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Ecological Studies on Selected Marine Intertidal Communities of Monterey Bay, California*

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Introduction

Marine sociological investigations have been carried out by various workers in several widely separated intertidal regions. Most of these studies are in the form of descriptive surveys, such as Verrill ('73), in the Vineyard Sound region; Sumner, *et. al.* ('11) and Allee ('23), in the Woods Hole vicinity; Hedley ('15) and Johnston ('17), on the Australian beaches; Shelford and Towler ('25), in the Puget Sound area of the Pacific coast; and Gislen ('31), in the Misaki district of Japan. Quantitative investigations in this field have been made on the Scottish coast, by Stephens ('28); in the Gullmar Fjord,

* This paper describes the results of part of the investigations carried out and submitted to the faculty of Stanford University as partial fulfillment of the requirement for the degree of Doctor of Philosophy.

Photograph of Cabrillo Point taken from the air.

by Gislen ('30) and Molander ('29); and on the coast of England, by Elmhirst ('32) and Pierrie ('32).

The results of these pioneer investigations have demonstrated the need of more extensive as well as intensive studies in other coastal rgions. By acquiring a detailed knowledge of the great variety of conditions represented in different littoral areas, more valid conclusions may possibly be drawn concerning the interrelationships of intertidal organisms and the effect of physico-chemical factors upon the restricted distribution of animal associations.

A survey of the literature published on the littoral faunas of the California coast reveals that, until the present time, practically all of the work has been of a taxonomic, morphological and embryological nature. The ecological aspect has been greatly neglected. It is true that scattered facts concerning the specific ecology of some of the animals are to be found in these papers and that the ecology of a few species has been dealt with in quite an exhaustive manner, but not a single paper dealing primarily with the sociological aspect of the littoral communities has been published.

The present paper is the result of a quantitative examination of the rocky beach faunas of the southern shore of Monterey Bay, California. The work was begun in October, 1931, and was carried on continually until June, 1933. Additional observations were made during the summer months of 1934.

The work was begun with the purpose of trying to determine more definitely the nature and causes of the vertical and horizontal zonation of the littoral invertebrates of a rocky shore. Notes on the prevailing physical and chemical conditions of the area were recorded throughout the period of investigation. In as many cases as the evidence permits, the effects of the physical factors upon the habits of the organisms are pointed out. The effects of some of the biotic factors upon the zonation were also studied and are recorded in this paper. Special attention was given to the feeding habits of the organisms.

The work is mainly concerned with 90 of the most commonly occurring macroscopic species of the intertidal area. A complete list of the species (170) identified during the course of the work is given at the end of the paper.

I wish to take this opportunity to express my appreciation to Professor Tage Skogsberg for many valuable criticisms and helpful suggestions offered in the course of this investigation.

Thanks are due Professor G. E. MacGinitie of the California Institute of Technology for having suggested the problem and for his untiring aid and sympathy in getting the project underway.

The work could not possibly have been carried out without adequate laboratory facilities and field equipment. For these and other courtesies I am indebted to Doctor W. K. Fisher, Director of Hopkins Marine Station.

In the study of an ecological problem, especially when dealing with marine communities where the relations of a great variety of species are concerned, one becomes indebted to a number of workers in special fields. The following taxonomists have very kindly aided in the determination of many of the organisms collected. Mrs. G. E. MacGinitie checked the identifications of all of the crustacea; Mrs. Ida Oldroyd, Curator of the Museum of Paleontology of Stanford University, assisted in the

determination of some of the gastropods; Doctor F. N. MacFarland identified most of the nudibranchs; Doctor R. L. Bolin aided in classification of the fishes.

Mr. H. W. Graham has very kindly given me certain photographs reproduced in this paper.

I.—Location of Investigated Area

The area studied in the present investigation is located on the southern margin of Monterey Bay, California, near the border line between the cities of Monterey and Pacific Grove. Here the granite base of the Monterey Peninsula projects out into the bay, forming the promontory called Cabrillo Point or Mussel Point, on which the Hopkins Marine Station of Stanford University is situated (Fig. 1). The area is about two miles east of Lighthouse Point which marks the southwestern extremity of the Bay, and is approximately in latitude 36° 37′ N. and longitude 121° 54′, Greenwich meridian.

The ecological transect which was chosen for this work extended across the intertidal zone directly north of the Jacques Loeb laboratory of the Hopkins

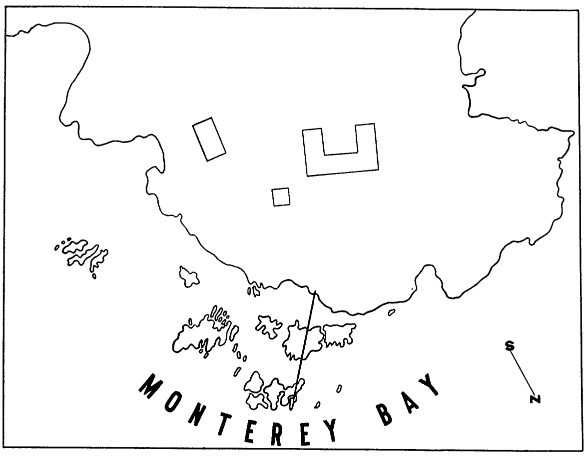


Fig. 1. Map of Cabrillo Point. The line extending from the shore indicates the investigated ecological transect.

Marine Station and was 108 yards long and one yard wide, with a bearing of N. 38° E.

This region was selected, first, because of its nearness to the laboratories of the marine station and, second, because the nature of the shore at this point allows several characteristic types of animal habitats to be exposed between the limits of the tides. By choosing this area, located near the laboratories, it was convenient to study the fauna throughout the entire year and to observe the seasonal changes in the inhabitants. Continuous and close observation was obviously one of the primary considerations in the investigation.

At Cabrillo Point a number of outlying, small granite islands project permanently above the sea level (Fig. 2). They protect the innermost portion

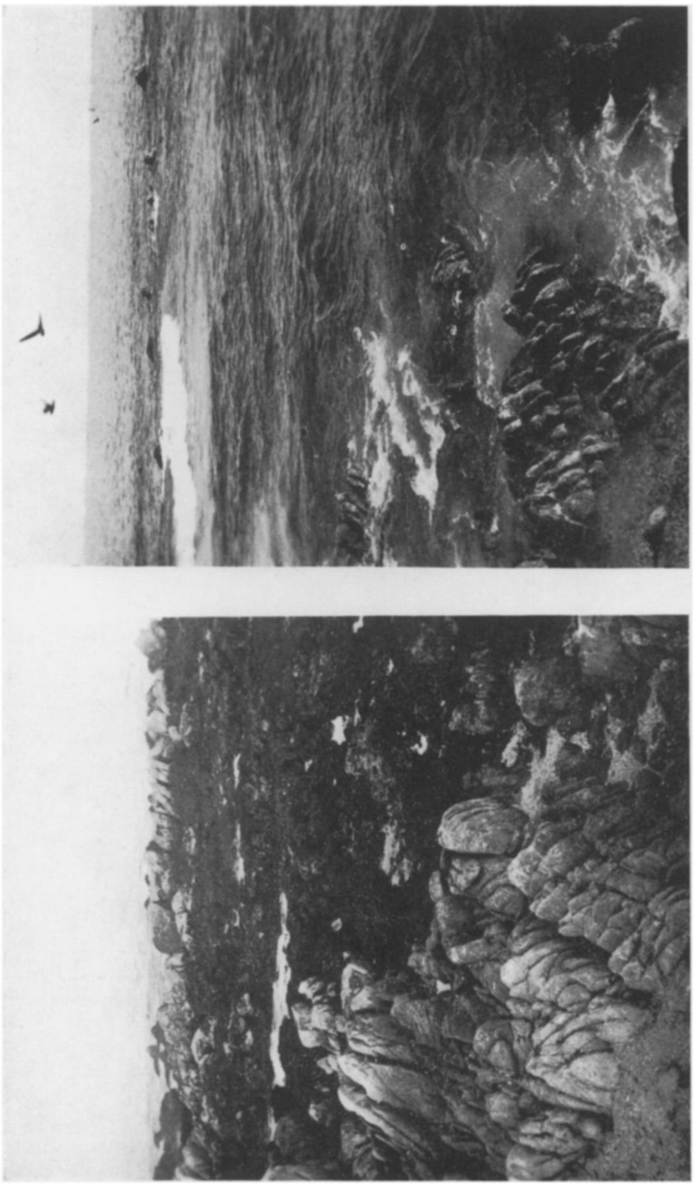


Fig. 2. A. View of the investigated area, taken from the shore during a period of low tide. B. View from the same location, taken during a period of high tide.

of the selected area from the intense wave action, characteristic of this region, while the outermost part of the line is exposed to the full force of the surf. Thus protected and exposed biotic associations occur within the tidal range.

The middle part of the selected strip crosses a fairly large tidepool which is covered with water even during the lowest range of the tides (Fig. 3). The strip also crosses two shallow channels between squares 41 and 48, and 85 and 90 (see p. 174). There is a repetition of low-tide level faunas on either side of these channels.

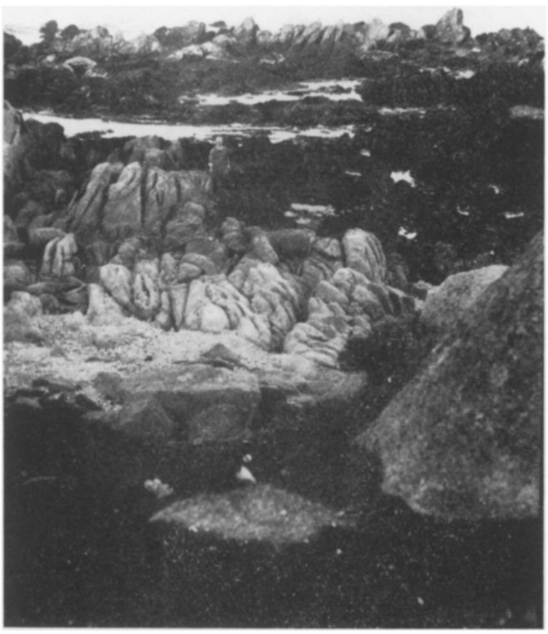


Fig. 3. Tidepool, in the background, across which the ecological transect passes.

It may finally be noted that the systematic study of the organisms of this locality has reached a state of perfection which allows an accurate determination of the material, a feature of paramount importance to the ecologist.

II.—General Environenmental Conditions

1. Geological Features

The substratum of the rocky shore at Cabrillo Point is a portion of the granite porphyry which forms the core of the Monterey Peninsula. According to Galliher ('32, p. 51), this porphyry is a local phase of the quartz-diorite which is of pre-Cretaceous age. The massive granite is cut by numerous pegmatite dikes. The removal of the granite, by weathering, from between the more resistant dikes produces a very rugged rock surface. The shore is also characterized by many large, granite boulders and by rocky islands which project above the water level near shore.

These features offer a very large surface for the attachment of sessile organisms and also present the varied animal habitats characteristic of a rocky coast.

2. Temperature of the Water

Daily temperature and salinity readings for the surface waters of Cabrillo Point are kept by the Scripps Institution of Oceanography, La Jolla, California. The data concerning these factors were very kindly placed at my disposal by Doctor E. G. Moberg, Acting Director of the Scripps Institution.

Figure 4 shows the records of the weekly mean and extreme temperatures of the surface water during the year 1932, in which period the greater part of this investigation was carried out. The weekly mean temperatures for a period of nine years are also given in this figure (see also Bigelow and Leslie, '28, p. 447).

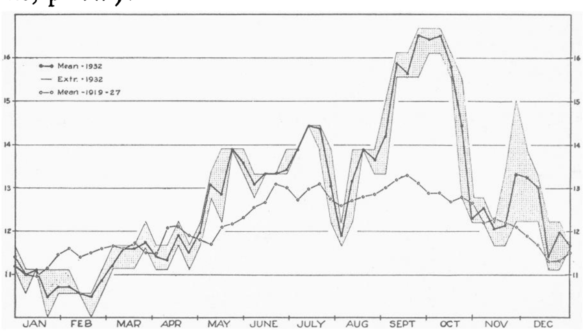


Fig. 4. Graph showing the temperature of the surface waters at Cabrillo Point.

It is evident from this graph that the temperature of the surface water at Cabrillo Point is characterized by two important features: first, the average temperature is moderately low to intermediate; and, second, the amplitude of variation is comparatively narrow. The lowest temperature, recorded in January and February, was as high at 10° C. The highest temperature, 16.8°, was reached in the latter part of September.

The figure shows that the highest temperatures occur regularly in the early fall. The mean weekly temperatures recorded over a long period of time range through approximately 2.5° C., a strikingly narrow amplitude.

A number of temperature readings were made at different hours of the day during all seasons in order to determine the variations throughout the day. These records demonstrate that the thermal variation is slight. The highest temperature recorded in this manner was 17.3°, on July 1, 1932, at 4 P.M. However, tidepool temperatures were recorded as high as 26° C. during July and as low as 3° C. during a severaly cold period in the winter of 1932.

The fact that the prevailing temperatures are fairly low to intermediate gives to the fauna of the area a comparatively northern aspect.

3. Salinity

There is practically no permanent fresh water drainage along the southern margin of Monterey Bay. The greatest fresh water supply of the Bay comes from the small Salinas River which enters the bay at a distance of approximately 20 miles northeast of Pacific Grove.

The daily salinity records for 1932 show a variation in salt concentration between 32.12 and 33.821 grams per liter. In this respect, too, the investigated area exhibits a very remarkable uniformity.

During the winter, when the rainy season occurs, the tidepools are greatly diluted. They often contain practically fresh water for short periods of time. Hardly any rain falls in this region from June to October 1, inclusive, and during the larger part of this period the drainage from the Salinas River is, for all practical purposes, negligible.

Figure 5 shows the weekly mean and extreme salinities for 1932 and the weekly means for the years 1919-1927, inclusive, according to the determinations made by Scripps Institution of Oceanography, ('28, p. 453).

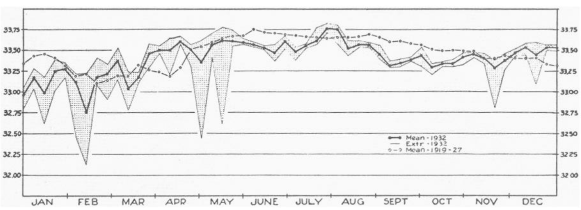


Fig. 5. Graph showing the salinities of the surface waters at Cabrillo Point.

4. Phosphate and Silicate

Weekly readings of the phosphate (PO_4) and silicate (SiO_2) of the surface waters near the laboratories were made during a full year, beginning in June, 1932. The results of these analyses are shown in Table 1. They demonstrate the presence of a perennial supply of these compounds sufficient for the development of the rich planktonic flora characteristic of this region.

