BEAUFORTIA

SERIES OF MISCELLANEOUS PUBLICATIONS

ZOOLOGICAL MUSEUM - AMSTERDAM

No. 148 Volume 12 Jan. 29, 1965

Community composition, structure, and interrelationships in the marine intertidal *Endocladia muricata* - *Balanus glandula* association in Monterey Bay, California

PETER W. GLYNN

TABLE OF CONTENTS

This study represents a slightly revised edition of a dissertation submitted to the Department of Biological Sciences of Stanford University in partial fulfillment of the requirements for the degree of Doctor of Philosophy. Contribution from the Institute of Marine Biology, University of Puerto Rico, Mayagüez, Puerto Rico.
Received February 12, 1964.

INTRODUCTION

Historical and perspective

When the tide recedes along the shores of the western coast of North America, a zone rich in living things is uncovered. In intertidal regions where soft substrates prevail, such as sandy beaches and mud flats, much of the life present may be concealed beneath the surface, but on rocky shores the profusion of life on the exposed surface is very evident. The assemblage here is rich, not only in quantity of life but also in number of species, and the diversity represented may be nearly overwhelming (BOLIN, 1949). The present study deals with the community ecology of a small portion of this assemblage.

Published studies on the ecology of the organisms and associations of the North American Pacific coast intertidal region may be grouped into three main categories. First, there are the studies which deal primarily with the qualitative delineation of intertidal zones and associations, and which attempt to correlate the occurrence of these with various factors of the physical environment (e.g., the studies of GISLÉN, 1943-44; RICKETTS & CALVIN, 1939 and later editions; DOTY, 1946; RIGG & MILLER, 1949). These studies are admirably summarized and reviewed by HEDGPETH (in RICKETTS & CALVIN, 1962). Second, there are the studies centering on the biology or ecology of a single species, or of a group of closely related species, such as the studies of TEST (1945), FRITCHMAN (1961-62), SEGAL (1956), YONGE (1962), and others, on limpets of the genus *Acmaea*. Works of this sort, far too numerous to list, are widely sampled in the large classified bibliographies of LIGHT, SMITH, et al. (1957) and RICKETTS & CALVIN (1962). A third main category of ecological investigations carried out in the Pacific coast intertidal region includes those studies in which a community-oriented approach is taken. In the present context, these deserve a review in some perspective.

The first significant contributions in the study of marine communities as such appeared in the literature largely during the latter half of the nineteenth century. These were studies dealing mainly with the benthic communities of the continental shelf in European and eastern North American waters, and stemmed from the excellent work of such famous pioneer students as FORBES (1844), VERRILL (1873), and MÖBIUS (1883). The historical development of these investigations is quite adequately covered by GISLÉN (1930), ALLEE (1934), and HEDGPETH (1957).

The analysis of rocky intertidal communities did not get underway until the early part of the present century. In GISLÉN's very interesting and comprehensive review of 1930, mention is made of quantitative community analyses carried out in the rocky intertidal zone of England in 1918 and 1919 by MAYNE & HERDMAN. These studies, in which the investigators recorded the numbers and weights of organisms per unit area, and calculated the numbers of *Balanus*, *Fucus*, limpets, and other forms present in square-foot frames, were among the earliest in the area of intertidal community analyses.

Since these pioneer explorations numerous quantitative community studies in the intertidal belt have been carried out in various parts of the world. In view of the ease of direct sampling at low water, however, it is somewhat surprising that so little work of this sort has been done on the Pacific coast of North America. HEDGPETH (in RICKETTS & CALVIN, 1962, p. 490) notes that "....quantitative population studies have been scarce on this coast. When the papers of Shelford and his students, the work of Hewatt, and the unpublished work of Pitelka & Paulson .... have been cited, this is about all we have."

SHELFORD and his students began in 1925 a survey of the intertidal and subtidal communities in the Puget Sound area which lasted for about five years. The associations found were quantitatively described and were named according to the abundant faunal elements present. The distribution and abundance of the organisms in one transect, across the entire rocky intertidal zone, was investigated by HEWATT (1937) at the Hopkins Marine Station, Pacific Grove, California. His study was particularly concerned with the zonation of the animals and with ecological succession in the *Mytilus californianus* association. The food relations of the more conspicuous species were also elucidated. The work of PITELKA & PAULSON (unpublished) consisted of a quantitative survey of the fauna of tidal flats in Tomales Bay, California. Probably the most comprehensive qualitative account of a community on the Pacific coast is MACGINITIE's, "Ecological aspects of a California marine estuary" (1935). Here an analysis was made of the environmental conditions and fauna of an extensive tidal flat, and much natural history information was gathered on the more abundant animals.

Two rather different viewpoints have developed among community ecologists on the matter of how one may best approach an understanding of the biotic community. One viewpoint has emphasized the importance of first learning the individual life histories of each species in the assemblage before attempting any generalizations of the whole complex. For example, MACGINITIE (1939) concluded his observations on a survey of littoral marine communities with this assertion: "Individual life histories of members of the community are absolutely necessary to a fuller understanding of the sociology of marine animal communities. Every animal is a part of the environment of every other animal in the community, and therefore, is a part of the environment of the community."

At the other extreme, in recent years a school has formed around what may be called the "ecosystem approach". This view seeks to reveal the nature of the higher-order principles operating at the community level, and omits from consideration most of the multifarious activities and interactions of the species populations making up the community. In 1957 ODUM proposed this approach for an ecology course, drawing an analogy between a frog specimen and a biotic community. He stated, "The philosophy of the ecosystem approach is almost exactly the same as that underlying the procedures commonly followed in the general biology laboratory. In general courses we first bring a whole organism of some kind such as the frog, Amoeba, Spirogyra or a flowering plant into the laboratory. After the student has studied the organism as a whole he then dissects (either actually or optically) the specimen and studies the various parts. It is important to note that the reverse procedure would be more or less ridiculous; that is, we would not first bring the student the liver of the frog (or the stamen of the plant) have him study that, then next day bring him the isolated stomach or each individual muscle one by one — and finally during the last week of the course attempt to assemble all the parts into a frog."

Numerous ecologists have recognized the importance of both of these approaches, and one of the first of them was C. S. Elton. As noted in the Bulletin of the Ecological Society of America in December 1961, when this society bestowed upon him the honorary title of "Eminent Ecologist", "While it became evident that ecosystems could be studied as single units, or organic machines, Elton also recognized that the respective roles of the components of such a system cannot be evaluated without measurements of their population characteristics." Elton was also one of the first ecologists to emphasize that " .... our knowledge of the social arrangements of animals will be most successfully and quickly advanced by elaborate studies of simple communities rather than superficial studies of complicated ones." (ELTON, 1927, Chapter 7).

Present approach and problem

In approaching the present study, it was decided to select for analysis a marine association sufficiently simple in composition that equal effort might be given to the study of the natural history relations of the more influential species and to the higher-order attributes of the whole complex. The intertidal region contains a biota which is not equally rich in all parts. The uppermost regions, splashed only by the highest waves, are relatively barren, and as one proceeds downward life becomes steadily more abundant and diversified. The biologist seeking rich, exotic collecting heads for the lower levels, but to the community ecologist the simpler upper levels present more attractive possibilities for fruitful study.

High in the intertidal region lies a strip or zone characterized most conspicuously by the presence of the red alga, *Endocladia muricata* and the acorn barnacle, *Balanus glandula*. The *Endocladia muricata-Balanus glandula* association was originally selected for study because of the following desirable attributes: (1) it appeared to contain relatively few species; (2) it is of common occurrence and easily recognized; (3) it is accessible for study the whole year and at most phases of the tide; (4) it appeared to be a reasonably consistent ecological entity; (5) the groups and species of organisms in this zone are comparatively well known taxonomically; and (6) most of the species are hardy and easy to maintain in the laboratory.

First appearances can be deceptive. While initially, this association appeared to contain relatively few species, it was discovered in the course of the study that about 90 species, mostly macroscopic forms, were commonly represented. Moreover, five new species of animals were found; *Musculus* sp. (Pelecypoda), *Runcina* sp. (Opisthobranchia), *Hyale* sp. and *Pontogeneia* sp. (Amphipoda), and *Hyadesia* sp. (Acarina). Two very common species present represented new records for the eastern Pacific; *Allorchestes ptilocerus* (Amphipoda), known formerly from the Sea of Japan and the east Asiatic coast, and *Syllis vittata* (Polychaeta), from European waters.

The present investigation was concerned with the qualitative and quantitative composition and structure of the *Endocladia-Balanus* association, the autecologies of the more influential species present in this association, and with the food interrelationships of these organisms. Research activities followed essentially the following scheme. (1) Qualitative and quantitative sampling of the association for numbers and biomasses of the species composing it was carried out in different places where the association occurs, and at different seasons of the year in essentially the same place, to determine variation in community composition with place and season. The composition of the benthos of the association was determined mainly from sixteen 20 × 20 cm quadrats and qualitative monthly samples collected from January, 1959 to December, 1961. Field observations were carried out during the day and night and at high and low water to determine conditions of the physical environment and the movement and density of the more transient members. (2) Autecological studies were made of the more abundant forms. (3) Qualitative determinations were made of the feeding habits and food interrelationships within the association and between members of the association and species inhabiting adjacent pelagic and benthic communities, to make possible a portrayal of a web diagram of the food relationships.

Acknowledgements

I take pleasure at this time in acknowledging the help given to me by several people. Listed below are some of these collaborators, identified mainly on the basis of the assistance provided. Not included here are many of my graduate-student associates, to whom I am also grateful for assistance and enlightening discussions.

Guidance and genuine interest were furnished throughout the course of the study by my major professor and friend, Dr. D. P. Abbott of the Hopkins Marine Station, Stanford University. Other staff members of this institution gave valuable assistance in certain areas. Dr. C. B. van Niel contributed helpful suggestions on theoretical and practical matters pertaining to determining the organic matter content of organisms. Aid was given by Dr. L. R. Blinks in the photosynthetic experiments with *Endocladia muricata*. Dr. R. L. Bolin provided constructive criticism on certain aspects of the study, and in cooperation with Dr. E. C. Haderlie of the Monterey Peninsula Junior College, helped in establishing the intertidal heights of the study plots. Thanks go to Dr. D. E. Wohlschlag for suggestions on field and statistical procedures, and for critically reading the thesis. In the author's absence, Mr. B. Fink, now with the Inter-American Tropical Tuna Commission, La Jolla, California, carried out the field work for a period of one week.

