspects of predation by muricid snails on mussels in Washington Sound. Veliger 2:41-47.
- Peterson, C. 1914. Valuation of the sea. II. The animal communities of the sea bottom and their importance for marine zoogeography. Rep. Dan. Biol. Sta. 21:44+ app. 68.
- Pielou, E. 1966a. Shannon's formula as a measure of species diversity: its use and misuse. Amer. Nat. 100 (914):463-465.
- Pielou, E. 1966b. Species diversity and pattern-diversity in the study of ecological succession. J. Theoret. Biol. 10:370-383.
- Pierron, R. and Y. Huang. 1926. Animal succession on denuded rocks. Publ. Puget Snd. Sta. 5:149-158.
- Redfield, A. and E. Deevy, Jr. 1952. Temporal sequence and biotic successions, p. 42-47. In Marine fouling and its prevention. U. S. Naval Institute, Annapolis, Maryland.
- Rees, T. 1940. Algal colonization at Mumbles Head. J. Ecol. 28:403-437.

- Ricketts, E. and J. Calvin and J. Hedgpeth. 1968. Between Pacific tides. 4th ed. Stanford Univ. Press, Stanford, Calif. 614 p.
- Rigg, G. and R. Miller. 1949. Intertidal plant and animal zonation in the vicinity of Neah Bay, Washington. Proc. Acad. Sci. 26:323-351.
- Risk, M. 1971. Intertidal substrate rugosity and species diversity. Ph. D. Dissertation. University of Southern California, Los Angeles. 84 p.
- Sanders, H. 1969. Benthic marine diversity and the stability-time hypothesis, p. 71-81. In G. Woodwell and H. Smith (eds) Diversity and stability in ecological systems. Brookhaven Symp. Biol. 22.
- Scagel, R. 1961. The distribution of certain benthonic algae in Queen Charlotte Strait, British Columbia, in relations to some environmental factors. Pacific Sci. 14:494-539.
- Scheer, B. 1945. The development of marine fouling communities. Biol. Bull. 89:103-121.
- Shelford, V. 1930. Geographic extent and succession in Pacific North American intertidal (Balanus) communities. Publ. Puget Snd. Biol. Sta. 7:217-223.
- Shelford, V. and E. Towler. 1925. Animal communities of San Juan Channel and adjacent areas. Publ. Puget Snd. Biol. Sta. 5:31-73.
- Shelford, V., A. Weese, L. Rice, D. Rasmussen, and A. MacLean. 1935. Some marine biotic communities of the Pacific coast of North America Part I. General survey of the communities. Ecol. Monogr. 5 (3):251-332.
- Shrere, F. 1942. The desert vegetation of North America. Bot. Rev. 8:195-246.
- Smith, R. 1973. Numerical analysis of a benthic transect in the vicinity of waste discharges in outer Los Angeles Harbor, p. 195-237. In D. Soule and M. Oguri (eds) Marine studies of San Pedro Bay. Part II, Biological investigations. USC-SG-2-73. Allan Hancock Foundation, Los Angeles.

- Smith, R. and R. Emerson. 1971. A survey of the distribution species, community structure, and species diversity on a wharf piling. Unpublished report, Dept. Biol., University of Southern California.
- Sokal, R. and P. Sneath. 1963. Principles of numerical taxonomy. Freeman, San Francisco, 359 p.
- Southward, A. 1958. The zonation of plants and animals on rocky seashores. *Biol. Rev.* 33:137-177.
- Stephenson, T. 1938. A further comment on the results described. *Ann. Natal Mus.* 9:45-82.
- Stephenson, T. and A. Stephenson. 1961a. Life between tidemarks in North America, IV A. Vancouver Island. I. *J. Ecol.* 49:1-29.
- Stephenson, T. and A. Stephenson. 1961b. Life between tidemarks in North America, IV B. Vancouver Island. II. *J. Ecol.* 49:227-243.
- Stephenson, T. and A. Stephenson. 1972. Life between tidemarks on rocky shores. Freeman, San Francisco. 425 p.
- Stephenson, W. 1972 (in press). The use of computers in classifying marine bottom communities. UNESCO, Oceanographic Symposium, Wellington, New Zealand.
- Stephenson, W. and W. Williams. 1971. A study of the benthos of soft-bottoms. Sek Harbour, New Guinea, using numerical analysis. *Aust. J. Mar. Freshw. Res.* 22:11-34.
- Stephenson, W., W. Williams, and S. Cook. 1972. Computer analysis of Peterson's original data on bottom communities. *Ecol. Monogr.* 42 (4):387-408.
- Straughan, D. 1971. Breeding and larval settlement of certain intertidal invertebrates in the Santa Barbara Channel following pollution by oil, p. 223-244. In D. Straughan (ed) Biological and oceanographical survey of the Santa Barbara Channel oil spill 1969-1970, I. Allan Hancock Foundation, Los Angeles, California.
- Towler, E. 1930. An analysis of the intertidal barnacle communities of the San Juan archipelago. *Publ. Puget Snd. Biol. Sta.* 7:225-232.

- U. S. Department of Commerce, Coast and Geodetic Survey. 1971. Tide tables, west coast North and South America. 1971. U. S. Government Printing Office, Washington, D. C. p.
- Wahlenberg, G. 1812. Flora laponica, exhibens plantas geographicæ et botanicae consideratas in Lapponiis suecicis. Reimer, Berlin. 550 p.
- Whedon, W. 1936. Spawning habits of the mussel Mytilus californianus with notes of the possible relation to mussel poison. Univ. Calif. Publ. in Zool. 41 (5):35-44.
- Widdowson, T. 1965. A survey of the distribution of intertidal algae along a coast transition in respect to salinity and tidal factors. J. Fish. Res. Bd. Canada 22 (6):1425-1454.
- Wilson, O. 1925. Some experimental observation on marine algal succession. Ecol. 6:303-311.
- Wulff, B. and K. Webb. 1969. Intertidal zonation of marine algae at Gloucester Point, Virginia. Chesapeake Sci. 10 (1):29-35.
- Zenkevitch, L. 1963. Biology of the seas of the U.S.S.R. Wiley, New York. 955 p.
- Zobel, C. 1939. Primary film formation by bacteria and fouling. The Collecting Net 14.