Table 1. Average Monthly Phosphate and Silicate (g. per L.)

Month	Phosphate	Silicate
June 1932	0.05818	1.0628
July, 1932	0.04776	0.8502
Aug., 1932	0.06060	1.0246
Sept., 1932	0.07071	0.6148
Oct., 1932	0.08280	0.8880
Nov., 1932	0.06734	0.6148
Dec., 1932	0.10657	0.8198
Jan., 1933	0.10704	0.8289
Feb., 1933	0.12310	0.6660
Mar., 1933	0.11487	0.5911
Apr., 1933	0.10122	0.7515
May, 1933	0.12323	0.8485

5. Air Temperature and Rainfall

No continuous records of the air temperature and precipitation are kept at the Hopkins Marine Station. These conditions, however, are recorded at a meteorological station which is maintained on the Monterey Peninsula by the U. S. Weather Bureau at the Del Monte Properties Company. Some of the data collected by this organization were kindly placed at my disposal by Mr. L. W. Perry, director of the Del Monte Station.

TABLE 2. Air Temperatures for 1932

	Max.	Min.	Mean.	Mean Max.	Mean Min.	Av.Daily Range
January	68°	30°	45.5°	55.5°	36.0°	19.0°
February	77	28	47.2	57.6	36.7	20.9
March	78	31	56.1	62.4	40.8	21.6
April	79	33	53.0	64.0	42.0	22.0
May	84	43	57.2	65.4	48.9	16.5
June	80	42	58.9	67.5	50.3	17.2
July	78	46	59.7	68.6	51.0	17.5
August	80	43	60.3	69.7	50.9	18.8
September	67	48	61.7	71.1	62.3	18.3
October	80	37	66.5	67.4	45.5	21.9
November	81	32	62.3	65.0	40.7	24.3
December	66	34	43.2	53.7	32.7	21.0

Table 2 demonstrates that the coldest temperatures prevail during the months of December, January and February. The minimum temperature recorded for 1932 was 24° F. (-4.4° C.). Such low readings, however, are extremely rare for the coastal area of the Monterey Peninsula. The highest temperatures were reached during the month of September. The average daily range for 1932 was 20° F. (11.1° C.).

From the viewpoint of ecology, the most important information to be derived from these data is that the animal and plant communities, when exposed by the tide, very seldom are subjected to freezing air temperatures. It is, indeed, very doubtful if exposure to cold air ever inflicts any serious damage to the fore-shores of this region. Other facts noteworthy in this connection are that during the warmer parts of the year foggy weather is very common and tidal exposure, generally speaking, occurs at night and in the early morning when the air temperatures still are comparatively low.

The average amount of rainfall in this area is very low as shown in Table 3.

TABLE 3. Precipitation for 1932

	Total Moisture	Greatest Daily	No. of Days .01″
January	4.06″	1.53″	15
February	3.07	1.17	10
March	0.33	0.24	3
April	0.39	0.22	5
May	0.72	0.55	5
June	0.00	0.00	0
July	0.00	0.00	0
August	0.01	0.01	1
September	0.00	0.00	0
October	0.00	0.00	0
November	0.18	0.18	2
December	0.56	0.56	12

Total precipitation—11.16″

6. Aeration

No records of the oxygen content of the waters of Cabrillo Point were taken during the course of this work. It may be safely assumed, however, that the intertidal water is almost continuously saturated with oxygen because of the vigorous surf action in the area. Moreover, the abundant growth of algae found on the littoral rocks also aids substantially in keeping the oxygen content high.

The photograph shown in Figure 6 gives evidence of the intensive action of the surf in this region.

Fig. 6. View showing the heavy surf on the rocks at Cabrillo Point.

7. Light Conditions

A record of the overhead conditions in the vicinity of the area investigated was taken twice daily during the year 1932. The light conditions were recorded at 8 A.M. and at 1 P.M. The records show that the region is protected from direct insolation during most of the forenoons and late afternoons. There were often a few hours of intervening sunlight during the middle of the day. The summer months were found to be exceptionally foggy.

These weather conditions, of course, prevent a wide variation in the air temperature and thereby greatly enhance the productivity of life in the intertidal communities.

8. Tides

In Monterey Bay there are two high tides and two low tides in every lunar day of approximately 24 hours and 50 minutes. It is apparent, therefore, that on each succeeding solar day the corresponding tides occur 50 minutes later than on the previous day. The heights of the two daily tides are comparatively equal only during the half-moon periods. At the full and new moon periods there is a great difference between the levels of the tides, especially in the case of the low tides, due to the varying declination of the moon. During these periods there are very pronounced higher high and lower low tides with intervening lower high and higher low tides. For instance, on June 14, 1932, there was a difference of 2.5 feet between the two high tides, and on the 18th of the same month there was a difference of 4.8 feet between the two low tides. From such conditions, it follows that there is a wide range in the extremes of the tides but the mean range is much less in extent. For the year 1932, during which the greater part of this investigation was made, the extreme range of the tide was 8.6 feet while the mean range for the same period was 3.5 feet.*

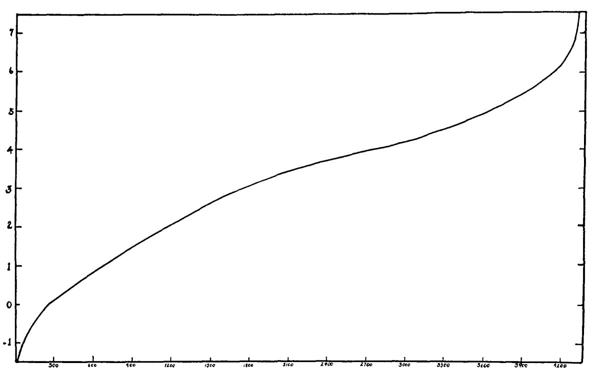


Fig. 7.
Graph showing the number of hours of exposure at various levels in the intertidal during a period of six months.

This variation in the two daily tides has a pronounced effect upon the animal and plant communities of the intertidal belt. The organisms living near the high tide limit are exposed for longer periods of time than similarly located forms in regions where the tides are approximately equal. Conversely, the organisms at or near the low tide limit are exposed less frequently and for shorter total time. This condition or variation in the periods of exposure at different depths causes definite breaks in the biotic sequence of the intertidal area which will be discussed later in this paper.

E. F. Rickets (unpublished manuscript) has constructed a diagram to show the time of exposure of organisms at different levels in the intertidal belt. His data were taken from the records of the tide recording machine at Crissy Wharf, just inside the Golden Gate at San Francisco, for the six month period from January 1, to July 1, 1931. He calculated the number of hours of exposure at each six inch level and thus obtained the total for the six month period. By his kind permission, the results are shown in Figure 7.

* These figures were calculated from data given by the Coast and Geodetic Survey in the "Pacific Tide Tables" for the Golden Gate at San Francisco, which is the port of reference for Monterey.

A study of this graph reveals the fact that the organisms below mean lower low water (the 0.0 of the tide tables) are exposed for relatively short periods of time. At the mean high water level there is a definite upward bend of the exposure curve. Organisms above this level are exposed for relatively long periods of time.

It is a fact of the most profound ecological significance that at the levels noted in the last paragraph, there are also breaks in the sequence of the biotic communities. Below the mean lower low water line, one finds associations which extend below the littoral into the sublittoral. The area above the 5 foot level is inhabited exclusively by such forms as, for example, *Littorina planaxis* which can withstand long periods of exposure.

A further discussion of the effect of the tidal rhythms upon the vertical distribution of the littoral organisms is given in Part V.

III.—Apparatus and Methods

For the benefit of those who, without previous experience, intend to enter upon this type of work, it may be advisable to present in this connection a list and brief description of the apparatus and other materials which were found useful or indispensable in the course of this investigation.

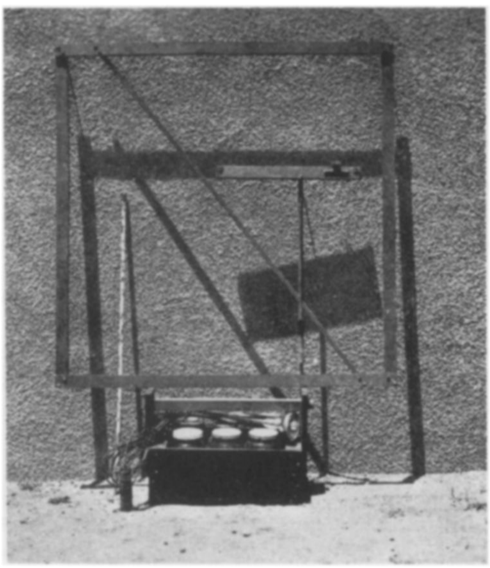


Fig. 8. Photograph of the field equipment used during this investigation.

The apparatus and materials were of three main types and may be listed as follows.

Field equipment: Square wooden frame of 1 square yard inside area; levelling instrument; stadia rod; iron rod, 3 feet long; thermometer; insulated wire line, 24 feet long; writing pad consisting of 20 white celluloid sheets, 8 x 4 inches.

Laboratory equipment: Aquaria; sorting pans; killing pans; glass tubing; preserving containers; finger bowls; syracuse dishes.

Chemicals: Formalin and ethyl alcohol, used as preservatives; magnesium sulphate, menthol, and chlorotone crystals, used as anaesthetics; Bouin's solution, used as a fixative.

The wooden frame, which was used to set off each square yard under analysis, was constructed of strips of hardwood (Fig. 8). Both sides of the frame were marked at one foot and 0.1 feet intervals in order that counts could be made and locations determined more accurately.

The instrument used in determining the levels along the ecological transect was constructed from angle brass. A piece of angle brass, 1.5 inches wide on each side and 17 inches long, was attached to the end of a brass tube, 20 inches long. A spirit tube of a level or "bubble" was fastened near one end of the angle brass and against the vertical portion. Above the bubble was placed a 1.0 x 1.5 inch mirror at an angle of 45° to the base. Small brass angles, each containing a 1/16 inch sight hole, were fastened at either end of the base at levels which caused a line connecting the sight holes to lie just above the level of the bubble. A brass rod, 20 inches long, was inserted into the bottom of the brass tube and was held in place by a brass sleeve containing a set-screw (Fig. 9). This simple apparatus can be made very cheaply and serves as well as a more expensive leveling instrument.

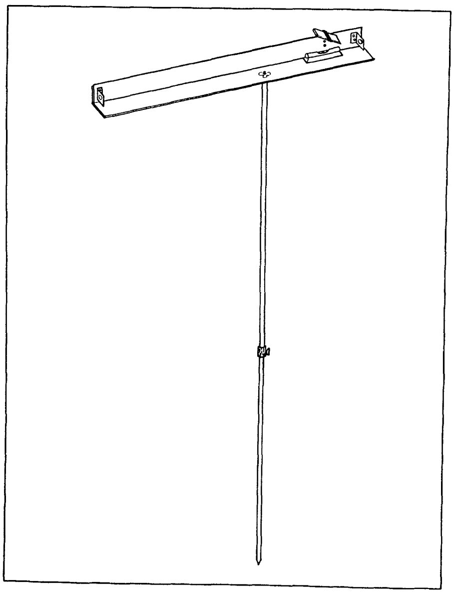


Fig. 9.
Diagram of
leveling instrument.

The collecting box was furnished with eight compartments, each large enough to hold one quart jar. Four holes for holding small vials, each 1 inch in diameter, were bored in the top of each end piece.

The small plankton net was used at various times for collecting the eggs and larvae. It was also useful in collecting small motile animals, e.g., isopods, amphipods, hetero-nereis, etc.

Several salt-water aquaria were used for observing the habits of various organisms.

Round pans, 12 inches in diameter, were used for sorting pans; and square pans, 12 x 12 inches, were employed for killing. Such an arrangement prevented the unintentional use of vessels which had contained a lethal substance.

The use of the remainder of the apparatus and chemicals will be explained in the following description of the methods used in the investigation.

In 1930, with the cooperation of the United States Coast and Geodetic Survey, Professor G. E. MacGinitie established four bench marks at intervals along a straight line, perpendicular to the shore, across the entire intertidal area directly north of the Jaques Loeb Laboratory of the Hopkins Marine Station. The first bench mark, at a level of18.38 feet, was imbedded in a granite base upon the shore. The second one was fixed about 25 yards out in the intertidal area, at a level of 3.82 feet. The third point was set in the granite base of a fairly large tide pool about one half the distance across the intertidal zone, at the 1.67 foot level. The last datum point was located in the mussel habitat near the low tide level, at 0.3 feet.

The early part of the investigation included a survey of this area, a topographic sketch being made of each square yard. A record was kept of the number of individuals of each species found within the square yard units. With the exception of the upper 25 square yards, this field work could be done only at low tide periods during which times most of the area was exposed for three to four hours.

An iron rod, 3 feet long, was inserted in a small hole in the first bench mark and a stadia rod, 10 feet high, was set up with the base resting on the second bench mark and thus in line with the first and fourth datum points. Three guy ropes, with an iron weight attached to each loose end, were used to hold the stadia rod in an upright position. An insulated wire, 24 feet in length, was stretched along the line to be investigated. Starting from the second datum point, a wooden frame one yard square, was placed serially along the west side of the line and the organisms within each square area were counted and recorded. A surface view of each unit was also sketched. This procedure was repeated until a strip 108 yards in length had been mapped and a census taken of its animals.

The records were made on white celluloid sheets which were not destroyed when handled with wet hands and after becoming moistened by wave splashes. The sketches were transferred to a long roll of graph paper with one square inch representing the actual square foot.

The levels of each square were recorded. The leveling instrument described above proved to be a very effective means of determining the heights of the various points above sea level. From the data thus collected a vertical section was constructed on the graph paper just above the topographic sketches of the squares. Those sketches and sections, reduced to one inch to the square yard, are appended at the end of this paper.

After the qualitative and quantitative survey had been completed for the entire 108 square yards, it was realized that an intensive survey could not possibly be made over this large area during each season through the period in which the investigation was to be completed. A study of the data, however, revealed that certain squares could be set aside as typical of a section of the transect. These typical squares were re-examined intermittently during the changing seasons and the new populations were recorded. The variations in the numbers of the different organisms are discussed in the section on Animal Distribution and Zonation.

During the course of the survey, representatives of each species were collected and brought into the laboratory to be determined and preserved. Others were placed in aquaria equipped with running sea water where their habits could be more easily observed.

IV.—Some Questions Concerning the Terminology of the Biotic Distribution and Zonation

There exists in the ecological literature, particularly in that dealing with marine communities, a great deal of confusion and inconsistency concerning the definition and application of the terms pertaining to the distribution and zonation of organisms. Such a condition is not surprising when one considers the small amount of quantitative investigation that has been done in marine sociology. It should also be kept in mind that the attempts to classify marine communities were made by workers in widely separated parts of the earth where the physical conditions, as well as the living forms, of the areas studied were far from similar. The gradual increase of knowledge of marine biotic communities has proven the futility of a general ecological classification based upon investigation in a few small areas.