The study was interrupted at the end of June 1960, when the author accepted a position in the Department of Biology, University of Puerto Rico, Mayagüez. Until the investigation at the Hopkins Marine Station was again continued in September 1961, Mr. A. T. Newberry collected and shipped monthly qualitative samples to Puerto Rico. In Mayagüez, Drs. H. E. Warmke and N. E. Delfel of the United States Agriculture Experiment Station, provided laboratory space and facilities for nitrogen analyses. Dr. Delfel also gave helpful suggestions on the statistical treatment of certain data. Drs. J. Maldonado-Capriles and M. Martínez-Picó of the Department of Biology, University of Puerto Rico, Mayagüez, were instrumental in making possible a return trip to the Hopkins Marine Station, to complete the study. During the period January 1-March 31, 1961, stipend support was received under United States Public Health Service Training Grant 2G-647, Division of General Medical Sciences, National Institutes of Health.

Temperature and salinity data were provided through the courtesy of Mrs. M. K. Robinson, Scripps Institution of Oceanography. Lieutenant R. W. Sallee and Chief J. C. Hansen of the United States Naval Air Facility, Monterey, kindly made available weather observations made there. Dr. W. Thompson, of the United States Naval Post Graduate School, Monterey, was very helpful in providing meteorological information. Dr. J. R. Borsting, also a member of this school, was equally helpful in discussing some of the theoretical problems involved in the statistical treatment of certain data. Mr. Vernal L. Yadon of the Pacific Grove Museum kindly assisted in collecting bird specimens for stomach analyses. Numerous workers aided in the identification of organisms, and these people are credited where their respective groups are taken up under „Qualitative composition of the association".

Finally, the author is appreciative of the time allowed for writing up these results, granted by Drs. J. A. Rivero and J. E. Randall of the Institute of Marine Biology, University of Puerto Rico, Mayagüez, and the aid given in the preparation of the illustrations by Mrs. C. Boyce and Mr. D. V. Mejía, also of the University of Puerto Rico, Mayagüez.

APPEARANCE AND OCCURRENCE OF THE ENDOCLADIA-BALANUS ASSOCIATION IN THE STUDY AREA AND ELSEWHERE

Studies were carried out on the intertidal shore directly in front of the Hopkins Marine Station (36° 37′ N; 121° 54′ W), Pacific Grove, California (figs. 1 and 2). The area most intensively studied is protected from the full impact of the shoreward-moving swells by marginal outcropping islands and reefs, and would be classified as "protected outer coast" according to the scheme of RICKETTS & CALVIN (1962). It is important to bear this in mind, for on some rock surfaces at the same level but exposed to greater wave action the *Mytilus californianus* association replaces the *Endocladia-Balanus*

FIGURE 1. Study area at a receding tide (ca. + 5.0 ft), looking eastward from the shore of the Hopkins Marine Station, Pacific Grove, California (February 7, 1962).

FIGURE 2. Study area at a receding tide (ca. + 2.0 ft), looking eastward from the shore of the Hopkins Marine Station, Pacific Grove, California (January 23, 1962).

FIGURE 3. A high rock bearing an *Endocladia-Balanus* association at the Hopkins Marine Station (February 3, 1962). A 30 cm ruler is shown in the foreground to the right. The most prominent components in this carpet are the dark tufts of *E. muricata* and the almost continuous, light sheet of *B. glandula*. A well-developed aggregation of *Mytilus californianus* extends obliquely in a crack to the bottom left of the photograph.

FIGURE 4. Appearance of the *Endocladia-Balanus* association from a distance of about six feet, Hopkins Marine Station (February 3, 1962). A 15 cm ruler is shown on the right.

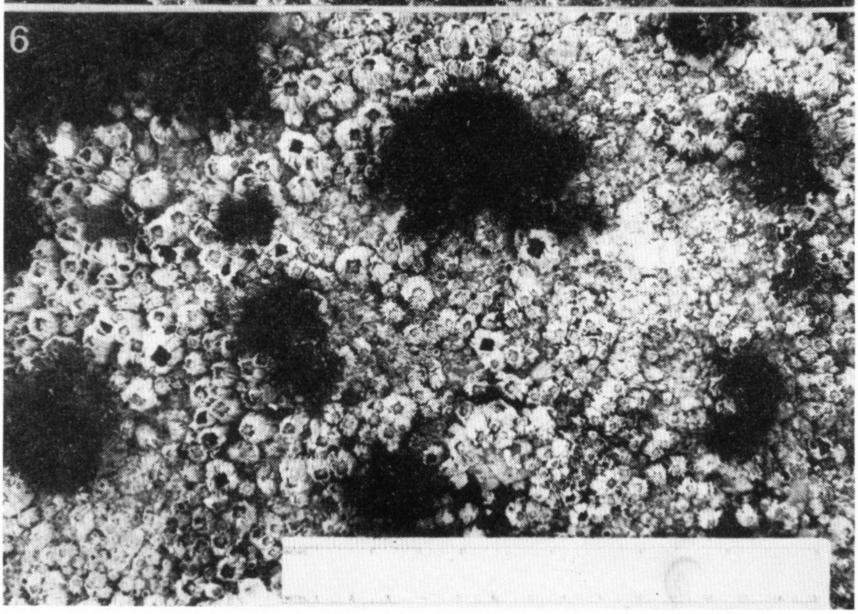


FIGURE 5. Close-up view of the *Endocladia-Balanus* association, Hopkins Marine Station (February 3, 1962). Close-up of the rock surface shown in fig. 4. Two thalli of *Gigartina agardhii* may be seen to the left, and one thallus of *Porphyra schizophylla* near the top center.

FIGURE 6. Close-up view of the *Endocladia-Balanus* association, Hopkins Marine Station (January 16, 1962). The proportion of large individuals of *B. glandula* is higher than in the area shown in fig. 5.

belt. The overall appearance of the association is well-illustrated in fig. 3. Figures 4, 5, and 6 show the association in more detail.

The specific locations where the quadrat samples were taken are shown in fig. 7. Quadrat samples I—XII inclusive were taken at or very near the center of the association at each spot, approximately halfway between the upper and lower vertical limits of the belt. Subsequent to collecting, these 12 quadrats were marked with coded lag screws turned into expansion shields. The Roman numeral of the quadrat was cut into the screwhead. Also, alternate corners of the square were drilled so that the exact collecting site could be re-identified. All of these markers were in good condition when last examined in March, 1962. At that time Quadrat I was three years old. In addition to the above, two quadrats (H_1 and H_2) were taken at the upper limits of the association, and two more (L_1 and L_2) taken at the lower limits of the belt. Locations of these are also shown in fig. 7.

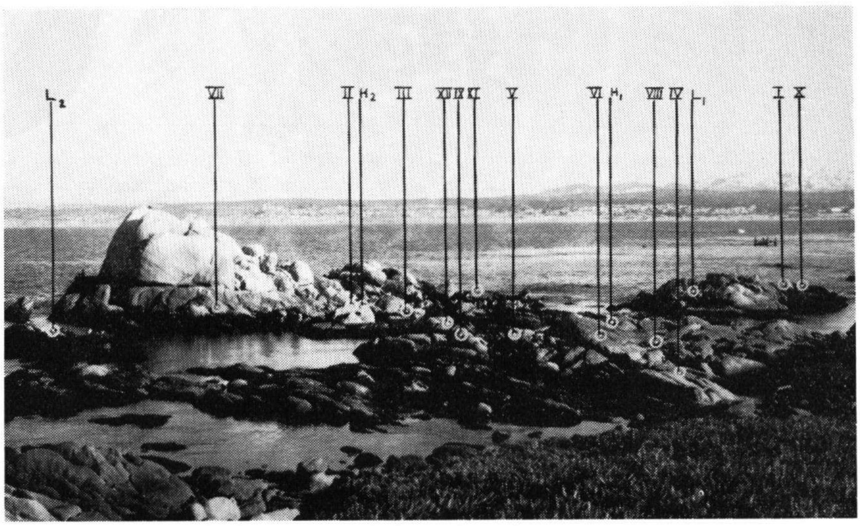


FIGURE 7. Location of 16 quadrat sites in the study area at the Hopkins Marine Station (January 16, 1962).

The intertidal height at the center of each 20 × 20 cm quadrat was determined, using as a reference point an intertidal brass peg at 3.82 ft above mean lower low water (MLLW). This is one of four markers established at the request of G. E. MacGinitie by the United States Coast and Geodetic Survey in 1930. A Dietzgen transit and Lietz staff were used for measuring the heights of the midpoints for each of the investigated plots. The elevations determined for each quadrat are shown in fig. 8. The average height of the 12 quadrats taken from or very near the center of the association was 4.6 ft above MLLW. However, it is clear from this figure that the center of the *Endocladia-Balanus* association varies significantly even within a limited area. When compared with the positions of the low (L) and high (H) samples, there appear to be three anomalously placed quadrats, viz. VII, X, and XII. Number VII is in one of the most exposed positions, subject to splash and surge, near the end of a surge channel. Numbers X and XII, low in relative position, are located in protected situations on the shore-facing sides of rocks. The two low sites (L_1 and L_2) are a bit displaced upwards, perhaps because of their locations in relatively exposed areas.

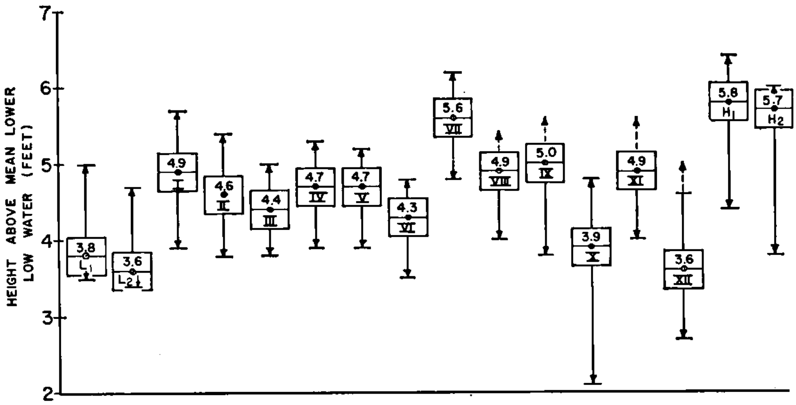


FIGURE 8. The vertical position in the intertidal zone of 16 quadrats taken in the *Endocladia-Balanus* association. Quadrat numbers are indicated by Roman numerals, while Arabic numerals show the heights of the centers of the quadrats in feet above mean lower low water level. The arrows above and below each quadrat point out the upper and lower limits of the *Endocladia-Balanus* belt at each site.

An estimate (± 3 in) of the vertical extent of the *Endocladia-Balanus* belt was determined for each quadrat sample site. This measurement was made by sighting along the margins of the belt with a rod and carpenter's level and reading off directly from a vertically placed yardstick in the center of the quadrat the distance to the upper and lower limits. Figure 8 shows the width of the belt for each of the sites. The vertical axis of this graph indicates the height in feet above sea level. Arrows terminating in broken lines indicate a discontinuity in the substrate, e.g. the top of a rock. In these situations the association might well have become established at a higher level had the opportunity to do so been available.

In perusing the literature on the subject of vertical distribution of intertidal species, sometimes it seems that the limits indicated for the same species at the same locality are more dependent on the author than anything else. For example, in Pacific Grove, California, DOTY (1946) gives the range for *E. muricata* as + 3 to + 4 ft above MLLW. GISLÉN (1944) sets the limits from + 1.1 to + 4.8 ft. For *B. glandula*, HEWATT (1937) has set the lower boundary one foot lower than Gislén, and the latter has the upper limit 3.7 ft higher than Hewatt, under exposed conditions. From the differences in the vertical distribution of the *Endocladia-Balanus* association from place to place in essentially one locality (fig. 8) it can be understood readily that the disagreement between workers probably is not significant. The vertical ranges of the species cited depend on such physical conditions as slope, degree of exposure to wave action, surges in rock fissures, and amount of spray, as well as on more subtle biological interactions, which may differ considerably from rock to rock or even on different faces of the same rock.

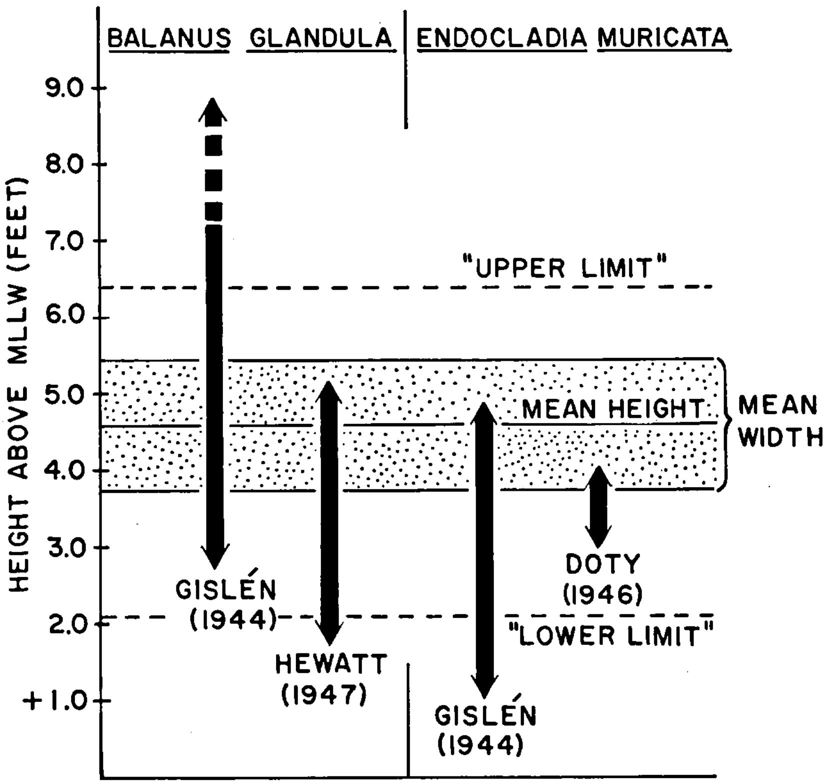


FIGURE 9. Comparison of the vertical ranges of *B. glandula* and *E. muricata* at the Hopkins Marine Station as established by various workers, with the vertical position of the 16 quadrats collected from the *Endocladia-Balanus* association. Upper and lower limits represent the over-all vertical range of the *Endocladia-Balanus* association in the vicinity of the quadrat sites.

The upper and lower limits of the *Endocladia-Balanus* belt at the 16 quadrat sample sites in the immediate area investigated, as compared to the vertical distribution of *E. muricata* and *B. glandula* as established by other workers, are shown in fig. 9. The ranges shown do not indicate the upper limits of distribution. In some situations of exposure to extreme exposure to wave action, e.g. a promontory jutting straight out into the open sea, one may find a well-developed carpet of *Endocladia* and *Balanus* displaced vertically upward by as much as 10 to 15 ft (fig. 3). However, the ranges indicated in fig. 9 show that *B. glandula* and *E. muricata* overlap vertically, the former occupying the highest level. The present study was centered in the region where the two species in association dominate the other biotic elements present. The margins of this comparatively narrow band of overlap, averaging roughly two feet in width, are delimited for one intertidal area in fig. 10.

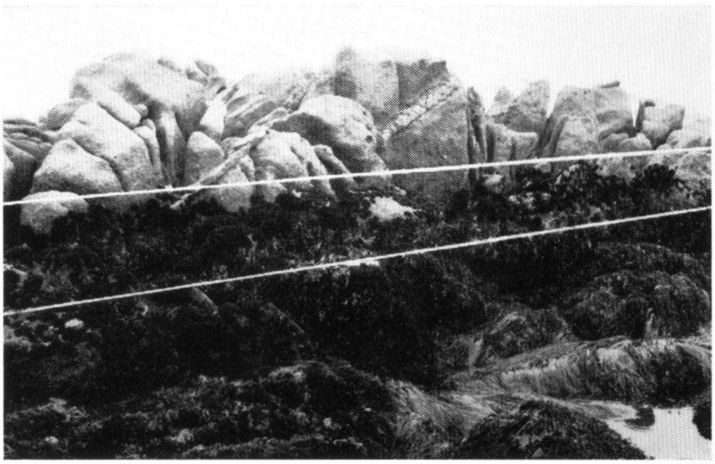


FIGURE 10. The upper and lower limits of the *Endocladia-Balanus* association in relation to other aspects of the intertidal zone (February 3, 1962). A 30 cm ruler is visible in the center of the photograph.

A field survey of the latitudinal extent of the association was not undertaken, but the possible range over which *B. glandula* and *E. muricata* could be found in association along the Pacific coast is indicated in fig. 11. SMITH (1944) gives the range of *E. muricata* as extending from La Jolla, California north to the Shumagin Islands, Alaska. RICKETTS & CALVIN (1962) state that the range of *B. glandula* extends from at least as far south as Ensenada, Baja California to the Aleutian Islands. Since these two species occupy essentially the same geographic range along the coast, it would be possible for them to occur together, on a firm substratum, along an irregular coastline for 20 degrees of latitude.

The known distributions of some of the other more important faunal components also are indicated in fig. 11. The most abundant mollusk, the minute bivalve *Lasaea cistula*, was reported by KEEN (1938) to extend as far south, probably, as the tip of Baja California. Actually, the specimens she examined were collected from several localities between Round Island, Baja California, and Point Arena, California. The geographic position of Round Island is not given on any of the standard maps of Baja California, but according to Keen (personal communication) it is probably one of the small islets in Los Coronados archipelago, just off-shore near the California-Mexico border line. Apparently *Littorina scutulata* has nearly the same distributional limits as *B. glandula* (cf. RICKETTS & CALVIN, 1962). From FRITCHMAN'S (1962)

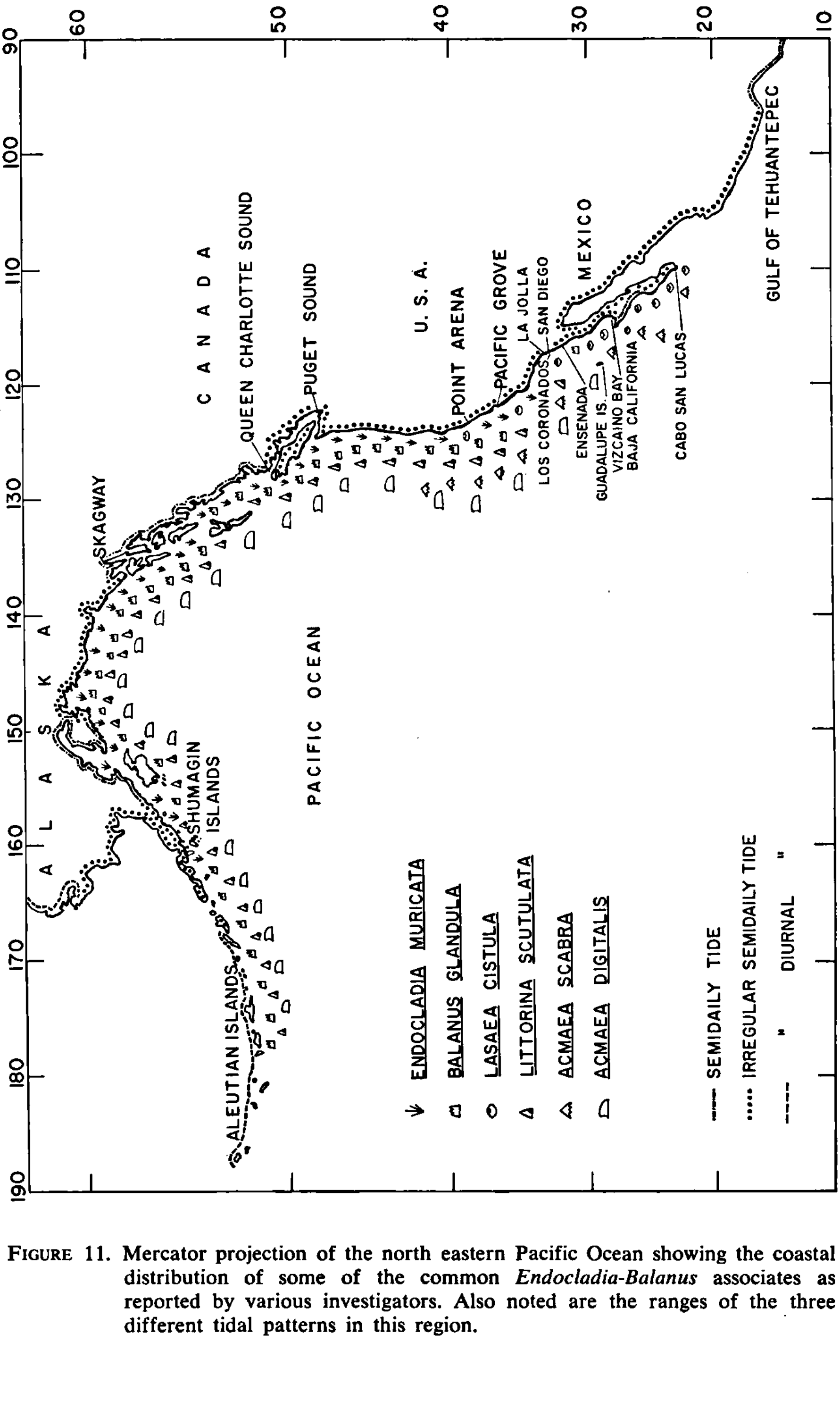


FIGURE 11. Mercator projection of the north eastern Pacific Ocean showing the coastal distribution of some of the common *Endocladia-Balanus* associates as reported by various investigators. Also noted are the ranges of the three different tidal patterns in this region.