Gislen (1930, pp. 46-62) presents an excellent account of the early history of the terminology used in the classification of the broader vertical regions of the sea. He calls attention to the fact that the attempts by the early investigators to classify the larger divisions of the sea floor upon the basis of biotic limits are of little value outside of the local areas. The different physical conditions which prevail in the various coastal regions may cause pronounced changes in the biotic levels. The organisms used in limiting the vertical zones may not even be present in some areas.

The littoral, with which we are concerned in the present work, has been defined in a number of ways by various investigators.

Some authors extended the lower limit of the littoral far below the intertidal area. For examples note the works of Peterson ('13), Murray and Hjort ('12), and Russell and Yonge ('23).

Most of the more recent writers limit the littoral to the intertidal area, but still there appears to be no agreement in regard to the definite limits.

Following the detailed definition of the littoral given by Gislen ('30, p. 48), the fundamental limits of the littoral are: *the mean higher high water line of spring tides and the mean lower low of spring tides.* It appears to me that this definition of the limits is justifiable, although, as pointed out by Gislen, the exact limits may be altered in certain regions by local physical conditions.

Those forms which inhabit the belt three or four feet above the high tide limit, and at the same time are definitely halobiotic, are referred to the supralittoral. This area is also inhabited by lizards and a few species of insects and arachnids. These are not taken into account in this work.

In the littoral region, where the physical and biological environments of the organisms are so complex, it is probably impossible to establish a perfect classification of the communities. This is demonstrated by the fact that some animals occur in one habitat during high tide periods and in others during the periods of exposure to the air. Moreover, some animals are active and roam only when complete darkness prevails. These constantly recurring variations in the communities require that the terms used in classifying the units of animal societies must be plastic. It must also be understood that the limits of the units are local and more or less arbitrary.

There are two main methods which are followed in the classification of ecological units. One group of workers bases the classification upon the obvious variations in the physical and chemical environment of the organisms. The other group designates the biotic units according to characteristic aggregations of organisms.

It was first pointed out by Peterson ('15) and later emphasized by Shelford ('25) that the units of animal communities of the sea bottom should be based upon the distribution of species which are closely similar as to the physical and chemical requirements. This method has been followed in most of the recent marine ecological works, *e. g.*,, in Molander ('28) and Gislen ('30). In all of these cases the investigations were carried out over wide areas of the littoral and sublittoral in which it was possible to observe the limits of the broader ecological units. It is claimed by these writers that the animal aggregation is the best index to the limiting factors of the environment. The *association* is designated by those following Peterson's lead, as the fundamental ecological unit of biotic communities. There is obviously no agreement among these writers concerning the valuation of the association, and as a consequence there has developed much confusion in the terminology of the ecological literature in this respect.

Those who classify the communities according to the type of the habitat also use the term *association*. Here again, there is comparatively little unanimity in the conceptions of the unit.

This confusion will continue until the units can be more clearly defined and until they cease to be indefinite concepts. It is certain that more extensive quantitative investigations with more exact knowledge of the interrelationships of the animal aggregations will help to solve this problem.

There are certain species each of which tends to form a characteristic community in the area which it inhabits. That is, these forms alter the environment to such an extent that the area becomes a favorable habitat to some species and unfavorable to others. This condition may be brought about by one or more of several characteristics of the predominating species, such as size, numbers, or methods of living. In an area inhabited by such forms, the biological factors are found to be more pronounced than the physical factors and a more definite relationship exists between the members of the society. In cases where there is a pronounced interdependence among the organisms, these may be said to form an association and the species which *controls* the environment may be called a dominant. It is on this basis that the term *association* is used in the following pages.

On the other hand, there are certain species, for example *Littorina planaxis,* which do not take part in any of the complex animal societies but are restricted to certain niches of the habitat limited by physical or chemical factors or both. Such isolated species are usually found in places where conditions are very extreme and thus where only specially adapted forms can exist.

Any investigation dealing exclusively with the associations will omit many interesting forms. It will, therefore, fail to give a complete description of the ecological conditions existing within a given area. In the present report an attempt has been made to include all forms which occur in appreciable numbers, even though some of them do not constitute a part of a definite association of organisms.

In discussing the distribution of the organisms of the intertidal region studied in the present investigation, the littoral has been divided into four vertical zones based upon the relative periods of exposure. As was noted in a previous sub-division (Tides), these zones are characterized by more or less definite communities whose limits are marked by obvious breaks in the faunal sequence. At the same time it should be emphasized that these zones do not correspond to the "associations" of other writers. Such a division has only a restricted applicability, but even so it is thought to be justifiable since it permits one to describe the faunal aggregates in this region in relation to the most pronounced local limiting factor, the tidal rhythms.

In brief, the following interpretations and considerations have been applied to the terminology of these ecological concepts in the present report:

1. *Littoral:* This is the area between the mean higher high water and the mean lower low water lines of spring tides.

2. *Supralittoral:* This is the area above mean higher high water level at spring tides which is inhabited by halobiotic forms.

3. *Zone:* This term has a restricted, more or less local, application in this report. It is used to designate a subdivision of the littoral, in the form of a horizontal strip. The development of the zone in the investigated area is connected either directly or indirectly with the physical environmental factors, especially the tides.

4. *Association:* This is an aggregation of organisms which is initiated by a single species and which depends for its existence upon this dominant form. It is a concept subordinate to that of the zone.

V.—Animal Distribution and Zonation

It has long been recognized by marine biologists that there is a definite zonation of the organisms found in the littoral. The most conspicuous elements marking this zonation are found among the plants and sessile animals. Upon the basis of these forms, the littoral has often been divided into several vertical zones. For example, King and Russell ('09) describe four zones characterized by both animals and plants; Pearse ('13) divided the littoral into four zones, one animal and three plant zones; Flattely and Walton ('22) recognize six. None of these writers offers any discussion of the factors which may be responsible for the zonation of the organisms.

Johnson and York ('15) recognize four littoral zones of the vegetation in Cold Spring Harbor, New York. They assert that the periods of exposure and submergence in the intertidal area are the most significant factors influencing the zonation of intertidal plants. Data are given to show the relative time of exposure of the foreshore at six inch intervals, but no correlation of exposure time with the plant zonation is indicated by these authors. However, when one plots the exposure curve from the figures given by these writers (ibid., p. 135), the result is of the same nature as that shown in Figure 7 of this paper. The limits of the upper and lower zones correspond very closely with the obvious bends in the exposure curve.

In a study of the littoral fauna and flora of Church Reef in Wembury

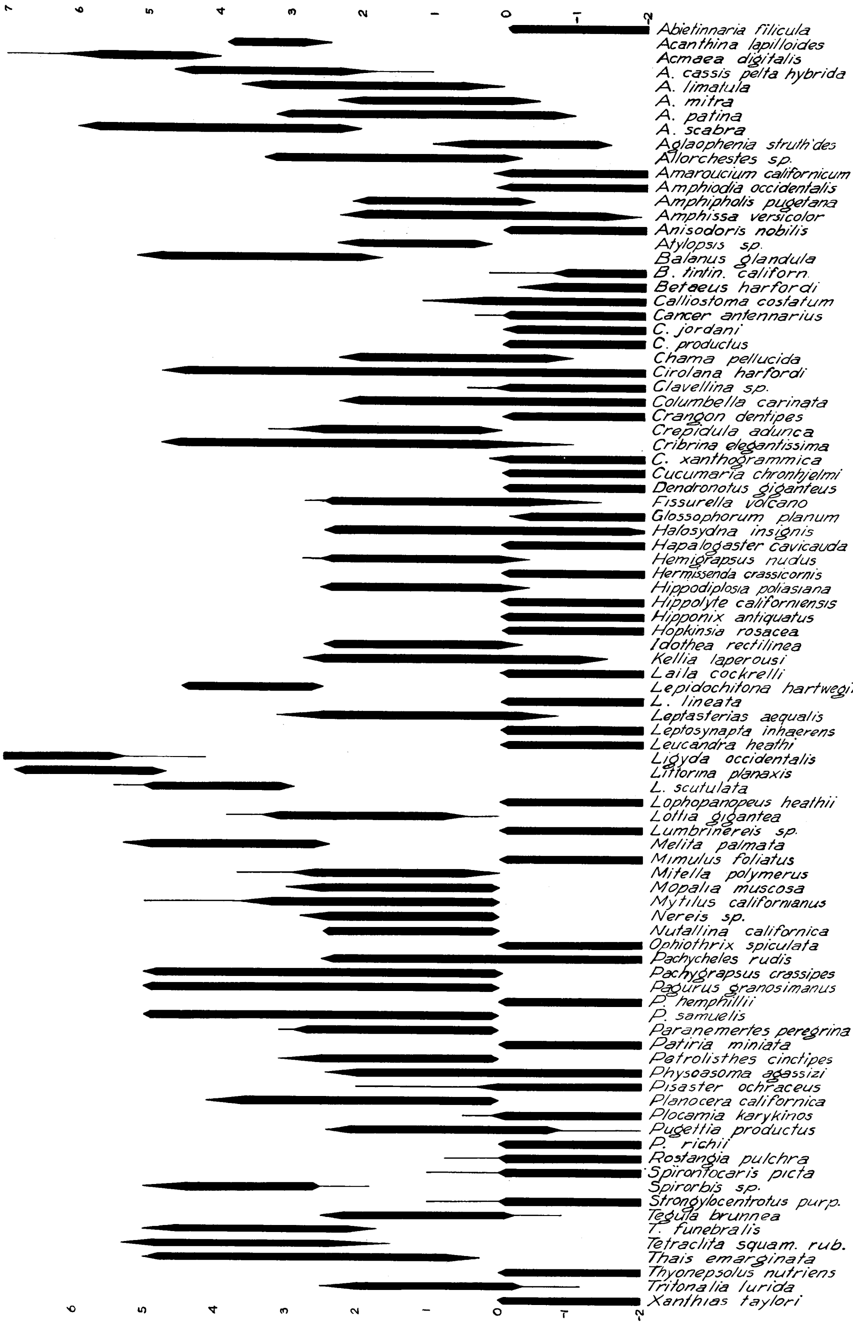


PLATE 1. Diagram showing the upper and lower limits of species of intertidal animals.

Bay, England, Colman ('33) points out the pronounced effect which the periods of exposure have upon the vertical distribution of the organisms. By determining the upper and lower limits of 22 species of plants and animals he shows that the most critical levels in the Wembury area are: "(a) between Mean and Extreme Low Water Springs; (b) between Mean Low Water Neaps and Springs; (c) at Extreme (Lowest) High Water Neaps."

From an analysis of the quantitative data, given in Table 10, and from the levels shown in the profile of the ecological cross section (Plate 2), it was possible to determine the upper and lower limits of the most common species found within the area studied in Monterey Bay. The results of this analysis are shown in the diagram of Plate 1. Some sources of error caused by the irregular nature of the rock surfaces were checked in the field by means of a transit level in order that the diagram would show, as nearly as possible, the exact vertical limits between which the organisms ranged.

It should be noted here that the predicted tide levels in areas exposed to an appreciable wave action can not be correlated exactly with the biotic limits. This fact has been pointed out by Orton ('29) and by Colman ('33). These investigators have allowed two feet for the extent of the "splash zone."

In an area such as the one under consideration, there would be no justification for allowing a strip of uniform width throughout the transect to represent the spray zone. In the outermost portion of the section, where surf action is great, especially during the stormy winter months, the upper limits of the ranges may be extended several feet, while in the innermost protected region the exaggeration of the levels is much less pronounced. The height of the splash zone also varies greatly with the seasons of rough and calm weather. Because of these variable factors of the surf, no allowance has been made for the wave action.

The limits of the ranges of the organisms found in the exposed littoral are less definite than those of the protected littoral. This condition is a result of the more irregular nature of the periods of submergence and emergence in the exposed area. In Plate 1, this has been indicated in some cases by a variation in the width of the lines; see, for example, *Mytilus californianus*.

The total number of upper and lower limits of the ranges of the organisms and the total number of species occurring between intervals of two-tenths of a foot in the intertidal were obtained from the data given in the graphic diagram of Plate 1. These figures are shown in Table 4 and are plotted in Figure 11.

The figures show three significant breaks in the faunal sequence of the intertidal area of this region. By far the most pronounced of these breaks is found at the level of mean lower low water, the zero of the tide tables. Many sublittoral inhabitants extend up into the littoral as far as the zero tide level but very few of them extend beyond this point. This is undoubtedly connected with the fact that above the mean lower low water level there is a sudden increase in the number of hours of exposure to which the organisms are subjected, as is shown in Figure 7.

Between the five and six foot levels there is also a definite change in the fauna, marked by the upper limit of the range of *Balanus glandula*. Several species of animals which are closely associated with these barnacles are not found above the five foot level. Between these levels, too, there is a marked change in the exposure curve as shown in Figure 7.

The distinct changes in the faunal sequence at the two levels, zero and five feet, thus appear to be the direct results of the relatively sudden changes in the amount of exposure at these levels. Furthermore, in each case, the level is most definitely marked by the upper limits of sessile animals.

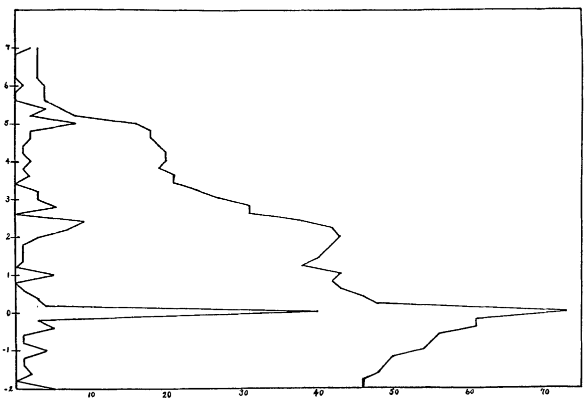


Fig. 10. Graph showing the total number of upper and lower limits of the ranges of organisms (left) occurring between the intervals of two-tenths of a foot.

TABLE 4. Total species and total upper and lower limits at intervals of 0.2 feet.

Level	Total Species	Total Limits	Level	Total Species	Total Limits
7.0	3	2			
6.8	3	0	2.4	38	9
6.6	3	0	2.2	42	7
6.4	3	0	2.0	43	3
6.2	3	0	1.8	42	1
6.0	4	1	1.6	41	1
5.8	4	0	1.4	40	1
5.6	4	0	1.2	38	0
5.4	6	4	1.0	43	5
5.2	8	2	0.8	42	0
5.0	16	8	0.6	43	1
4.8	18	2	0.4	46	3
4.6	18	2	0.2	48	4
4.4	19	1	0.0	73	40
4.2	20	1	–0.2	61	3
4.0	20	2	–0.4	61	5
3.8	19	1	–0.6	56	1
3.6	21	2	–0.8	55	1
3.4	21	0	–1.0	54	4
3.2	24	3	–1.2	50	1
3.0	27	3	–1.4	49	1
2.8	31	6	–1.6	48	2
2.6	31	0	–1.8	46	0

A third critical level occurs between the tide levels of two and three feet. The animal limits which mark this level are scattered through a vertical distance of one foot. In other words, this level is not so sharply defined as the other two.

The middle level appears to be the direct result of the heavy growth of *Pelvetia* and *Fucus* which are attached to the rocks of this area. The upper limit of this algal belt occurs at 3.5 feet. It forms by far the most obvious and striking line to be found in the littoral of this region (Fig. 11). The

Fig. 11. View of the intertidal area showing the prominent line formed by the upper limit of the Pelvetia-Fucus belt and the lower limit of the *Balanus glandula association.*

heavy growth of the fronds of the algae covers a belt between the levels of two and three feet. It is within this belt that the upper limits of the ranges of a number of intertidal animals are found.

Practically all of the animal species found in the zone between the zero and three foot levels are roving forms; and there is a very close ecological relationship between the fauna and the flora existing in the area. The rock surfaces retain their moist condition throughout the periods of exposure since they are covered by the algal fronds. The covering of the algae also protects the area from strong insolation. Thus a number of types of animals such as limpets, chitons, and snails which wander about during periods of darkness and at high tide periods, are to be found only beneath the layer of algae during times of exposure. Since all of the quantitative data presented was collected during the hours in which the area was exposed to air and sunlight, these factors of exposure apparently account for the definite critical level in faunal distribution which is noted at this point. This is an excellent example of the difficulty facing the ecologist in his attempt to classify the animal communities noted above. The classification accepted in this report is intended to be a practical one. It holds for the low tidal periods when the ecologist is at work but not for the high tide intervals. During the low tidal periods a concentration and during the high tidal periods a scattering of the animals occurs.

The upper limit of the *Pelvetia-Fucus* habitat which is so definitely marked at the 3.5 foot level may be the result of tidal frequencies. It corresponds exactly with the point in the littoral which is crossed most frequently by the oscillating tidal waters (Fig. 12). The zonation of the animals in this area thus appears to be caused by the tide. The effect of the tide is partly direct, partly indirect through its influence over the *Pelvetia-Fucus* belt.

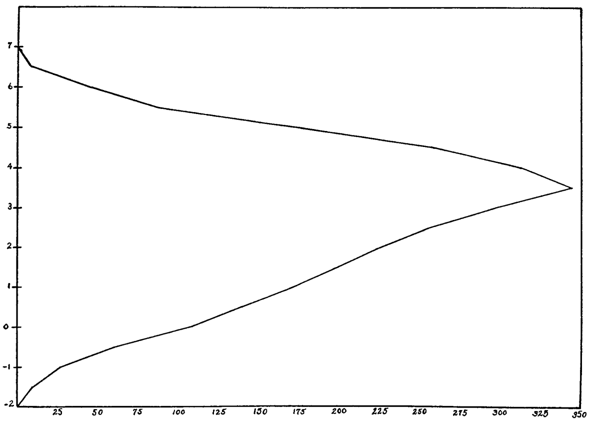


Fig. 12. Graph showing the frequency of the tidal waves at intervals of two-tenths of a foot in the intertidal area. (Data taken from Tide Tables.)

The middle faunal level is further emphasized by the lower limit of *Balanus glandula*. The range of this barnacle ends abruptly along the level at which *Pelvetia* fronds cover the rock surface (Fig. 11).

On the rocks of the exposed littoral which do not support any growth of *Pelvetia* and *Fucus* the zone between zero and three feet is densely populated with *Mytilus californianus* and its associated faunas.

On the basis of this zonation of the littoral animals, the intertidal has been divided vertically into four zones. In the following pages, each of these zones with its main inhabitants is described and at the end of each description a table is given showing the species and numbers of individuals of each found in a representative square yard. At the end of the section is a table showing the quantitative distribution of ninety of the most commonly represented species found along the ecological transect.

1. Supralittoral

The only halobiotic species commonly found among the supralittoral rocks, above the high tide line, is *Ligyda occidentalis*. These large isopods are found in rock crevices high above the spray zone. They apparently constitute a transition form between the marine and terrestrial life which has not as yet completely lost its affiliation with the marine habitat. During low tide periods and particularly after darkness, they make excursions into the upper region of the littoral in search of particles of detritus which constitute their food.

Several species of insects and arachnids, as well as one lizard, not belonging to the halobiosis, were noted in the supralittoral but were not identified.

2. Littoral

Zone I. The uppermost zone of the rocky shore at first appears to be a barren area. A close examination, however, will reveal that it supports a thin coating of small algae, a meagre pasture upon which a few animals browse. Only those organisms which have the ability to survive long periods of exposure to the strong insolation and to the fresh water of the winter rains are able to survive in this habitat.

Littorina planaxis is the most characteristic animal on the rock surfaces of this zone. At low tide they are found congregated in cracks and crevices in which water is retained after the tide has receded. Exiccation experiments carried out in the course of this investigation have shown that these periwinkles can withstand a maximum period of not less than 64 days without being submerged in sea water.

Two limpets, *Acmaea scabra* and *A. digitalis*, are found in the lower half of this zone. The former species is numerous in the protected areas, while a small growth form of *A. digitalis* is most abundant on the exposed rocks. Since the splash zone in the exposed littoral extends much higher than in the protected littoral, *A. digitalis* appears to range up to a higher level than does *A. scabra*. The large "homing" specimens of *A. scabra*, however, have a higher range on the rocks which are not exposed to wave action.

In the highest tide pools a eurythermal copepod, *Tigriopus fulvus*, is extremely abundant in all seasons. The temperature of the water in these pools fairly often reaches 29° C. during the summer months, and was recorded as low as 3° C. in the winter of 1932.

Square No. 12 is typical of this zone. Its contents are given in Table 5.

Table 5. Contents of Square No. 12

Acmaea digitalis	2
Acmaea scabra	19
Ligyda occidentalis	4
Littorina planaxis	28
**Tegula funebralis* (small)	27

* In a shallow tide pool.

Zone II. The rock surfaces between the levels of three and five feet are densely inhabited by rock barnacles and their associated fauna. Horizontal surfaces are completely covered with *Balanus glandula* which are greatly elongated because of the crowded condition. The presence of these barnacles gives to this belt of the foreshore a characteristic physiognomy (Fig. 13). Practically all forms found in the zone are dependent upon the barnacles for food or for protection against desiccation.

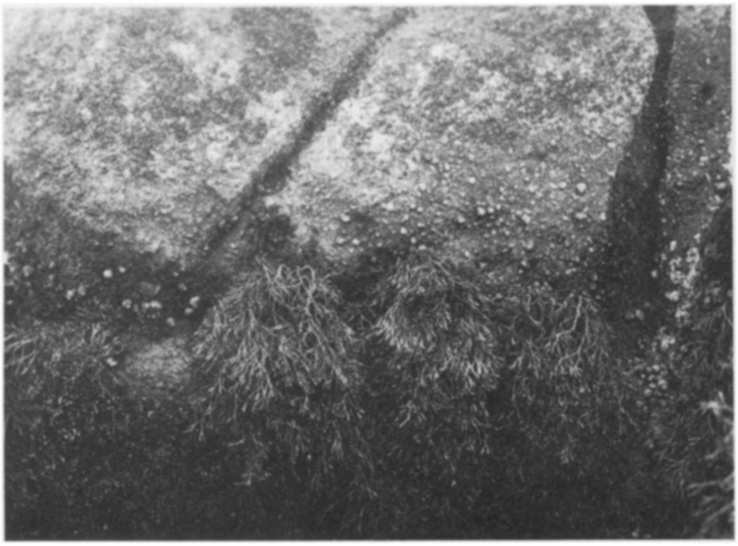


Fig. 13. A characteristic view of the *Balanus glandula* habitat on the rocky shore of Cabrillo Point.

During the periods at which this habitat is exposed to the drying effects of insolation and winds, the small periwinkle *Littorina scutulata* retreats into the empty barnacle shells or into the spaces between the barnacles where moisture is retained for comparatively long periods. These snails do not secrete the mucus for attachment and protection as does *L. planaxis*. As soon as the area is covered with water, they begin to move about over the barnacles and scrape encrusting and mat-forming algae from the substratum.

Acanthina lapilloides is always found associated with *Balanus glandula* in areas which are protected from violent wave action. They are easily detached from the rocks and hence are never found in the exposed littoral. Their food consist of the rock barnacles and of the small littorines. The peculiar feeding habits of this predaceous gastropod will be described later in another paper.

Three species of *Acmaea* are found in this zone. Small specimens of *A. scabra,* ranging from 3 to 10 mm. in length, are numerous among the barnacles. *A. limatula,* the file limpet, is abundant on the shaded vertical rock faces at this level. These habitats, protected from the direct sunlight, present a fairly smooth surface due to the heavy growth of film-forming algae. A small growth form of *A. digitalis* is very common in the *Balanus* habitat of the exposed rocks.

In the tide pools of Zone II, *Cribrina elegantissima, Pagurus samuelis, P. granosimanus, Tegula funebralis,* and *Leptasterias aequalis* are found. These forms also occur beneath moist rocks at this level.

Table 6 gives the contents of a typical square of this level.

TABLE 6. Contents of Square No. 24

Acanthina lapilloides	6
Acmaea limatula	4
Acmaea scabra	361
Amphithoe sp.	Rare
Balanus glandula	14,000
Cirolana harfordi	Rare
Cribrina elegantissima	44
Leptasterias aequalis	9
Littorina scutulata	378
Pagurus granosimanus	23
Pagurus samuelis	18
Spirorbis sp.	Common
Tegula funebralis	37

Zone III. In the intertidal area studied in this survey there is, between the levels of zero and three feet, a distinct difference between the fauna of the protected littoral and the fauna of the exposed littoral. For this reason, the species of the two habitats are treated separately.

a. *Protected rock habitat:* The protected rocks of this zone are covered by a thick growth of algae which makes a uniform and sheltered habitat for the animals. The upper half of the zone supports a heavy layer of *Pelvetia* and *Fucus*. Of these two plants, the former is by far the most abundant alga in this region. The lower part of the zone is covered by several species of algae, most of which are brown.

This community is not characterized by any one dominant species such as one finds in the *Balanus* habitat above. On the other hand, it is easily distinguished by the presence of several species of animals, each of which occurs in moderate or small numbers. The most common species, arranged according to the degree to which they characterize this habitat, are *Acmaea cassis pelta, Leptasterias aequalis, Mopalia muscosa, Hippodoplosia pallasiana, Atylopsis* sp., *Tetraclita squamosa rubescens, Pachygrapsus crassipes, Spirorbis* sp., *Fissurella volcano, Pagurus samuelis* and *Idothea rectilinea.* These forms range throughout this zone of the littoral.

In the uppermost part of the zone, beneath the *Pelvetia* and *Fucus,* large specimens of *Tegula funebralis,* the black turban snail, are very abundant. At lower levels this form is replaced by the brown turban, *Tegula brunnea.* Individuals of the black species frequently carry dunce-cap limpets, *Crepidula adunca,* attached to their shells.

The two forms occurring in the greatest numbers are: an isopod, *Cirolana* *harfordi,* and an undetermined amphipod of the genus *Atylopsis.* The amphipod was collected only in this zone but the isopod is found throughout the lower half of the littoral beneath the algae, rocks, and mussels.

Two gastropods, *Amphissa versicolor* and *Columbella carinata,* are common in this algal belt. Their lower limits extend down into the sub-zero zone. Another snail, *Tritonalia lurida,* is found only in Zone III.

In the "under-rock habitat" of this zone many characteristic species are found. *Pachycheles rudis, Hemigrapsus nudus,* and *Petrolisthes cinctipes* are

TABLE 7. Contents of Square No. 35

Acmaea patina	162
Amphipholis pugetana	4
Amphissa versicolor	24
Chama pellucida	1
Cirolana harfordi	Abundant
Columbella carinata	293
Cribrina xanthogramnica	1
Halosydna brevisetosa	8
Hippodiplosia pallasiana	Few
Kellia laperousi	4
Leptasterias aequalis	10
Pachycheles rudis	122
Pagurus samuelis	35
Paranemertes peregrina	Few
Pentidotea resecata	19
Petrolisthes cinctipes	9
Physcosoma agassizi	14
Pisaster ochraceus	4
Planocera californica	25
Pugettia producta	9
Spirontocaris picta	47
Strongylocentrotus purpuratus	49
Tegula funebralis	4

always present beneath the rocks. Small specimens of *Pagurus samuelis* are abundant in this habitat. Other animals found under boulders are *Planocera californica, Leptasterias aequalis, Nereis* sp., *Physcosma agassizi, Amphipholis pugetana, Acmaea scutum, Kellia laperousi,* and small specimens of *Strongylocentrotus purpuratus.*

Table 7 gives the species and the number or representatives of each species found in a typical square yard of the protected littoral of Zone III.

b. *Exposed rock habitat:* There are certain organisms which apparently can survive only on the rocks which are subjected to severe wave action. *Mytilus californianus* forms beds several inches in thickness on the rocks of the surf swept area. *Mitella polymerus,* the goose barnacle, is most commonly found in clusters among the mussels. The owl limpet, *Lottia gigantea,* inhabits the smooth rock surfaces along the upper margin of the *Mytilus* beds.

Practically all of the other animals found at this level of the exposed littoral may be classified into two ecological groups. First, there are those forms which depend upon the mussels for protection against the intense force of the waves and for protection from desiccation. The second group includes those animals which depend upon the mussels as a source of food . (See Hewatt, W. G., 1934).

The species commonly found beneath the mussel beds are *Cirolana harfordi, Petrolisthes cinctipes, Physcosoma agassizi, Allorchestes* sp., *Amphissa versicolor, Columbella carinata, Tegula brunnea, Pachygrapsus crassipes* and small specimens of *Strongylocentrotus purpuratus.* It should be noted here that the population corresponds very closely to that of the under-rock habitat of the protected littoral.

The most common predaceous animals of the zone are *Thais emarginata* and *Pisaster ochraceus.* The whelks are the greatest enemies of the mussels in this region since they ocur in such large numbers. *Leptasterias aequalis,* the six-rayed star, feeds on the small mussels, ranging from 2 to 10 mm. in length.