tabulation of the ranges of the Acmaeidae, *Acmaea scabra* extends from 23° N. latitude (Cape San Lucas), to an uncertain point near 42° N. (near the California-Oregon border). *Acmaea digitalis* has a more northerly distribution, between 30° and 60° N. latitude, from Guadalupe Island, Mexico, to the Aleutian Islands. Pacific Grove lies closer to the southernmost extensions of *E. muricata*, *B. glandula*, and *A. digitalis,* and it seems possible, then, that the association is better established in the north.

SHELFORD (1930) recognized and studied a *Balanus-Littorina* biome in the vicinity of Puget Sound, and remarked that it ". . . . probably extends from central Alaska to San Diego or beyond. . . .". In 1935 SHELFORD and his co-workers concluded that communities of the *Balanus-Littorina* type (because of the worldwide occurrence of certain genera, and the ecological equivalence of species in both the North Atlantic and North Pacific Oceans) cover much of the suitable shores of the northern hemisphere.

Physical environment

Substrate

A brief account of the geological nature of the Monterey Peninsula shoreline and its environs was given by Galliher in 1932 in connection with investigations of the sedimentary deposits of the Monterey Bay. According to Galliher this is a highly complex region composed of the three major types of rock. Underlying the littoral zone are igneous and sedimentary formations, while metamorphic rock underlies the drainage basin of the bay. The rocky littoral zone at the Hopkins Marine Station is composed of a pre-Cretaceous, eroded granite porphyry. Occasionally a pegmatite dike cuts through this system, as is evident near the center-top in fig. 10. In addition, at the shoreline between and around many of these granite outcroppings are well-developed patches of shell debris on the surface of the eroded granitic sand. The action of the sea moves this sand and shell debris and causes considerable abrasion on some rocks. Often the tests of *Balanus glandula* and *Chthamalus* spp. are worn smooth under these conditions. These areas were always avoided when collecting quantitative samples.

Exposure and submersion

One of the most striking events to occur along the littoral belt of the northeast Pacific Ocean is the periodic rise and fall of the tide. Tidal fluctuations in the study area follow an irregular semi-daily pattern. This pattern extends from the Gulf of Tehuantepec into the Puget Sound region and as far north as the Alaska Peninsula. It is interrupted by a regular semidaily pattern along three stretches, viz. south of Vizcaíno Bay, Baja California for about 200 miles; from the Queen Charlotte Sound area to Skagway, Alaska; and along approximately 1,500 miles of the coastline in the vicinity of the Cook Inlet (Doty, 1957). These positions are marked on the map of the eastern Pacific Ocean in fig. 11.

The intertidal area represents a tension zone or region of overlap between the marine and terrestrial realms; submersion is essential for the life activities of the aquatic populations and exposure for the air-breathing forms. The physico-chemical characteristics of the sea and the atmosphere are markedly distinct; thus when the tidal level changes the intertidal populations are subject to an abrupt shift of environmental conditions. To the marine organisms at flood tide come such essential factors as food, dissolved oxygen, and a medium in which to discharge gametes or larvae. On the other hand, the air-breathing species must somehow become adjusted to the periods of submergence. Also, the same intertidal region can be invaded by different predators, depending on the phase of the tide.

An attempt was made to observe the occurrence and duration of periods of submergence and exposure in the association, and to compare these observed periods with corresponding periods predicted for the area from the U. S. Coast & Geodetic Survey Tide Tables. Procedure was as follows.

Quadrat VI, shown in figs. 7 and 8, was selected for study because it could be observed conveniently at high water. The center of this quadrat, at + 4.3 ft, lies 0.3 ft below the mean heights of the centers of Quadrats I through XII. The quadrat lies on an inclined surface, and extends over a vertical distance of approximately four inches. This quadrat was observed from shore during selected periods on eight different occasions during a three month period, September 21—December 13, 1961. The conditions noted were recorded in terms of whether the quadrat was exposed to air, awash, or submerged. These conditions, as used here, are defined as follows:

Exposed — whole quadrat exposed to air, without wetting by waves or splash.

Awash — quadrat alternately exposed to air and wetted by the sea, but not wetted for more than 50% of the time.

Submerged — quadrat wetted or covered with water more than 50% of the time.

Precise timing of the occurrence of these conditions was not possible because of irregular wave washing and the fluctuating rise and fall of the water line, but a reasonable approximation was made.

Since more wave action and splashing can be expected during periods of high seas or strong winds, and since a higher water level on the shore can be expected during periods of well-developed and prolonged westerly winds, observations were carried out under different weather conditions. The system employed for designating the character of the weather and sea was scaled according to the existing conditions in the study region. Thus "calm" conditions were characterized by swells of less than three feet from peak to trough and a wind velocity of no more than 10 mph. The height of the swells on a "moderate" day ranged between three and five feet and the wind, blowing from 10 to 20 mph, usually caused whitecaps to form. During the one "rough" day of observation the swells were over six feet in height, and a 30 to 40 mph northwest wind was blowing. The observations made on Quadrat VI are recorded in fig. 12 (see lines labled "observed") along with the predicted tidal curve. The predicted tidal curve for each of the days of observation was plotted by using data in the U.S.C.G.S. Tide Tables (1961), the 1/4—1/10 rule as outlined in that reference, and the correction factors for Monterey, California. The curves are shown in relation to the 4.3 ft level of Quadrat VI.

Comparison of the actual timed observations of exposure and submersion for Quadrat VI with predicted periods of exposure and submersion based on calculations from the Tide Tables, was done as follows. The predicted tidal curve was superimposed on a line drawn at + 4.3 ft, the measured height of the center of Quadrat VI. When the predicted water level exceeded this height, the quadrat was represented as submerged; when the water level was below this point the area was represented as exposed. No attempt was made to predict the time the quadrat might be awash. The predicted periods of exposure and submersion are shown in fig. 12.

This figure shows several things worthy of note. First, from these limited observations it is seen that the duration of the periods designated "awash" and "submerged" is not markedly correlated with roughness of sea conditions. The awash phase for a falling or rising tide was usually less than 30 minutes and never longer than one hour. This can be understood in view of the rapid rise and fall of the tidal curve. Second, the actual duration of the submerged period always amounted to more than that predicted. For example, the total duration of submersion on December 13 was three times the predicted value. Although no significant amount of wetting was expected on the basis of the predicted curves on November 5 and December 1, sub-

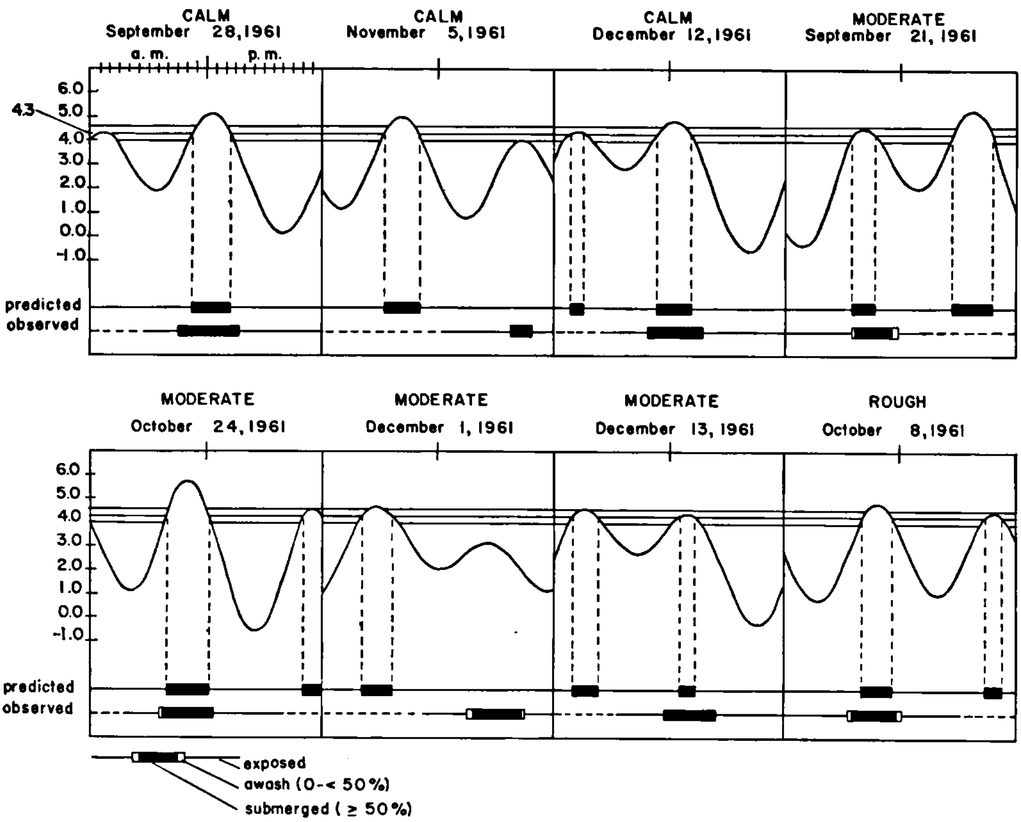


FIGURE 12. High water observations under calm, moderate, and rough sea conditions, showing the predicted and observed time of cover for Quadrat VI at the 4.3 ft level. Predicted tidal curves were drawn from data tabulated in U. S. Coast and Geodetic Survey Tide Tables (1961). Dashed lines under observed indicate observer not present. Times indicated are Pacific Standard Time.

mersion lasted for two hours and three and one-half hours, respectively. October 24 showed the least discrepancy between the observed and predicted periods, but even here the period of complete submersion was 13% longer than predicted.