TABLE 8. Contents of Square No. 105

Acmaea digitalis	204
Allorchestes sp.	1052
Amphissa versicolor	80
Balanus glandula	448
Balanus tintinabulum californicus	4
Calliostoma canaliculatum	4
Calliostoma costatum	4
Cirolana harfordi	12260
Columbella carinata	8
Lacuna sp.	4
Leptasterias aequalis	4
Lottia gigantea	8
Mitella polymerus	556
Mytilus californianus	2452
Pachygrapsus crassipes	4
Petrolisthes cinctipes	720
Physcosoma agassizi	672
Strongylocentrotus purpuratus	32
Tegula brunnea	44
Thais emarginata	240

Balanus glandula extends lower on the exposed rocks than on the protected. On the protected shore, the lower limit of its range is very abrupt and definite. In exposed places these rock barnacles attach themselves to the mussels. This is especially true during the spawning season of the barnacles.

The population of a typical square yard of the exposed mussel habitat is given in Table 8.

Zone IV. The upper limit of this zone is the zero level of the tide tables. It is the level of the mean lower low tides and is the highest point reached by any of the sublittoral animals, with the exception of a few which are found beneath rocks of the higher littoral.

The lowest intertidal zone is the most productive area found along the rocky shore. In contrast to the higher parts of the littoral, there is not the great abundance of individual representatives of each species; but the number of species of animals greatly exceeds that of the higher zones. This is the region most frequently visited by shore collectors in search of specimens of the rarer species.

This zone has no dominant species. In other words, it does not have a characteristic physiognomy so apparent in the *Mytilus* beds.

The most characteristic animals found between the zero tide level and the lowest range of the tides are hydroids, colonial tunicates and sponges. *Aglaophenia struthionides* and *Abietinaria filicula* are familiar hydroids of the area studied. *Amaroucium californicum* is the commonest colonial tunicate; and *Lissodendoryx noxiosa* is the prevalent sponge.

TABLE 9. Table contents of Square No. 90

Abietinnaria filicula	Abundant
Aeolidia sp.	2
Aglaophenia struthionides	Common
Amaroucium californicum	Abundant
Amphiodia occidentalis	10
Amphiporus bimaculatus	2
Amphissa versicolor	67
Anisodoris nobilis	4
Betaeus harfordi	19
Bugula nereitina	Abundant
Calliostoma canaliculatum	2
Calliostoma costatum	12
Cancer antennarius	4
Cancer jordani	3
Cancer productus	3
Caprella sp.	Abundant
Cardita subquadrata	6
Chama pellucida	6
Cirolana harfordi	Abundant
Clavellina sp.	112
Columbella carinata	281
Corynactis sp.	13
Crangon dentipes	24
Cucumaria chronhjelmi	17
Dendronotus giganteus	2
Dirona picta	3
Epiactis prolifera	7
Eudistylia polymorpha	9
Fissurella volcano	3
Halosydna brevisetosa	37
Hapalogaster cavicauda	2
Hermissenda crassicornis	4
Hopkinsia rosacea	12
Ischnochiton mertensii	3
Isociona lithophoenix	Common
Kellia laperousi	5
Laila cockerelli	5
Leptasterias aequalis	22
Leucosolenia eleanor	Common
Lissondendoryx noxiosa	Few
Lophopanopeus heathi	11
Lumbrinereis sp.	Common
Megatebennus bimaculatus	4
Mimulus foliatus	4
Modiolus capax	7

Mopalia muscosa	2
Nereis sp.	Abundant
Ophiothrix spiculata	7
Orthopyxis caliculata	Common
Pachycheles rudis	62
Pagurus granosimanus	Common
Pagurus hemphilli	Common
Petrolisthes cinctipes	22
Physcosoma agassizi	127
Pisaster ochraceus	2
Plocamia karykinos	Common
Pododesmus macroschisma	4
Pugettia productus	2
Pugettia richii	4
Rhabdodermella nuttingi	Common
Rostangia pulchra	3
Saxicava arctica	12
Sertularia pulchella	Abundant
Spirontocaris picta	Common
Strongylocentrotus purpuratus	17
Styela stimpsoni	10
Synalpheus lockingtoni	2
Tanystylum intermedium	Abundant
Tegula brunnea	30
Tegula funebralis	3
Thyonepsolus nutriens	3
Xanthias taylori	3

The thick beds of sponges and tunicates offer an ideal habitat for shelter-seeking forms. Beneath the masses of colonial animals are found many retiring organisms such as the pistol shrimps, *Crangon dentipes, C. bellimanus* and *Synalpheus lockingtoni;* crabs, *Petrolisthes cinctipes, Pachycheles rudis, Lophopanopeus heathi, Xanthias taylori,* and *Hapalogaster cavicauda;* the isopod, *Cirolana harfordi;* the prawn, *Spirontocaris picta;* and the worms, *Halosydna brevisetosa, Nereis* sp., *Lumbrinereis* sp., *Physcosoma agassizi,* and *Eudistylia polymorpha.*

The hermit crabs are mainly represented in this sub-zero zone by *Pagurus hemphilli* and *P. granosimanus.*

There are a great number of different species of nudibranchs living on the substratum of this zone; for example, *Anisodoris nobilis, Hermissenda crassicornis, Hopkinsia rosacea,* and *Rostangia pulchra.*

Seventy-four species of animals were recorded from one square yard of the lowest littoral unit. The quantitative analysis of this square yard is given in Table 9.

3. Seasonal Migrations

After the preliminary quantitative survey of the transect was completed, it was possible to select typical squares, each of which was representative of a fairly homogeneous portion of the transect. A recounting of the inhabitants of these typical squares was made during each season of the year. In this way any pronounced seasonal migrations of the animals could be detected.

O'Donoghue (1924) found that *Pisaster ochraceus* and *Evasterias*

	1-10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	48	49	50	51
Abietinnaria filicula																																			
Acanthina lapilloides						5		2		8	5	5	11	6	1																			
Acmaea digitalis																																			
A. cassis pelta hybrida																																			
A. limatula				4	5	11	48	42	103	21	19	57	6	4	15	12	4		3		24	21													
A. mitra							1													2		3										9	12	6	4	5
A. patina																								121	162	222	170	75	56						
A. scabra		6	19	7	1	7	16	20	31	37	2	4						3																		
Aglaophenia struthioides																																			
Allorchestes sp																																			
Amaroucium californicum																				R						C	R						R	C		
Amphiodia occidentalis																															6		21	118	
Amphipholis pugetana																								2	4	29	13	16	21					
Amphissa versicolor																								38	24				22	37	49	43	31	2	43
Anisodoris nobilis																															3				
Atylopsis sp.															C	C	C	C	C	C	C	C	C	R										
Balanus glandula				10	75	105	20	98	3609	4605	117	95	208	8100	14004	9018	4536																	
B. tintin californ																																			
Betaeus harfordi																														4	12	27	16	16	8
Calliostoma costatum																						3	4							7	12	22	15	8	2
Cancer antennarius																																4	3	1	3
C. jordani																																5	3		
C. productus																																6	4	3	2
Chama pellucida																									1	3							2	15	6	3
Cirolana harfordi														R	C		A		C	A	C	A	A	A	A	A	A	A	A	C	C	A	A	C	C
Clavellina sp																										215	179						72	68	17
Columbella carinata																								277	293	371	452	526	397	215	272				
Crangon dentipes																														6	8	18	22	16	
Crepidula adunca																7	8	13	11	7	4								6	11	5	9	7		
Cribrina elegantissima							1				12	42	49	27	44	6		2			3	3		2							6	4				
C xanthogrammica																									1	1									
Cucumaria chronhjelmi																																			
Dendronotus giganteus																																9	3		
Fissurella volcano																						2	3			10						4	2	3	2
Glossophorum planum																																21	2		
Halosydna insignis																								4	8	4	2	24	23	6	32	41	12		
Hapalogaster cavicauda																																4	2		
Hemigrapsus nudus																								2			2	3	6						
Hermissenda crassicornis																																2	4	2	
Hippodiplosia poliasiana																								A	R	A	A						A		
Hippolyte californiensis																																			
Hipponix antiquatus																															7	4	6	3	6
Hopkinsia rosacea																													2	5	3	6	3	5	6
Idothea rectilinea																																		4	7
Kellia laperousi																								6	4							7	3	4	2
Laila cockrelli																																2	1		
Lepidochitona hartwegii											3	6	8				4	3																	
L. lineata																																	2	4	5
Leptasterias aequalis							1			1		3	8	11	9	23				5			7		7	10	27	30	55	41	23	56	11	12	9	
Leptosynapta inhaerens																																			
Leucandra heathi																																R	C	C	
Ligyda occidentalis	7	3	4	1	1																															
Littorina planaxis	12	89	96	127	49	75	6			12																										
L scutulata				99	85	195	77	48	375	645	10	230	365	273	378	948	231																	
Lophopanopeus heathii																															6	9	5	3	
Lottia gigantea																																			
Lumbrinereis sp																	C			C									R	R	R	A	A	C	C
Melita palmata													C	A	A	A					A	A	A	A	A	A	C									
Mimulus foliatus																															9	5	3		
Mitella polymerus																																			
Mopalia muscosa							2												1	10	1		3	1				3					13	4	1	
Mytilus californianus					1		1		1	2							6	18	6		22	4	3										6	12	8	
Nereis sp.																													R	C	C		C	C		
Nutallina californica																																			
Ophiothrix spiculata																															2	17	7	3	4
Pachycheles rudis																								64	122					24	18	79	62	3	27
Pachygrapsus crassipes							2	1			3					4				2	18	12	15	3				5	2				7	6	13	6
Pagurus granosimanus															R	R														C	C	C	C	C		
P. hemphillii																																C	C		
P. samuelis				R				C	C	R	C	C	C	C	R	R	R	R	C	C	C	C	R	C	C	R	C			C	R	R				
Paranemertes peregrina																				R						R	C	A	A	A						
Patiria miniata																															2				
Petrolisthes cinctipes																								11	9	9	55	34	10			48	28	20	14
Physcasoma agassizi																				6			29		18	14		47	19		72	104	68	81	52	44
Pisaster ochraceus																								7	4	6	8	15	22			9	12	9	7
Planocera californica																								C	C	A	A	A	A						
Plocamia karykinos																						R						C	C	R			C			
Pugettia productus																			1	1	1	4			10	9		2	5	21		4	2	4		
P. richii																														8	7	5	2		
Rostangia pulchra																										1	3		1			2	3	1	3
Spirontocaris picta																									R	C	C	A	A	C	C	C	C	C	C
Spirorbis sp.														A	A	A				A							C	C	C	C	C					
Strongylocentrotus purp.																								10	49	35	51	78	15	52	73	27	41	37	32
Tegula brunnea																														17	36	43	22	14	2
T. funebralis		12	27	78	21	16	80	155	125	85	765	475	203	48	37	195	57	81	27	115	108	114	65	17		4	5				8	7	2	9	9	7
Tetraclita squam. rub.																																			
Thais emarginata																																			
Thyonepsdus nutriens																															4	12	13	6	2
Tritonalia lurida																															18	32	27	12	7
Xanthias taylori																														2	4	7			

TABLE 10. Quantitative distribution of 90 of the most common species of animal it was impossible to count individuals the relative population of the species is indicated

53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	90	91	92	93	94	95	96	97	98	99	100	105
																																	A	C	A	C	R							
																										210	241									11	25	169	227	174	138	320		204
																		34		19	11	19	12	4	4	17	14	17		37	28	19								13	4			
					6				3	4	23	12	27							11	12	12					4	6								56	110	71	67	22				
8	6	4	7	8						9																																		
																17																												
																		2		32	209	365	289	312	172	276	322									21	175	215	197	27	49	121	223	
					C	C	C																							A	A	A	A	A	C	C	C	R						
																										R												C	C	C	C	C	C	1052
																		R											A	C		A	A	A	C									
																																	10	14	11									
21	12	4										12	17																															
86	62	49	71	68	42								63	42	39	21	14	62											39	20	32	27	67	78	56	25							12	80
	1																																4	5	2	2	1							
												R							C	C	C	C	R	R																				
																				78	327	5040	3519	1647	207	59												1566	1255	178	96	3370	146	448
	6	4				2		6					21					12																									2	4
																																	19	22										
									4																								12	15	4	2								4
6	6	2							1	2						2														1	2	3	4	5	3	6	4							
		1																															3	2	1									
4	4	2						3	2	3																							3	3	1	3	2							
										2		3																					6	2										
A	A	A	A	A	A	A	C	C	A	C	A	A	C			A					R	R					R			C	C	C	A	A	C	C	C	A	C	C	R		A	12260
																14															59	271	112	17	26	39	16	22						
691	590	615	481	376	401	426	342	79	317	209	269	115	65	93	71	249	67	319											381	441	492	419	281	268	117									8
																																	24	6										
									15	45	37	41	33	42		26		27	8																									
		2																4	4	15		31	109	156	53	7	1											33	53	2	1		6	
								1	1	4	4	4		7	3			1	2	5	11	9	12	6	2	2									2	14	10	13	10					
	4																																14	12	5	2	2							
										1		1																					3	1	2			2						
												2																																
14	17								33			29	13			29																	37	41										
																3																	2	4										
6	2																													5	1	5	4	3	1									
					C	R			C	A	A	A									C							C	A	A	A	A												
				27	39	22	34																																					
4	8	2	2	3	4		4	3	3	1									2											3	5	9	12	8	3									
				5	7	9	17	11																														3						
3	4																																5	9										6
																																	2	3										
																																							1	3				
4	7	4							1									21												2	3	5												
8	10	3														5				11	5					6	11	15	9	2			22	17	9	14	12							4
6	3								3	2																																		
																																	R	C										
																						752	112	109	38																			
																																	11	6										
																										4	1											6	9	8	6	16	6	8
																																	A	A	C	C	C							
																																	4	6	2									
			4	6																		29	311	7	55	102	11											516	479	376	257	119	653	556
24	29	31								1											3		6	7	6	18	14	6		4	2	3	2											
2	3	5	15	18	6		12	27	27	38	45	29	5	6							14	21	127	17	71	118	3									47	252	759	1475	980	920	195	2205	2452
		C							C	C		C								C								A	A	C			A	A	C									
																																	1	6	9	6		42	82	7			7	
																																	7	12	4									
8	3							2	4	2		4				47																	62	58	52	12	14							
												3								18	12	7	21	16	17	4		4	4		4	2			12	7	14	25	28	12	13		19	4
A	A	A	A	A	A	C	C	C	C	C	C		R				A	R															C	C	C			C						
																																	C	C	R									
A	A	A	A	A	A	A	A	A	A	A	A	A	R	A	C	A	C	A	C	C	A	A	C		C		C	C	C	A	A	A												
		C												C	C	C				C	C																							
3	1	1	1		2											2					1																							
14	2															18					12												22	36	29	19	28	31	39	44	61		54	720
																3										9							127	107									7	672
					1	1										2			23	14	1	1	3			1	1	1	7	2	7	9	12	4	3	9	8	7	10					
A	A	C			C	C			C																																			
C	C				C																																							
	3	1	2	2	5	2	2	5				17									3								2	4	2	5	2	4	3									
																																	4	2										
3	4					1																								6	4	3	3	1										
C	A	A	A	A	A	A	A	A				R	C			C	C	R															C	C	C	A	A	A						
A	A	A											C																															
26	28	10	12	8	21	16	9		8			23	2			21														22	31	29	17	14	15	21	21							32
												3				18		47	24								14	12	46	34	46	39	30	23	3									44
12	8	3			26		14	22	35	156	140	45	68	74	17	178		12	31	14	25	31	33	18	46	9		4					3	8	16									
																23			13	31	82	57	632	240	362		73	26							15	210	407	436	475		10		72	
																						3	81	27	42	16	6											2	9	43	29	21	178	240
																																	3	3										
												4				17	19		6																									
																																	3	2	2									

found along a transect across the intertidal region at Cabrillo Point. Cases in which
by: A—abundant; C—comm n; R—rare.

troschelli, the two common starfishes of the littoral of Departure Bay, British Columbia, migrate to a subtidal level during the hot summer months and return to the intertidal as the cooler season approaches. Seasonal migrations of this and other kinds are known from various regions where the vicissitudes of the seasons are more or less severe, for instance, along the Scandinavian Peninsula.