The differences between predicted and actual periods of submersion tend to be somewhat greater during moderate and rough sea conditions (fig. 12), especially September 21, October 8, December 1, and December 13, but the differences are less than might be expected. The really striking point is that, even when the sea is calm, Quadrat VI is receiving the conditions of exposure and submersion that might be predicted if it were several inches lower in elevation. By averaging the effective vertical heights of the initiation and termination of the six awash observations, it is seen that Quadrat VI, at + 4.3 ft above MLLW behaves as if it were actually -0.8 ft lower, i.e., at + 3.5 ft. The reasons for the discrepancies between observed and predicted periods of submersion are not clear. Many factors could be involved, including the fact that the predictions apply to the nearest U.S.C.G.S. reference station at Monterey Harbor, more than a mile from the study area. The greatest discrepancy, noted in the afternoon of December 1 (fig. 12) might be explained by the fact that the observation occurred when a low-pressure cell was centered from 500 to 1,000 miles to the northwest of Monterey Bay over a period of three days. It is possible that this anomalous high-water level resulted from the difference in the pressure head between the off-shore low and the continental high pressure centers. In this connection SAUR (1962) found that the small, non-tidal variation of the sea level at San Francisco is greatest in the winter, when barometric fluctuations are also most pronounced.

On two occasions the periods of washing and submersion of Quadrat VI were compared simultaneously with those for Quadrat IV. Quadrat IV is located on a gradually sloping surface with its center at an elevation of 4.7 ft, whereas Quadrat VI is on a more steeply inclined surface and in a more protected position, with its center at 4.3 ft. Observations showed that Quadrat IV was exposed and submerged as if it were actually located at about + 3.9 ft, about 0.8 ft below its actual height of 4.7 ft. The qualitative and quantitative consistency of the biotic elements in quadrat samples I—XII supports the assumption that conditions of exposure and submersion are approximately the same for all quadrats, regardless of actual height. The average measured height of the centers of quadrats I—XII is + 4.6 ft. On the average, these points experience periods of submersion and exposure that would be predicted from the Tide Tables if they were about 0.8 ft lower down, that is, if they averaged about + 3.8 ft in elevation.

For calculating the frequency of the periods of exposure and submersion on a long term basis, the average height of the 12 quadrats was assumed to be + 3.8 ft rather than + 4.6 ft, in order to better approximate the time the *Endocladia-Balanus* zone is bathed by sea water and exposed to atmospheric conditions.

The predicted tidal pattern for Monterey, for the months of September, October, and November, 1961, is shown in fig. 13. The heights predicted for consecutive low and high waters are joined by straight lines to show the continuity for the three-month period. Each complete tidal cycle represents a lunar day, and the bi-monthly occurrence of neap and spring tides are seen to be associated with the phases of the moon. The effective or ecological height of the center of the *Endocladia-Balanus* belt in the study area is shown at 3.8 ft as compared with its absolute height (averaging 4.6 ft). Throughout the remainder of this paper, the average effective height of the study plots, for exposure calculations, is assumed to be + 3.8 ft. The observations have pointed out that the predicted tides more closely approach the existing conditions of exposure when the vertical level is dropped by -0.8 ft.

As can be seen in fig. 13, the ecological height of the center of the association in the study area is located just above the level of the lowest of the lower high waters, therefore it is usually bathed twice daily by the sea. (From its average absolute height, + 4.6 ft, it should never be reached by the highest of the low water tides). During the three-month period shown, the association was wetted twice every day except for four days in mid-September, two days in mid-October, and for brief periods at the beginning and end of November. In 1961, the 3.8 ft level was submerged daily by two high waters on 271 days, or 74% of the year. The peaks of these periods of submergence are separated by about 12 hours. At the very least, then, for three-quarters of the days of the year the *Endocladia-Balanus* belt is washed by the tides twice daily.

For calculating the duration of the periods of submersion and exposure on a long term basis it was assumed that "moderate" conditions of weather and sea probably best represented the most frequent conditions. The extreme moderate-day observation on December 1, 1961, was deleted from these calculations.

When the tide rises up to the level of the *Endocladia-Balanus* association, and then again falls from it, two awash phases will accompany one period of submergence. To determine the duration of awash versus submerged, an average of the time relations was calculated for each of these periods on the three moderate-day observations, September 21, 1961, October 24, 1961, and December 13, 1961 (fig. 12, table 1). The anomalous moderate-day observation of December 1, 1961 was not considered in this connection. The duration in minutes of each awash and submerged phase can be read directly from the observed horizontal bars in fig. 12. Of the total time the *Endocladia-Balanus* level is subject to high water wetting, then, the awash phase is here assumed to be 13% and the submerged phase 87%.

Another matter of importance is the percent of the total time during which the *Endocladia-Balanus* belt is exposed, and the percent of the total time it is submerged. This may be calculated in two ways.

First, one may draw a curve like that shown by Ricketts & Calvin (1952, p. 5, fig. 1, constructed from tide predictions for the six-month period, January 1—July 1, 1931, at Crissy Wharf in San Francisco Bay).

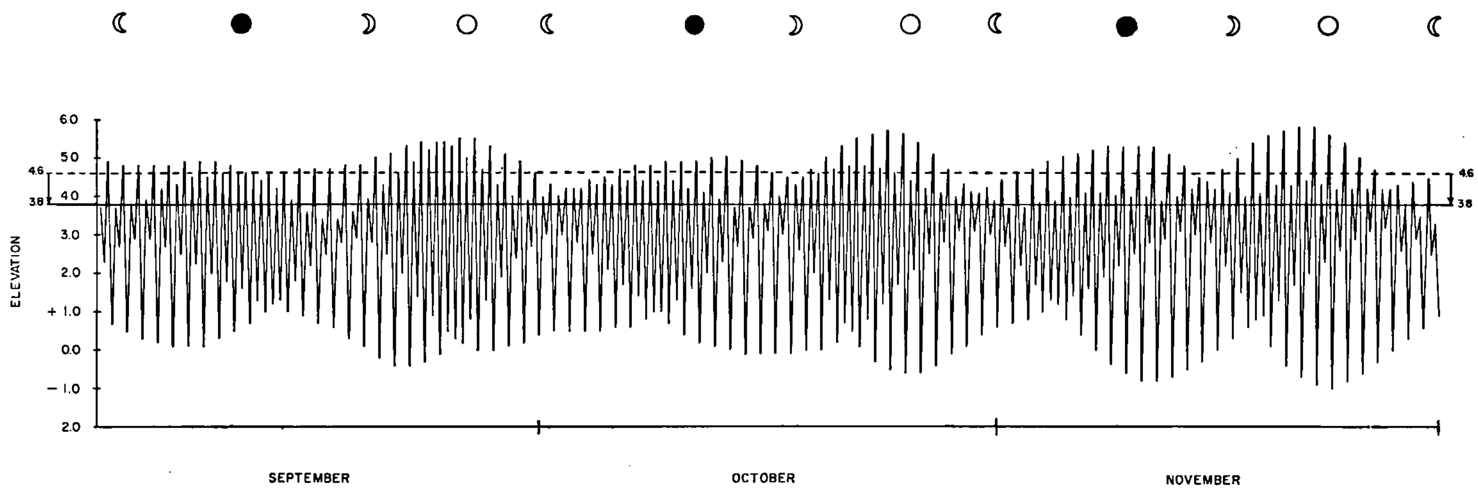


FIGURE 13. The predicted tidal pattern for Monterey, California from September through November, 1961, in relation to the 3.8 ft ecological height of the *Endocladia-Balanus* association. The phases of the moon are also shown in relation to the tides.

Such a curve is shown in fig. 14, indicating relative times of exposure to sea and atmosphere as determined on a long-term basis. Since the mean range of the tide in Monterey Bay is 0.5 ft less than at Fort Point, San Francisco (the reference station from which the data were obtained for the curve), a correction factor of 4.0 (mean range of tide at San Francisco)/3.5 (mean range of tide at Monterey), or 8/7 must be used. This simply means that although ".... the relative heights and the character of the exposure curve are the same for any point on the open Pacific coast." (RICKETTS & CALVIN, 1952), the curve will take on a more stretched-out configuration if the mean

TABLE I. Time relations of the awash and submerged phases in one complete tidal cycle for three moderate-day observations, 1961.

Observation	Minutes covered			% Time covered	
	Awash (flooding)	Submerged	Awash (ebbing)	Awash (total)	Submerged
Sept. 21	20	221	40	21	79
Oct. 24	30	294	10	9	91
Dec. 13	10	290	15	8	92
			Average	13	87

tidal range exceeds that at Fort Point, or will become more compressed in form if the mean tidal range is less than that at Fort Point. On this basis the corrected elevation of 3.8 ft at Monterey is 8/7 × 3.8, or 4.3 ft.