This phenomenon was not evident in the case of the Monterey Bay fauna. The small variations in the air and water temperatures of Monterey Bay probably account for the absence of seasonal migrations in this area. The marine climate of this region is, indeed, in this respect quite unique for the temperate seas.

The results of the periodic rechecking of the animal populations along the transect were not, however, altogether negative. It was noted that a generally lower level is obtained by *Leptasterias aequalis* during the breeding season. These six-rayed starfishes are found in the *Balanus glandula* habitat at all seasons except in late spring during which time they are brooding their young beneath the *Pelvetia* fronds.

The predaceous snail, *Acanthina lapilloides,* also migrates downward during the spawning season.

On account of the small changes in the number of specimens of the various species present during the different seasons, the results were not considered significant enough to justify the inclusion of these seasonal data in the present section. The examples given in the tables for each zone must suffice to illustrate the relative frequency of the species at all seasons.

VI.—Food Relationships

Generally speaking, in an intertidal community the basic food supply of the animals is of four main types, as follows:

1. *Larger benthonic plants.* These consist mainly of algae, although in certain regions a few phanerogam genera are more or less important, even playing the dominant role in particular localities. In the warmer parts of the oceans, the benthonic plants of large sizes are subordinate, while in the cold and temperate seas, the brown algae, especially, constitute a very conspicuous food component in the communities of the intertidal and subtidal regions. As a consequence, what is stated below in regard to the significance of these plants has a distinctly limited application. Probably the most striking, not to say paradoxical, result brought forth by the investigation of the food relations of the coastal regions is that, in spite of the enormous productivity of organic matter represented by the growth of the larger benthonic plants, nevertheless, relatively few of the animals feed directly upon these forms while they are still alive. The enormous algal pastures along the edges of the continents serve the animals almost exclusively as a substratum and as a means of protection, and hardly at all as a direct source of food.

2. *Encrusting or mat-forming algae.* These algae are usually very small, predominantly microscopic forms, a large number of them being diatoms.

They cover practically all surfaces of the foreshore; they even penetrate above the regions generally covered with water where they form an inconspicuous but important pasture. Many animals subsist by browsing on this filmy growth. Most important among the browsers are certain gastropods.

3. *Plankton*. Enormous quantities of plankton are formed, particularly in the colder and temperate waters. The warmer regions are comparatively barren of plankton and of large benthonic algae. This plankton material is constantly carried over the foreshore by currents and tidal streams and is sprayed over the higher levels of the coast belt by the waves. A large number of the animals feed on this supply, especially on the microscopic constituents.

4. *Detritus*. The particulate matter, or detritus, which is formed by the disintegration of plants and animals, is of great importance as a source of food in most intertidal areas. Included in this material are, of course, enormous quantities of micro-organisms. These unquestionably are of profound importance as a direct source of nourishment for the higher animals, although so far no attempt has been made to estimate their relative significance. Most of the detritus in the intertidal belts of the cold and temperate seas is derived from the larger benthonic plants. It is in this condition that these plants mainly contribute to the food cycles of these regions.

Thus the first of these four types of food always seems to be of but slight significance. It may also be stated with safety that the second type is of subordinate importance (with possible exceptions in certain habitats of the tropical seas). The last two types are unquestionably the dominant ones. There is disagreement, however, among the ecologists concerning the relative value of the living plankton and of the detritus as a food supply for bottom-dwelling marine animals. The early investigators were prone to draw too broad conclusions from observations in localized areas. A large number of recent investigations have shown that these early generalizations concerning the food supply of marine organisms were not justified. No sufficiently broad, quantitative survey has been carried out in this field, and thus the problem must still be considered as unsolved.

MacGinitie (1935, p. 648) emphasizes the fact that the plankton constitutes a very insignificant link in the food chains of the mud-living animals of Elkhorn Slough, California. In this environment, where bacterial action is enhanced by relatively high temperatures and by the enclosed nature of the habitat, it was found that detritus formed by far the greater portion of the basic food supply. Most of the inhabitants live beneath the surface and pass the mud, rich in detritus, through their digestive tracts. This condition, however, applies only to organisms found in sloughs and similar surroundings.

According to the work of Blegvad (cit. Shelford, 1929, p. 114), the living plankton is not significant as a food for bottom living forms of the sea. Blegvad states that

> Detritus forms the principal food of nearly all the invertebrates of the sea bottom, next in order of importance being plant food from fresh benthos plants. The value of the live plankton in this connection is absolutely minimal, amounting in any case to nothing more than an indirect significance through the medium of the plankton copepods.

Here again, too broad conclusions should not be drawn from observations made in a local area. The conditions of the Danish coastal waters, upon which Blegvad based his conclusions, are far from typical of coastal regions in general. The broad expanse of shallow water off the coast of Denmark, especially the Lim Fjord where most of these observations were made, permits an extremely abundant growth of Zostera and other marine plants. A large supply of detritus results from the disintegration of these plants. Even moderate wave activity in these shallow waters keep a part of the detritus almost continuously in a state of suspension so that the so-called "plankton feeders," such as mussels and barnacles, probably subsist to a very large extent on suspended detritus.

In the region investigated in the present work there is an abundance of algal growth, although limited in area due to the steep slope of the bottom. The supply of micro-plankton is also extremely plentiful. It is certain that this living plankton forms an important link in the food chains of the bottom living invertebrates of the area. The stomach contents of a large number of mussels and barnacles, which live on the minute food, were examined. These examinations revealed the presence of many of the dinoflagellates and diatoms which are known to be common in the adjacent waters. The contents of the lower portion of the alimentary canals of these animals showed a decidedly increased proportion of the empty shells of these plankton organisms. This indicated that these organisms were digested and hence that live plankton is used as a food.

Several samples of sea water from the intertidal region were centrifuged and examined. The results showed a high percentage of living micro-plankton as well as much detritus. Bigelow and Leslie (1928, p. 530) examined the waters of Monterey Bay in the mid-summer of 1928. Even during this season of supposedly low productivity in temperate seas, these investigators found the quantity of phytoplankton in the surface waters to be very high. They estimated the average diatom production at that time to be over one million cells per liter of surface water in the Bay.

It should be emphasized that these statements are not to be interpreted as implying that live micro-plankton forms the most important food of plankton feeders. Generally speaking, detritus when strongly particulated, is very difficult to estimate quantitatively. No attempt was, therefore, made to establish the relative value of these two types of food. Both of them unquestionably are essential. The live plankton is, however, not subordinate as suggested by investigators of other habitats but on the contrary it is a very essential component.

Because of pronounced differences in the feeding habits of the organisms of the exposed and protected areas, the food cycles of the two regions have been discussed separately.

a. *Protected habitat:* In the protected part of the littoral *Balanus glandula* is the most abundant form which obtains its food from the material suspended in the surrounding water. As soon as these barnacles are covered by the tidal waters, they begin feeding. At the lower level of this community are found sponges, hydroids, dunce-cap limpets *(Crepidula adunca)* and *Spirorbis* which also feed on the suspended detritus and its bacteria, as well as on the living plankton. Beneath stones, *Petrolisthes cinctipes* is found straining suspended matter from the water.

Next in abundance to the plankton and suspended detritus feeders are the forms which scrape encrusting and mat-forming algae, inclusive of benthonic diatoms, from the rock surfaces. This group of browsing organisms consists mainly of gastropod molluscs such as periwinkles, turban snails, and limpets. In Zone I, this type of feeder is represented by *Littorina planaxis* and two species of *Acmaea: digitalis* and *scabra*. In Zone II, *Littorina scutulata, Acmaea cassis pelta,* and *Tegula funebralis* scrape the rock surfaces for food. The snails, *Columbella carinata, Amphissa versicolor, Tegula brunnea,* and the limpet *Fissurella volcano,* also of this feeding type, are abundant at the lower levels.

The only organism in the protected habitat which is known to feed on the living benthonic growth of large algae is *Pugettia producta*. The stomach contents of a number of these forms revealed the presence of small rectangular pieces of the fronds of algae, mostly *Iridaea*.

Among the predaceous species of the protected area, *Acanthina lapilloides* is the most numerous. Members of this species feed mainly upon the barnacles but they have been seen devouring periwinkles. The interesting feeding habits of this form are described elsewhere.

Leptasterias aequalis feeds upon a variety of animals, such as barnacles, littorines, young limpets and young snails.

An examination of the stomach contents of several species of fishes, for example, *Clinocottus analis, Montereya recalva, Xiphidion ruprestre,* found in the lower tide pools and under rocks in this area, showed that their food supply consisted mainly of amphipods and isopods.

The pure detritus feeders include a large number of species, most of which are represented by relatively few individuals. Some of the most important animals which subsist on the disintegrating parts of other organisms are: *Cirolana harfordi, Pentidotea resecata, Pachygrapsus crassipes, Hemigrapsus nudus, Pachychelus rudis, Pagurus samuelis, P. granosimanus,* and *Halosydna brevisetosa*. A number of burrowing annelids also comes under this category.

A diagram showing the main chains in the food cycles of the protected littoral is given in Figure 14.

b. *Exposed habitat:* The food relationships of the animals in the exposed littoral are shown in Figure 15. The main differences between the protected and exposed habitats consist in the presence of the large numbers of *Mytilus californianus* found in the exposed habitat. This is a form which subsists on microplankton and suspended detritus. Plankton feeders, other than Mytilus californianus, which are found in abundance in this habitat, are the rock barnacles, *Balanus glandula* and *Tetraclita squamosa rubescens,* and the goose barnacle *Mitella polymerus*. The two rock barnacles are restricted to areas which are not favorable for the growth of the mussels, while the goose barnacle

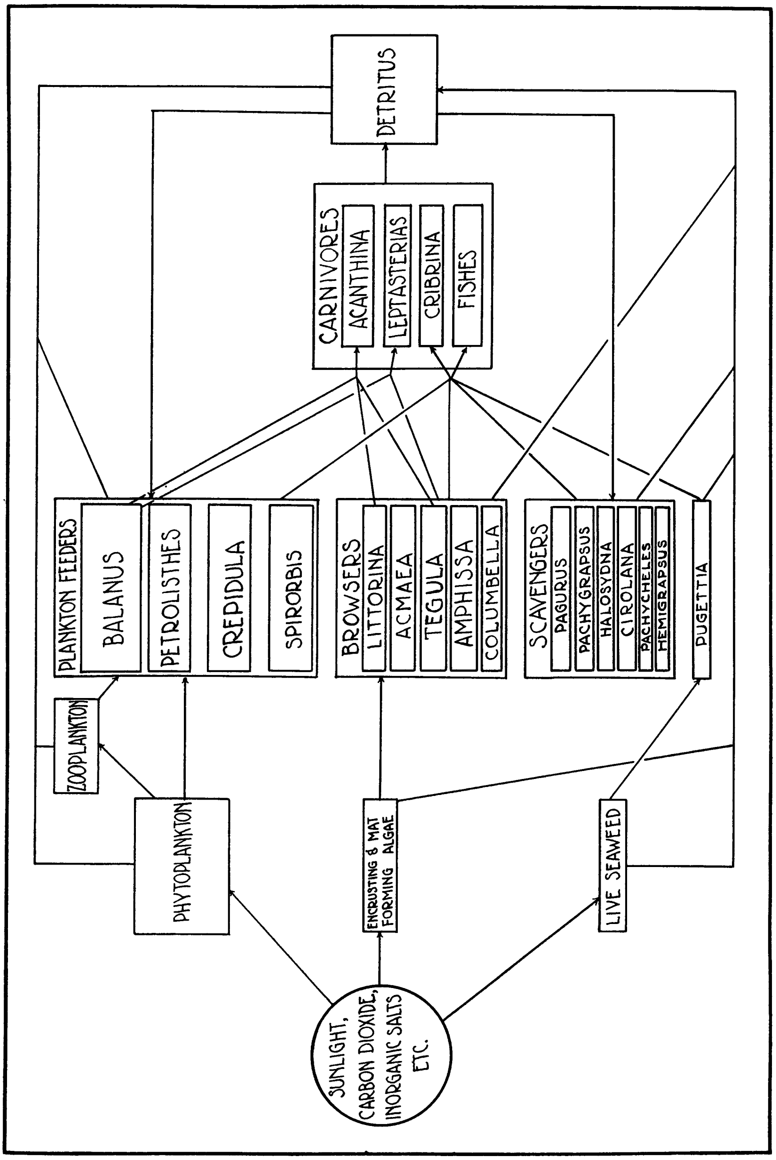


Fig. 14. A diagram of the food cycle of the animals found on the protected littoral rocks of Cabrillo Point.