By dropping the average absolute height of the 12 study plots from + 4.6 to + 4.3 ft, it remains only to follow the point of intersection of the vertical height with the predicted tracing to the time axis on the exposure curve (fig. 14). The + 4.3 ft level was found to be exposed for 3,150 hours

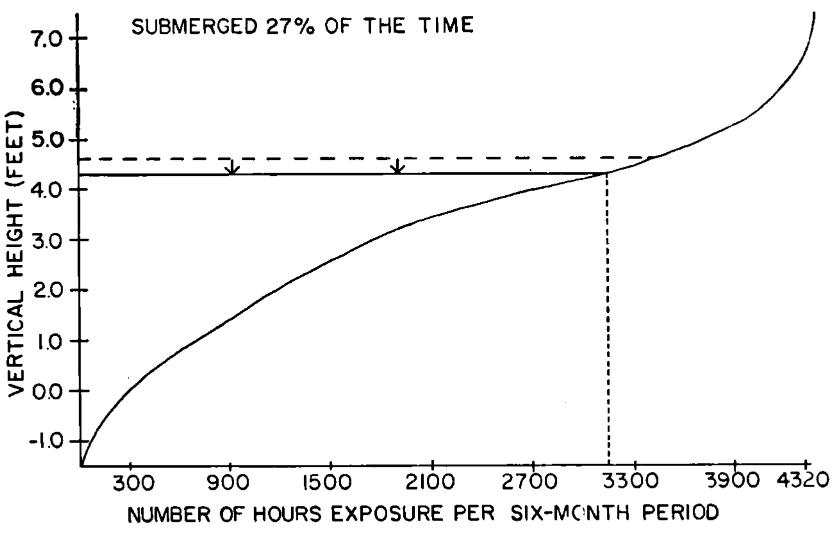


FIGURE 14. The predicted exposure curve for the six-month period, January 1—July 1, 1931, for Crissy Wharf, San Francisco, California.

for this six-month period in 1931. The percent of the time submerged, then, is simply the total number of hours for the period, minus the hours exposed (4,320-3,150), or 1,170 hours, 27% of the time.

A second way in which percent of total time the *Endocladia-Balanus* belt is exposed or submerged may be calculated is by means of a mean tidal curve, such as that shown in Ricketts & Calvin's fig. 132 (1952, p. 383). This mean tidal curve has been used for fig. 15. Since this curve is also based on data obtained at Crissy Wharf, San Francisco, the 8/7 correction factor for Monterey is used.

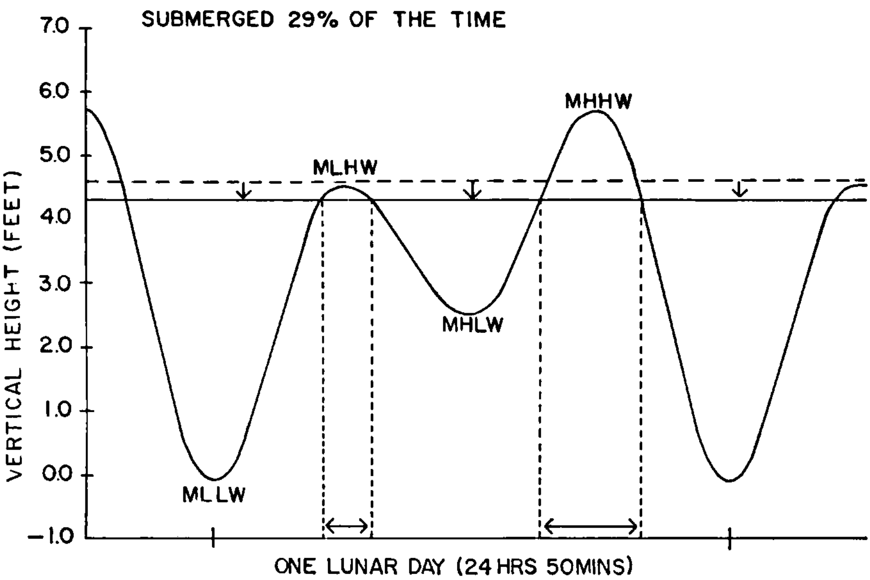


Figure 15. The predicted mean six-month tidal curve for Crissy Wharf, San Francisco, California (January 1—July 1, 1931).

When the 4.3 ft is added to the mean tidal pattern (fig. 15) the mean total time of submergence is easily calculated to be 7 hrs 8 min/lunar day or 6 hrs 54 min/solar day. For the six-month span this amounts to 1,242 hours, or submergence for 29% of the time. This exceeds the first estimate by only 72 hrs, with a difference of 6%.

It is important, in calculating such figures as those presented above, to make use of field observations as well as tide table predictions of water height. If the calculations had simply been carried out using the average measured height of the quadrats (+ 4.6 ft) rather than on the effective ecological height, quite different and deceptive results would have been obtained.

One other aspect of the time relations of exposure and submersion deserves consideration here. In the intertidal zone on most temperate shores a rather abrupt demarcation in the vertical distribution of organisms is usually evident at certain levels. It seems that this phenomenon is correlated with "critical levels" which are related to the longest continuous periods of submersion or exposure some organisms will have to withstand at a stretch (Colman, 1933; Doty, 1957). The longest continuous periods of exposure and submersion to which the mean elevation of the upper, center, and lower quadrat levels were subject are summarized in table II. Also included is the percent of the total time the mean heights of the sampling levels are exposed to air.

The mean center elevation experiences a longest continuous period of exposure of slightly more than 20 hrs. A considerable deviation from the center level is noted in the lower, and particularly upper margins. At the lower margin, the longest continuous period of exposure is 9 hrs, less than half that of the center. However, the upper margin is continuously exposed for a maximum period of nearly 24 days when the height of the higher high water tides is less than 5.0 ft.

Table II. Summary of longest continuous periods of exposure and submergence, and percent of total time exposed to air of the mean elevations of the upper, center, and lower quadrat levels. The calculations are based on the U. S. Coast and Geodetic Survey tidal predictions for Monterey Bay, California, 1961.

	PORTION OF ENDOCLADIA-BALANUS BELT		
	Upper margin	Center	Lower margin
Absolute height	5.8	4.6	3.7
Effective height	5.0	3.8	2.9
Longest continuous period of exposure	23 3/4 days	20 1/4 hrs	9 hrs
Longest continuous period of submergence	4 3/4 hrs	6 1/2 hrs	8 1/5 hrs
Percent of total time region is exposed to air	95	72	46

Differences between the center, and upper and lower margins are considerably less with respect to the longest continuous periods of submersion. The center portion of the *Endocladia-Balanus* belt is submerged for a maximum time of 6½ hrs, and the lower and upper margins for maximum times of $8^1/_5$ hrs and $4^3/_4$ hrs, respectively. The small magnitude of these time differences is related to the fact that the highest of the higher low waters (3.2 ft in 1961) does not wet the lower margin of the assemblage. The duration of the longest continuous period of submersion is directly proportional to the time the highest, single high water period covers a particular *Endocladia-Balanus* level.

The mean center level is exposed to the atmosphere for 72% of the total time over a period of six months. The lower margin is exposed for 46% of the time, while the upper margin is exposed for 95% of the time.

Exposure and submersion in relation to time of day and season

Since the time of low and high water progresses about 50 minutes each day, periods of submersion and exposure can occur at any time of the day. It is therefore important to consider, as did GISLÉN (1943), when the organisms of the *Endocladia-Balanus* belt are exposed and submerged with respect to the time of day and year. In 1961 they should have been exposed to the air at every low water and at the lower high water on 94 days; on the remaining 271 days they were exposed only at every low water. The longest continuous exposures to air were for about 20 hrs; such exposures occurred during two periods of seven days each in May and June. Typical patterns of submersion and exposure are shown in fig. 16.

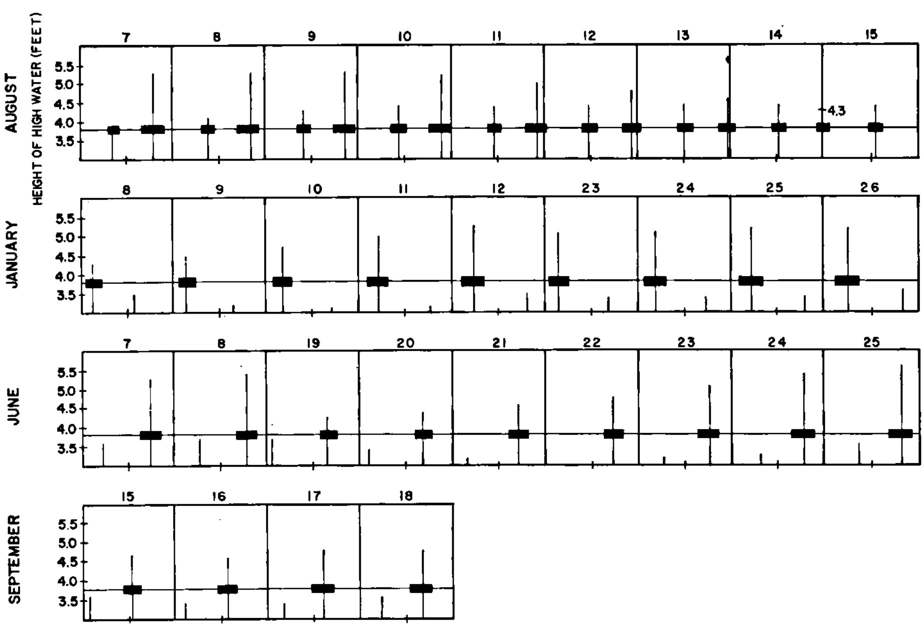


FIGURE 16. Occurrence of semidaily and daily high water periods at the 3.8 ft level in relation to season and time of day, Hopkins Marine Station, 1961. The date of the months is given just above each 24-hour graph. The horizontal bars indicate the duration of submergence, and the vertical lines represent the predicted heights of the two high tides. The prevailing semidaily pattern is shown at the top for a nine-day period in August. Examples illustrating a single daily submersion are represented, respectively, by two periods in January, 8—12 and 23—26, two periods in June, 7—8 and 19—25, and one period in September, 15—18.

The longest continuous exposures to air in the center of the association were for about 20 hrs; such exposures occurred during two periods of seven days each in May and June. The longest continuous periods of submergence at this level were considerably less. In 1961 the two maximum periods of submergence lasted for about 6½ hrs. These high tides occurred at 9:05 A.M. on January 16 and at 10:34 P.M. on July 27. The predicted level on these two occasions was 6.2 ft.

The longest continuous period of exposure at the upper margin of the association lasted for nearly 24 days, from March 20, early A.M. to April 12, late P.M. Also, this level experienced continuous exposure for about 21 days, from February 19, early A.M. to March 12, late A.M. Organisms living at the upper margin of the association, then, are exposed completely to the atmosphere for two prolonged periods in the winter and spring months.

Since most of the organisms in the *Endocladia-Balanus* association are marine forms, and hence probably better equipped to withstand prolonged submersion than prolonged exposure to the atmosphere, the periods likely to present the greatest hazards to them are the periods during which they are covered by the sea only once a day, and receive exposures to air of up to 20 hrs at a stretch. For 1961 the number of days during which the association received only one submersion per day, and the maximum duration in days of this single daily submergence are presented in table III.

TABLE III. The number of days for each month of the year (1961) during which the *Endocladia-Balanus* belt received only one submersion per day, and the maximum number of days over which this daily submergence extended.

	Jan.	Feb.	March	April early	April late	May	June	July	Aug.	Sept. early	Sept. mid	Oct.	Nov.	Dec.
Number of days with single daily submergence	9	10	8	4	6	7	9	10	9	2	4	2	4	10
Maximum number of days per period	5	5	4	4	3	7	7	6	5	2	4	2	2	4

Climate

It has been shown that the *Endocladia-Balanus* belt is usually covered and uncovered by the sea twice each day, that during certain periods it may receive continuous exposures to air for up to 20 hrs, and that these periods of exposure occur at all seasons and may occupy different portions of a 24-hour day. On the other hand, the belt may remain submerged for periods of up to about six hours, and these periods of submersion also occur at all seasons and times of day. The question now arises: to what climatic conditions, marine and atmospheric, are the organisms of the belt exposed? In the following sections selected aspects of the marine climate and atmospheric climate are discussed, and studies on the microclimate in the *Endocladia-Balanus* association during exposure to air are presented.

The marine climate

SKOGSBERG (1936) discovered that the thermal properties of the surface waters in the Monterey Bay exhibit a distinct annual rhythm. This fact was revealed in spite of the relatively small annual range and the frequent fluctuations resulting from local meteorological disturbances. More recently, the existence of these hydrographic seasons has been corroborated by BOLIN & ABBOTT (1963).

Essentially, these marine seasons are as follows. The Oceanic Period occurs in September and October and is characterized by relatively high temperatures. It appears that this warm-water phase is caused mainly by the shoreward movement of offshore surface waters, including those of thc California Current, which have a relatively higher temperature than the inshore waters. The so-called Davidson Current Period, characterized by declining temperatures and a low vertical thermal gradient, lasts from November through February. It has its origin in the Davidson Current system, which is a northerly-moving stream generated by southerly winds. This stream tends to bank up along the shore as a result of Corioli's Force. Finally, the third or Upwelling Period is the longest, occurring in March and lasting through the spring and summer, until July or August. This phase is caused by the inshore upwelling of deep water, resulting from a lateral displacement of the surface water seaward.

Prior to the present study a definite warming trend of the surface waters was observed from 1956 through 1958 (SETTE & ISAACS, 1960). The trend is well shown by comparing monthly averages of daily shore temperatures taken at the Hopkins Marine Station. The highest monthly averages recorded each year (usually in the fall) for the years 1955, 1956, 1957, and 1958, were 13.17, 15.55, 16.24, and 15.99° C, respectively. Figure 17 shows the shore temperature for the same locality for the three-year period, 1959—

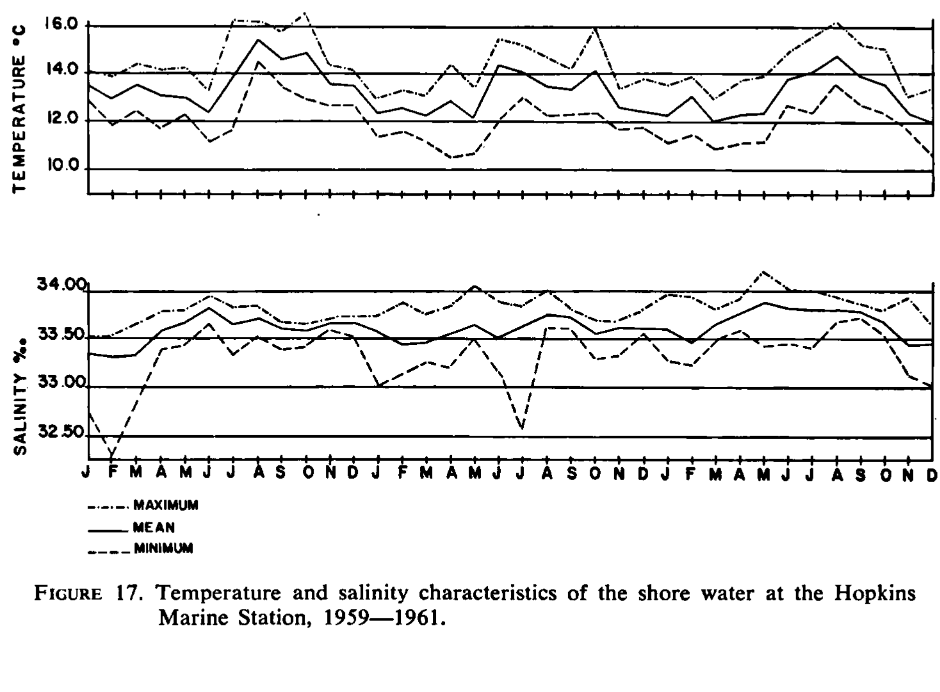


FIGURE 17. Temperature and salinity characteristics of the shore water at the Hopkins Marine Station, 1959—1961.

1961. The highest monthly averages in the fall for each of the three years were 15.36, 14.22, and 14.73° C, respectively, marking the end of the three-year warming phase. Extreme individual temperatures noted during the period were 16.5 and 10.5° C. The rather abrupt drop in temperature at the initiation of the Davidson Current Period is evident toward the end of October, as are the low temperatures prevailing during the Upwelling Period.

The salinity characteristics of the Monterey Bay shore waters for the period 1959—61 are also presented in fig. 17. It is observed that the range in the monthly mean curve is very slight, viz. from 33.32‰ in February, 1959, to 33.89 ‰ in May, 1961. A slightly higher trend is evident during the summer months. On only two occasions did the minimum salinity value for the month fall below the 33.00‰ level. These observations, 32.32‰ in February, 1959, and 32.59‰ in July, 1960, could have resulted from fresh water run-off directly into the sampling area.

In considering the marine climate to which shore organisms are subjected, it is useful to consider temperature and salinity simultaneously. The general marine conditions prevailing are shown in fig. 18, a scatter diagram of the monthly means of the daily shore temperatures versus the monthly means of the daily shore salinities. More useful to the ecologist, however, is information on the extreme Temperature/Salinity conditions which occur (fig. 19), since these are likely to be limiting for organisms. These extreme conditions are not distributed evenly over the entire year, as can be seen in table IV.

TABLE IV. Frequency of occurrence in various months of yearly extreme temperature and salinity observations along the shore at the Hopkins Marine Station, 1919—1939, 1941—1961.

	HYDROGRAPHIC SEASON											
	Davidson Current ←→				Upwelling ←→						Oceanic ←→	
	N.	D.	J.	F.	M.	A.	M.	J.	J.	A.	S.	O.
High salinity of the year	1				1	2	6	15	12	3	7	
Low salinity of the year		7	6	11	11	3	1	1		1		
High temperature of the year						3	1	8	11	4	18	8
Low temperature of the year	5	9	13	9	6	4	1	3				

High salinities are most frequent when both upwelling and surface warming inshore are occurring, while low salinities inshore result from winter rains and run-off. High and low temperature extremes reflect local atmospheric conditions in summer and winter, respectively.

The atmospheric climate

GISLÉN (1943, 1944) has investigated the climatic conditions of temperate shores, especially the central coasts of California and Japan, and concluded that the climate of the central California coast is one of the mildest in the

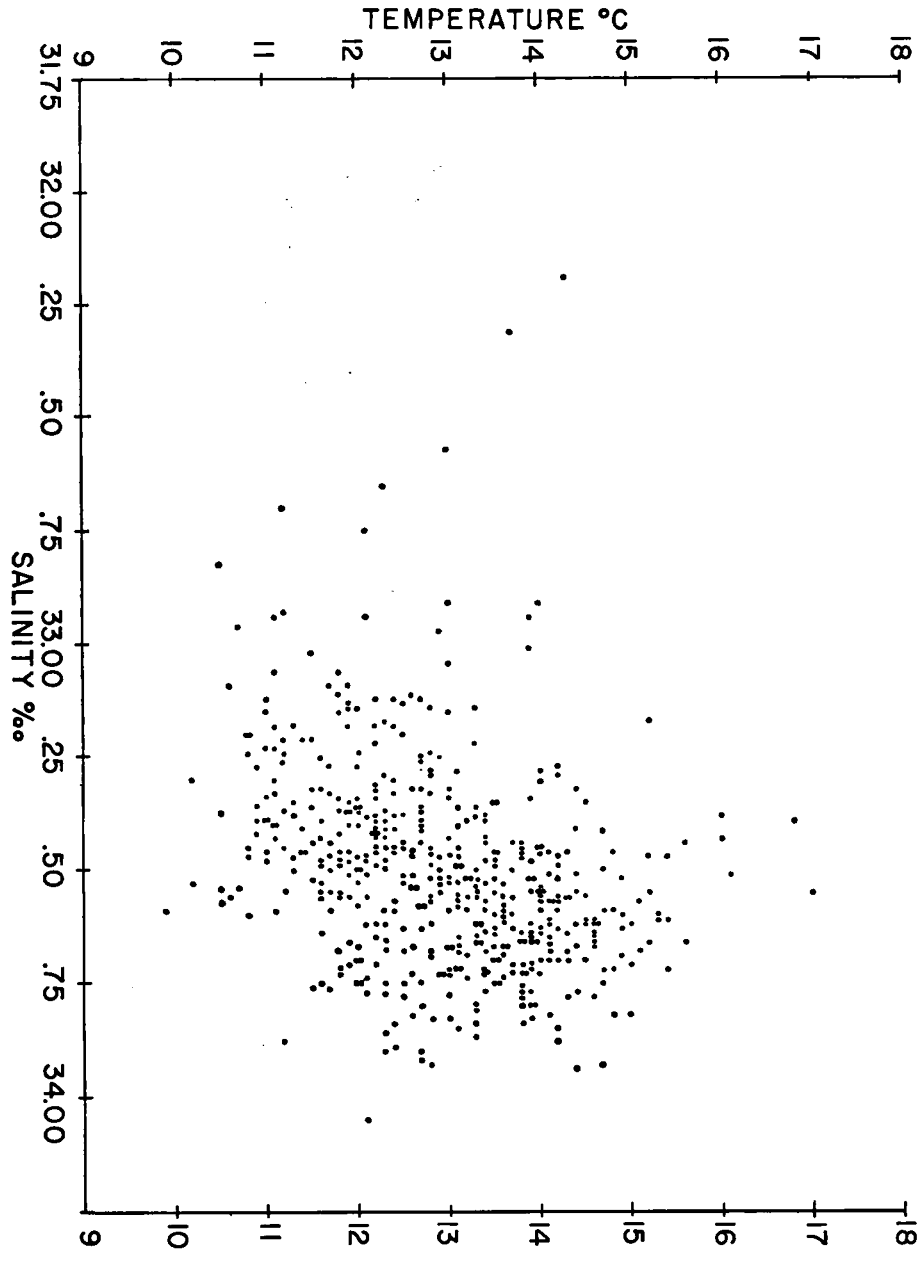


FIGURE 18. Monthly averages of temperature and salinity of the shore waters at the Hopkins Marine Station, 1919—1939, 1941—1961. The averages are based on daily measurements, made between 0800 and 0900.