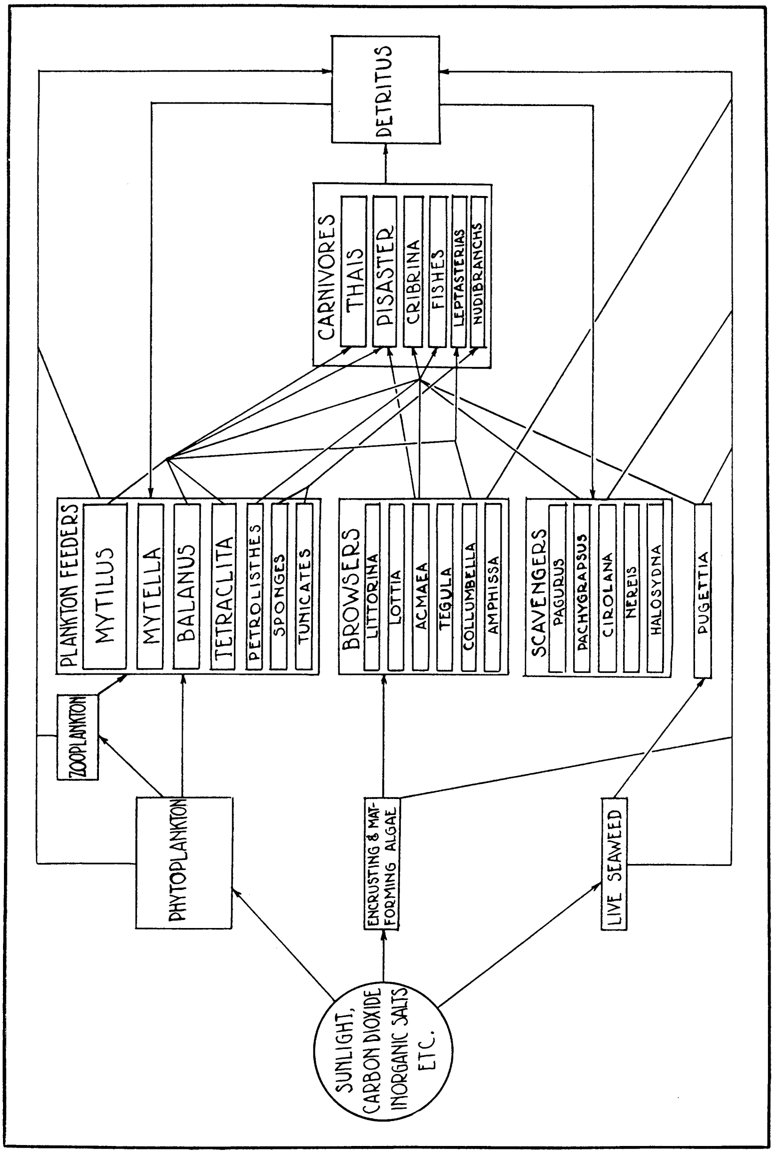


Fig. 15. A diagram of the food cycle of the animals in the exposed littoral of Cabrillo Point.

is only found associated with these bivalves. Beneath the mussel beds, *Petrolisthes cinctipes* feeds on the plankton and suspended detritus.

On the protected sides of vertical rock faces in the surf-swept region, there is a small, green anemone, thought to be identical with *Cribrina elegantissima,* which apparently feeds to a great extent upon the plankton and nectonic invertebrates. In a large number of individuals examined, the gastrovascular cavity revealed the presence of partially digested copepods, isopods, and amphipods, as well as many diatoms and dinoflagellates. It is supposed that these anemones are partially nourished by the large quantities of symbiotic algae which are found in their tissues. Along the water channels, at lower levels, many hybroids, bryozoa, sponges, and tunicates feed on the microplankton and on the bacterial contents of the suspended detritus.

Among the organisms which scrape their food from the substratum, *Littorina scutulata* is the most abundant form on the surfaces covered by rock barnacles. Here, also, are found numerous specimens of *Acmaea scabra* and *A. digitalis* which range down into the upper part of the mussel habitat. A small black species of *Acmaea,* which was not determined, is the most common limpet of the mussel beds. These animals are found scraping food from the mussel shells to which they are attached. *Lottia gigantea,* also this type of feeder, is found only on the exposed rocks.

At the lower levels, thes nails, *Tegula brunnea, Calliostoma costatum, C. canaliculatum, Columbella carinata,* and *Amphissa versicolor,* are the most common browsing forms.

Pugettia producta feeds on the abundant algal growth at the lower levels of the exposed littoral.

The mussels, which are found in large numbers in areas exposed to wave action, furnish food for a variety of predaceous animals. *Thais emarginata,* the purple whelk, bores through the mussel shells and extracts the soft parts. *Pisaster ochraceus,* the common large starfish of this intertidal region, lives in the crannies and cracks at the base of the *Mytilus* beds and is found feeding on the mussels, especially during the night. The large green anemone, *Cribrina xanthogrammica,* is not an active enemy of the mussels but feeds upon the specimens which are torn loose by wave actions. During the stormy winter months, large mussels drop down into the channels which are thickly populated by the large anemones. The crabs, *Cancer antennarius, C. productus, Pachygrapsus crassipes,* and *Petrolisthes cinctipes* are also eaten by these anemones. The food of *Leptasterias aequalis* found in this area consists mainly of small mussels, limpets, and barnacles.

Many of the subtidal fishes visit the intertidal zone during periods of high tide, but little is known of their food habits. However, the mussels, limpets, and crabs probably form a large part of their food supply.

Pagurus hemphilli, Pachygrapsus crassipes, Cirolana harfordi, Nereis sp., and *Halosydna brevisetosa* depend for their food upon decaying remains; *i.e.,* they are the detritus feeders of the exposed littoral.

VII.—Systematic List of Species

Porifera

Isociona lithophoenix (de Laubenfels)
Leucandra heathi (Urban)
Leucosolenia elenor Urban
Lissodendoryx noxiosa de Laubenfels
Ophalitospongia pennata (Lambe)
Plocamia karykinos de Laubenfels
Reneira cineria Bowerbank

Coelenterata

Abietinnaria filicula (Ellis and Solander)
Aglaophenia struthionides (Murray)
Corynactis sp.
Cribrina elegantissima (Brandt)
Cribrina xanthogrammica (Brandt)
Epiactis prolifera Verrill
Orthopyxis caliculata (Hinds)
Plumularia setacea (Ellis)
Sertularia pulchella (d'Orbigny)

Platyhelminthes

Planocera californica Heath & McGregor

Nemertina

Amphiorus bimaculatus Coe
Micrura verrillii Coe
Paranemertes peregrina Coe

Bryozoa

Bugula neritina (Linnaeus)
Hippodoplosia pallasiana (Moll)
Membranipora tehuelcha (d' Orbigny)

Annelida

Arenicola sp.
Eudistylia polymorpha (Johnson)
Halosydna brevisetosa Kinberg
Polynoe lordi Baird
Lumbrinereis sp.
Nereis sp.
Sabellaria sp.
Serpula columbiana Johnson
Spirorbis sp.

Gephyrea

Physcosoma agassizi Keferstein

Arthropoda

Crustacea

Allorchestes sp.
Amphithoe sp.
Atylopsis sp.
Balanus glandula Darwin
Balanus tintinnabulum californicus Pilsbry
Betaeus harfordi (Kingsley)
Cancer antennarius Stimpson
Cancer jordani Rathbun
Cancer productus Randall
Caprella sp.
Cirolana harfordi (Lockington)
Crangon bellimanus (Lockington)
Crangon dentipes (Cuerin)
Exosphaeroma oregonensis (Dana)
Hapalogaster cavivauda Stimpson
Hemigrapsus nudus (Dana)
Hemigrapsus oregonensis (Dana)
Hippolyte californiensis Holmes
Idothea rectilinea (Lockington)
Ligyda occidentalis (Dana)
Lophopanopeus heathii Rathbun
Melita sp.
Mimulus foliatus Stimpson
Mitella palymerus (Sowerby)
Pachycheles rudis Stimpson
Pachygrapsus crassipes Randall
Pagurus granosimanus (Stimpson)
Pagurus hemphilli (Benedict)
Pagurus samuelis (Stimpson)
Pentidotea resecata (Stimpson)
Pentidotea wosnesenskii (Brandt)
Petrolisthes cinctipes (Randall)
Polycheria osborni Calman
Pugettia producta (Randall)
Pugettia richii (Dana)
Scyra acutifrons Dana
Spirontocaris paludicola Holmes
Spirontocaris picta (Stimpson)
Synalpheus lockingtoni Coutiere
Tetraclita squamosa rubescens Darwin
Xanthias taylori (Stimpson)

Arachnida

Pycnogonum stearnsi Ives
Tanystylum intermedium Cole

Molusca

AMPHINEURA

Callistochiton crassicostatus Pilsbry
Ischnochiton magdalenensis (Hinds)
Ischnochiton mertensii (Niddendorff)
Katharina tunicata (Wood)
Lepidochitona lineata (Wood)
Lepidochitona hartwegii (Carpenter)
Mopalia muscosa (Gould)
Nuttallina californica (Reeve)
Placiphorella vollata Carpenter

GASTROPODA

Acanthina lapilloides Conrad
Acmaea asmi (Niddendorff)
Amaea cassis pelta hybrida (Eschscholtz)
Acmaea digitalis Eschscholtz
Acmaea insessa (Hinds)
Acmaea limatula Carpenter
Acmaea patina (Eschscholtz)
Acmaea scabra Gould
Aeolida herculea Bird
Aeolidia papillosa Linnaeus
Amphissa versicolor Dall
Anisodoris nobilis (MacFarland)
Bittium eschrichtii (Niddendorff)
Cadlina marginata MacFarland
Calliostoma canaliculatum (Martyn)
Calliostoma costatum (Martyn)
Calliostoma gloriosum Dall
Columbella carinata Hinds
Crepidula adunca Sowerby
Crepidula nivea Adams
Dendronotus giganteus O'Donoghue
Diadora aspera (Eschscholtz)
Diaulula sandiegensis (Cooper)
Dirona picta MacFarland
Discodoris heathi MacFarland
Fissurella volcano Reeve
Haliotis cracherodii Leach
Haliotis rufescens Swainson
Hermissenda crassicornis (Eschscholtz)
Hipponix antiquatus Linnaeus
Hopkinsia rosacea MacFarland
Lacuna porrecta Carpenter
Laila cockrelli MacFarland
Lamellaria stearnsiana Dall
Leptothyra carpenteri (Pilsbry)
Littorina planaxis Philippi
Littorina scutulata Gould
Lottia gigantea Gray
Megatebennus bimaculatus (Dall)
Philodina sp.
Polycera atra MacFarland
Pseudomelatoma torosa Carpenter
Purpura nuttallii (Conrad)
Rostangia pulchra MacFarland
Tegula brunnea (Philippi)
Tegula funebralis (Adams)
Thais emarginata (Deshayes)
Triopha carpenteri (Stearns)
Triopha maculata MacFarland
Tritonalia interofossa (Carpenter)
Tritonalia lurida (Middendorff)

PELECYPODA

Cardita subquadrata (Carpenter)
Chama pellucida Sowerby
Hinnites giganteus Gray
Kellia laperousi (Deshayes)
Mytillimaria nuttallii Conrad
Modiolus capax Conrad
Mytilus californianus Conrad
Pecten circularis Sowerby
Pododesmus macroschisma Deshayes
Saxicava arctica (Linnaeus)

CEPHALOPODA

Paroctopus apollyon (Berry)

Echinodermata

Amphiodia occidentalis (Lyman)
Amphipholis pugetana (Lyman)
Cucumaria chronhjelmi Theel
Henricia leviuscula (Stimpson)
Leptasterias aequalis (Stimpson)
Leptosynapta inhaerens (Muller)
Ophiothrix spiculata LeConte
Patiria miniata (Brandt)
Pisaster ochraceus (Brandt)
Strongylocentrotus franciscanus (Agassizi)
Strongylocentrotus purpuratus (Stimpson)
Thyonepsolus nutriens Clark

Chordata

TUNICATA

Amaroucium californicum Ritter and Forsyth
Clavellina sp.
Glossophorum planum Ritter and Forsyth
Styella stimpsoni Ritter

VERTEBRATA

Clinocottus analis (Girard)
Dialarchus snyderi (Greeley)
Greeleya rubellio (Greeley)
Xiphidion ruprestre (Jordan and Gilbert)

Summary

On the southern margin of Monterey Bay, California, a transect, one yard wide and 108 yards long, across the littoral was subjected to an ecological study.

The area investigated is rocky and characterized by the unusual monotony of most of the factors of its physicochemical environment. For instance, the average annual range of the temperature of the surface water is only 2.5° C., from 11° to 13.5° C.; the salinity of the surface water exhibits variations between 32.12 and 33.82 grams of salt per liter and the water is apparently always saturated with oxygen; the average daily thermal range for the air, 11.1° C.; and fog prevails during the warmer part of the year. The most pronounced environmental factor is the tide, which is unequal, with striking differences particularly between the two daily low tides.

A quantitative and qualitative analysis of this ecological transect showed that there is a definite zonation of the intertidal animals in the area. Upon the basis of the accumulated data, the littoral of this area was divided into four vertical zones. The factors which cause this zonation are elusive in nature and thus are not readily determined. It was found, however, that two of the zonal limits located at the 0.0 and 5.0 foot levels, are closely correlated with the relative *lengths* of the periods of tidal exposure to which the animals are subjected. The remaining limit, represented by a less definite level between two and three feet above the zero tide level, corresponds to the upper limit of the area which is covered by the fronds of *Pelvetia* and *Fucus*. This faunal level may, indirectly, be due to the *frequency* of tidal exposures since the upper limit of the *Pelvetia-Fucus* growth coincides with the line across which the tide most frequently passes. This level in the animal zonation, however, is evidently the direct result of the protection against dessication and insolation afforded the animals by these algae.

It was also established that the limits of the ranges of some of the animals result rather from biological than physico-chemical prenomena. Interspecific relationships of food and shelter are particularly conspicuous. Examples of animals which are thus limited in their vertical ranges are, *Acanthina lapilloides, Thais emarginata,* and *Littorina scutulata.*

Some species have developed certain adaptations which enable them to occupy niches of the habitat where competition is less severe. For example, *Littorina planaxis* has penetrated into the upper littoral due to its capacity to withstand relatively long periods of exposure to air and fresh water. It also maintains its position on the foreshore by its ability to attach itself to the substratum by a mucous secretion. *Acmaea scabra,* on acount of its remarkable homing habit, can also live in the upper littoral.

With the exception of certain spawning migrations, no pronounced seasonal migrations were noted in the investigated area. This condition is undoubtedly the result of the extreme monotony of the physical and chemical environment.

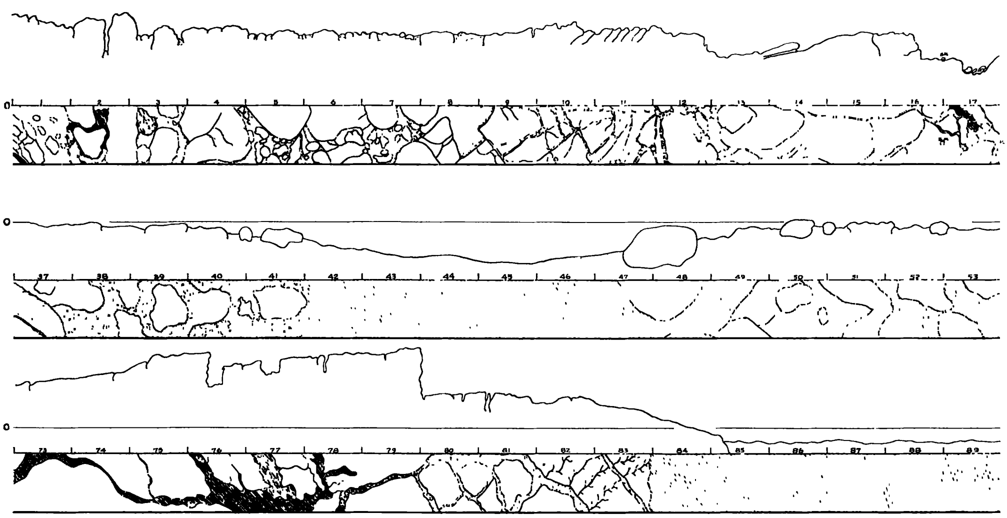


PLATE 2. A diagram showing a superficial and profile view of the ecological transect. The mean lower low water line is indicated on the chart. The first 12 squares represent an uneven rocky area characterized by many cracks and crevices in which loose boulders and sand are found. In squares 17, 18, 19 and 20 is located a high tidepool in which water is retained after the tide recedes. From squares 20 to 41 the basic granite projects above the sandy bottom and the spaces

REFERENCES

ALLEE, W. C. 1923a—Studies in marine ecology: I. The distribution of common littoral invertebrates of the Woods Hole region. III. Some physical factors related to the distribution of littoral invertebrates. Biol. Bull. **44**:167-191; 205-253.

———1923b.—Studies in marine ecology: IV. The effect of temperature in limiting the geographical range of invertebrates of the Woods Hole littoral. Ecology **4**:341-354.

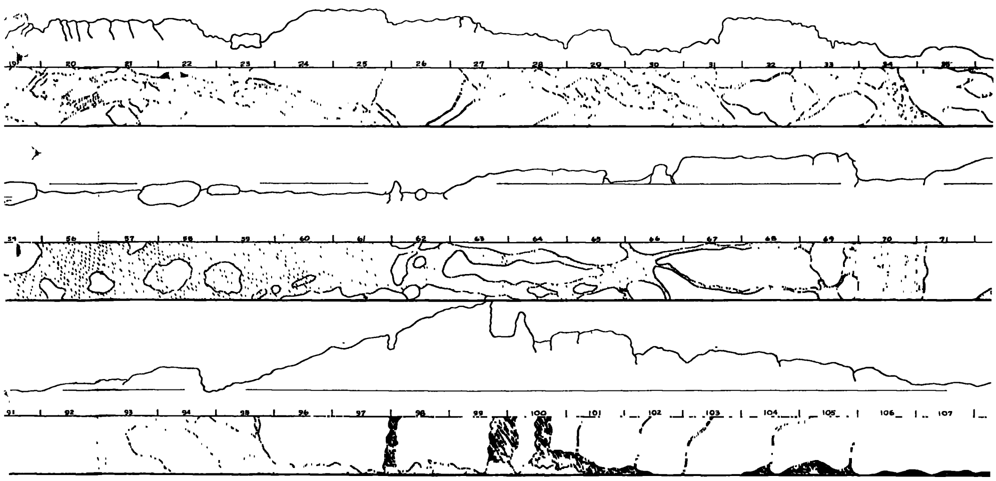
BIGELOW, H. B. AND M. LESLIE. 1928—Reconnaissance of waters and plankton of Monterey Bay. Bull. Mus. Comp. Anat. **70**:427-581.

BOHART, R. M. 1929—Observations on the attachment of *Balanus crenatus* Brugeiere, found in waters of Puget Sound. Amer. Nat. **43**:353-361.

BOVARD, J. F. AND H. L. OSTERRUD. 1918—Partial list of the animals yielding embryological materials at the Puget Sound Biological Station. Publ. Puget Sound Biol. Sta. **2**:127-137.

BRUCE, J. R. 1928—Physical factors on the sandy beach. Part I: Tidal, climactic and edaphic. Jour. Mar. Biol. Assoc. **15**:535-557.

COLE, WM. H. 1932—The sensitivity of cirri and variability of their movements in the barnacles *Balanus tintinabulum* and *B. balanoides*. Jour. Exp. Zool. **63**:143-153.



between the projections are filled with shell and sand and loose rocks. The transect crosses a permanent channel between the squares 41 and 48. A permanent tidepool covers the area between squares 49 and 63. Between squares 63 and 83 the surface is characterized by a granite projection which rises several feet above the zero tid level. Another water channel is shown between squares 85 and 90. The outermost granite projection is located between squares 90 and 108. This portion is the area which is most exposed to the wave action.

COLEMAN, J. 1933—The nature of intertidal zonation of plants and animals. Jour. Mar. Biol. Assoc. **18**:435-476.

DAVENPORT, C. B. 1903—The nature of intertidal zonation of plants and animals. Jour. Mar. Biol. Assoc. **18**:435-476.

DAVENPORT, C. B. 1903—Animal ecology of the Cold Spring sand pit. Chicago Dec. Publ. **10**(1):157-163.

DAVIS, J. R. AND H. J. FLEURE. 1903—*Patella.* Liverpool Mar. Biol. Cttee. Memoir, (London) **10**:1-76.

DURIETZ, G. E. 1930—Algbälten och vattenståndsväxlingar vid svenska Östersjökusten. Botaniska Notiser, (Lund.) **1930**:421-432.

ELMHIRST, R. 1932—Quantitative studies between tide mark. Glasgow Nat. **10**:56-62.

ELTON, C. 1927—Animal Ecology. New York. 207 pages.

FIELD, I. A. 1922—Biology and economic value of the sea mussel, *Mytilus edulis.* Bur. Fish. **38**:127-260.

FLATTELY, F. W. AND C. L. WALTON. 1922—The Biology of the Seashore. New York. 336 pages.

GAIL, F. W. 1918—Some experiments with Fucus to determine the factors controlling its vertical distribution. Publ. Puget Sound Biol. Sta. **2**:139-151.

GALLIHER, E. W. 1932—Sediments of Monterey Bay, Calif. Mining in Calif., Division of Mines, San Francisco. 42-77.

GEE, W. 1913—Modifiability in the behavior of the California shore anemone, *Cribrina xanathogrammica*. Jour. Animal Behavior **3**:305-328.

GERSBACHER, W. M. AND M. DENNISON. 1930—Experiments with animals in tide pools. Publ. Puget Sound Biol. Sta. **7**:209-215.

GISLEN, T. 1929—Epibiosis of Gullmar Fjord I. Kristineberg's Zool. Sta., 1877 to 1927, n:r **4**:1-123.

———1930—Epibiosis of Gullmar Fjord II. Kristineberg's Zool. Sta., 1877 to 1927, n:r **4**:1-380.

———1931—A survey of the marine associations in the Misaki district. Jour. Fac. Sci. Imp. Univ. Tokyo **2**:389-444.

GOWANLOCH, J. N. AND F. R. HAYS. 1926—Contribution to the study of marine gastropods, I. Contr. Canad. Biol. and Fish., N. S., **3**:133-166.

HASEMAN, J. D. 1911—The rhythmical movements of *Littorina littorea* synchronous with ocean tides. Biol. Bull. **21**:113.

HAYS, F. R. 1929—Contribution to the study of marine gastropods, III. Development, growth and behavior of Littorina. Contr. Canad. Biol. and Fish., N. S. **4**: 413-431.

HEDLEY, C. 1915—An ecological sketch of the Sydney beaches. Jour. Roy. Soc. New So. Wales **49**:15-77.

HERDMAN, W. A. 1919—Notes on the abundance of some common marine animals. Spolia Runiana IV. Jour. Finn. Soc. Zool. **34**:247-259.

HESSE, R. 1924—Tiergeographie auf ökologischer Grundlage. Jena, 313 pages.

HEWATT, WILLIS G. 1935—Ecological succession in the *Mytilus californianus* habitat as observed in Monterey Bay, California. Ecology **16**:244-251.

HUMPHREY, R. R. AND R. W. MACY. 1930—Observations on some probable factors controlling the size of certain tide pool snails. Publ. Puget Sound Biol. Sta. **7**:205-509.

HUNT, O. D. 1925—The food of the bottom fauna of the Plymouth fishing grounds. Jour. Mar. Biol. Assoc. **13**:560-899.

HUNTSMAN, A. G. 1918—The vertical distribution of certain intertidal animals. Trans. Roy. Soc. Canada, **12**(3):53-60.

JOHNSON, M. E. AND H. J. SNOOK. 1927—Seashore animals of the Pacific Coast. New York. 659 pages.

JOHNSON, D. S. AND H. H. YORK. 1915—The relation of plants to tide levels. Carnegie Inst. Publ. **206**:1-162.

JOHNSTON, T. H. 1917—Ecological notes on littoral fauna and flora of Colundra, Queensland. Queensland Nat. **2**:53-63.

KANDA, S. 1916—Studies on the geotropism of the marine snail, *Littorina littorea*. Biol. Bull. **30**:57-84.

KING, L. A. L. AND E. S. RUSSELL. 1909—Method for study of animal ecology of the shore. Proc. Roy. Soc. (London) **17**:225-253.

KIRSOP, F. M. 1922—Preliminary study of methods of examining life of the sea bottom. Publ. Puget Sound Biol. Sta. **3**:129-139.

KLUGH, A. B. 1923—Common system of classification in plant and animal ecology. Ecology **4**:366-377.

———1924—Factors controlling the biota of tide pools. Ecology **5**:192-196.

LAUBENFELS, M. W. DE. 1932—Marine and fresh water sponges of California. Proc. U. S. Nat. Mus. **81**:1-140.

MACGINITIE, G. E. 1935—Ecological aspects of a California Marine estuary. Amer. Midl. Nat. **16**:629-765.

MAY, R. M. 1924—Ophiurans of Monterey Bay. Proc. Calif. Acad. Sci., Ser. 4, **13**:261-303.

MAYNE, C. 1918—Report of Edward Forbes Exhibitions. 32nd Ann. Rept. Liverpool Mar. Biol. Comm. 10-13.

MOLANDER, A. 1928—Animal commities on soft bottom areas in Gullmar Fjord. Kristineberg's Zool. Sta., 1877-1927, n:r **2**:1-90.

MURRAY, J. AND J. HJORT. 1912—Depths of the Ocean. London, 821 pages.

O'DONOGHUE, C. H. 1924—On the summer migration of certain starfish in Departure Bay, B. C. Contr. Canad. Biol. S. S. **1**:455-472.

ORTON, J. H. 1920—Sea temperature, breeding and distribution in marine animals. Jour. Mar. Biol. Assoc., N. S., **12**:339-366.

———1932—Studies on relation between organism and environment. Trans. Liverpool Biol. Soc. **46**:1-16.

PEARSE, A. S. 1913—Observations on the fauna of the rock beaches at Nahant, Mass. Bull. Wisconsin Nat. Hist. Soc. **11**:8-72.

———1926—Animal Ecology. New York, 1926, 417 pages.

———1929—Observations on certain littoral and terrestrial animals at Tortugas, Fla. Carnegie Inst. Publ. **391**:205-223.

———1931a—The beaches at Misaki. Jour. Pan-Pacific Rsearch Inst. **6**:3-8.

———1931b—Ecology of certain crustaceans on the beaches at Misaki, Japan. Jour. Elisha Mitchell Sci. Soc. **46**:161-166.

PERRY, E. M. 1916—Distribution of certain invertebrates on a restricted area of sea bottom. Publ. Puget Sound Biol. Sta. **1**:175-176.

PETERSON, C. G. J. 1913—Valuation of the sea II. Rept. Danish Biol. Sta. **21**:1-67.

———1918—The sea bottom: Valuation of Danish Waters, 1883-19917. Rept. Danish Biol. Sta. **25**:1-62.

———1924—A brief survey of the animal communities in Danish waters. Amer. Jour. Sci., **7**(3):1-343.

PHILLIPS, JOHN F. V. 1931—Quantitative methods in study of numbers of terrestrial animals in biotic communities. Ecology **12**:633-650.

PIERRIE, M. E. ET. AL. 1932—Quantitative study of the fauna of the sandy beach at Fort Erin. Jour. Mar. Biol. Assoc. **18**:279-296.

PIERRON, R. P. AND Y. C. HUANG. 1925—Animal succession on denuded rocks. Publ. Puget Sound Biol. Sta. **5**:149-158.

RICE, L. 1930—Peculiarities in the distribution of barnacles in communities and their probable causes. Publ. Puget Sound Biol. Sta. **7**:249-257.

SCHMITT, W. L. 1921—The marine decapod crustacea of California. Univ. Calif. Publ. in Zool. **23**:1-470.

SHELFORD, V. E. 1916—Physiological differences between marine animals from different depths. Publ. Puget Sound Biol. Sta. **1**:157-174.

———1929—Laboratory and field ecology. Baltimore, 608 pages.

———1930—Geographic extent and succession in Pacific North American intertidal (Balanus) communities. Publ. Puget Sound Biol. Sta. **7**:217-224.

———1932—Basic principles of the classification of communities and habitats and use of terms. Ecology **13**:105-120.

———AND E. D. TOWLER. 1925—Animal communities of the San Juan Channel and adjacent areas. Publ. Puget Sound Biol. Sta. **5**:33-74.

STEGGERDA, M. 1925—Rock bottom fauna of a restricted area near Friday Harbor, Wash. Publ. Puget Sound Biol. Sta. **5**:29-32.

STEPHENS, A. C. 1928—Notes on quantitative distribution of molluscs and polychetes in intertidal areas of the Scottish coast. Proc. Roy. Phys. Soc. (Edinburgh) **21**:205.

———1929—Studies on Scottish marine fauna. Trans. Roy. Soc. (Edinburgh) **56**:291.

SUMMER, F. B., OSBURN, R. C. AND L. J. COLE. 1911—A biological survey of the waters of Woods Hole and vicinity. Bull. U. S. Fisheries **31**:Pt. 1, 1-443; Pt. 2, 547-795.

TOWLER, E. D. 1930—An analysis of intertidal barnacle communities of the San Juan Archipelago. Publ. Puget Sound Biol. Sta. **7**:225-232.

VERRILL, A. E. 1873—Report on the invertebrate animals of Vineyard Sound and adjacent waters. U. S. Fish Comm. Pt. 1 :295-778.

WEESE, A. O. AND MACNAB. 1930—Seral communities of a muddy sea bottom. Proc. Okla. Acad. Sci. **10**:26-28.

WILSON, D. P. 1929—A habit of the common periwinkle *(Littorina littorea)*. Nature **124**:443.

WORLEY, L. G. 1930—Correlation between salinity, size and abundance of intertidal barnacles. Publ. Puget Sound Biol. Sta. **7**:233-240.

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