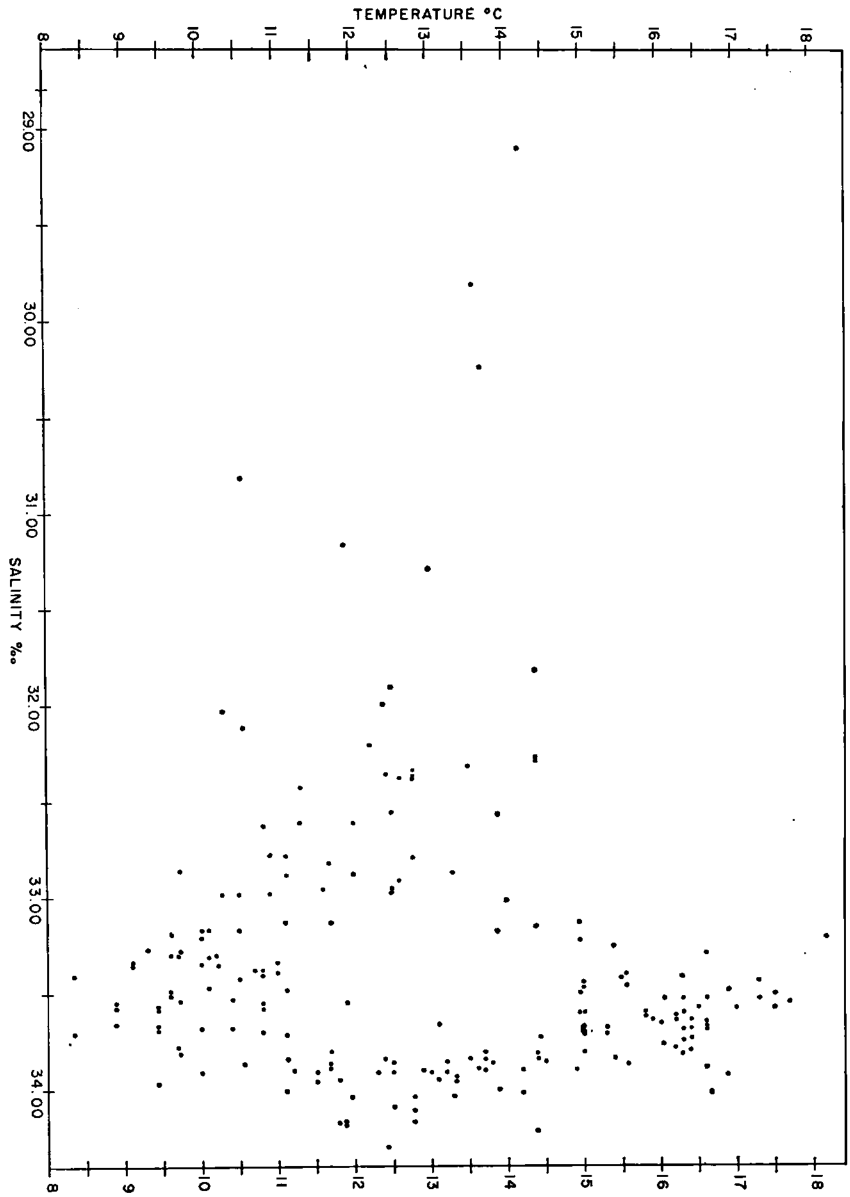


FIGURE 19. Yearly Temperature/Salinity extremes in the shore waters at the Hopkins Marine Station over a 42-year period (1919—1961, inclusive, except for 1940). All observations are based on daily measurements made between 0800 and 0900. For each year the following is plotted:
Maximum salinity of the year with its accompanying temperature.
Minimum salinity of the year with its accompanying temperature.
Maximum temperature of the year with its accompanying salinity.
Minimum temperature of the year with its accompanying salinity.

temperate zone. For this region he reviewed air temperature, rainfall, humidity, and winds. These four meteorological factors are briefly considered here, especially with regard to their action upon the associates in the *Endocladia-Balanus* assemblage at low water. Since most of the organisms making up the association are marine forms, it is reasonable to assume that during exposure they would be most susceptible to extreme atmospheric conditions. It is also important, then, to consider the precise time intervals when low water coincides with extreme atmospheric stress conditions.

Most of the weather observations reported here were made available by the United States Naval Air Facility, Monterey. Although this installation is 3.5 miles from the Hopkins Marine Station and 1.25 miles from the seashore, the more general atmospheric conditions prevailing at the two localities approximate one another rather closely. For example, the difference between the maximum atmospheric temperatures on September 4, 1961 at these stations was 0.8° C (fig. 21). The erratic movement of fog banks, best developed from May through September, may occasionally cause great differences between the two localities in the temperature and moisture characteristics of the atmosphere.

Figure 20 shows the mean maximum and minimum, and the extreme maximum and minimum atmospheric temperatures at the United States Naval Air Facility for a 12-year period and for 1961. The greatest range between the mean maximum and mean minimum temperatures for the 12-year period was 7.6° C in November. Below-freezing temperatures were rare, occurring only during the months of December, January, and February. However, maximum temperatures above 30° C were recorded in May, June, September, October, and November. The highest temperatures tend to come during the summer months and in the fall, and the lowest temperatures in the winter. This same pattern appears in SKOGSBERG's (1936) earlier tabulation of the air temperatures taken at the Del Monte Hotel, Monterey, for the period 1929—1933.

Of the three years of study, 1961 was rather unusual in that the extreme maxima of June (33.6° C) and October (35.8° C), exceeded the extremes for

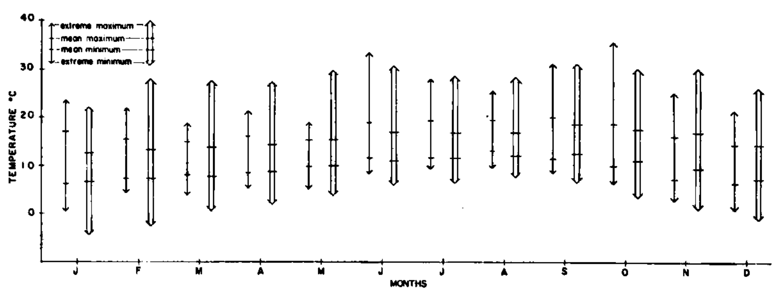


FIGURE 20. Air temperatures in 1961 (vertical lines) compared with the 12-year trend, 1948—59 and 1945 (vertical bars), at the United States Naval Air Facility, Monterey, California. Extreme maxima and minima as well as mean maxima and minima are indicated in each month. The interpretation in reading these values is shown in the inset key.

these months over the 12-year period. Although the lowest temperature recorded in 1961 was above freezing (0.6° C in January), the extreme minima in May and November were close to the greatest extremes recorded for these months over the long-term trend. On January 22, 1962, the mercury dropped to a low of -1.6° C.

At times low water occurs in the afternoon hours during the warmest months of the year. Observations were made on one such instance on September 4, 1961. As the tide receded, and the wave splashing discontinued, the exposed rock surface received the sun's rays directly. The temperature at submersion was the sea water temperature, 12.8° C. The temperature of three microhabitats was recorded at hourly intervals with a mercury thermometer accurate to the nearest tenth degree. These habitats were a two-cm deep pool, the shaded interior of a tuft of *E. muricata*, and the exposed surface of the granite rock. The rise in temperature in these three diverse situations is shown in fig. 21. The extent to which animals living in an algal tuft are protected against insolation can be appreciated by the 8° C difference in temperature between the inside of the tuft and the adjacent bare rock surface. With the incoming tide the temperature dropped suddenly to 14.5° C. During this very warm day even the sea water experienced a rise in temperature of 1.7° C. The air temperature and wind velocity as recorded at the United States Naval Air Facility are also shown in fig. 21. The rather close correspondence of the temperatures there and in the study area is well brought out here. The maximum temperature recorded at the Hopkins Marine Station was 0.8° C higher, and occurred one hour later than that at the Naval Air Facility. The maximum occurred relatively early in the day as compared with Gislén's average time for the summer maxima, about 4:00 P.M. A maximum wind velocity for the day of seven knots was noted at 3:00 P.M. The drop in the atmospheric temperature between 1:00 and 2:00 P.M. might be explained partly by the increased wind velocity during those hours.

Generally, the system of winds in the environs of the Monterey Peninsula is made up of two rather distinct elements: a northerly component, resulting from the high pressure area off the coast, and a land-sea breeze effect. The well-developed northerly component frequently occurs as a strong northwest or west wind, resulting from both the high pressure and land-sea breeze effects. This tendency is shown in the "wind roses" in fig. 22 by the length of the westerly wind vectors from March through August, and especially in May, June, and July. In October the easterlies became more prominent and dominated the wind system until February. In March, April, May, and June a wind velocity below three knots was recorded for only 19, 26, 16, and 16% of the time, respectively.

The land-sea breeze phenomenon occurs throughout the year, but has its maximum development during the summer months when there is a sharper thermal gradient between the air masses over the land and sea. Sporadically the two wind systems are interrupted by strong winds from the southerly quarter, as in March and April.

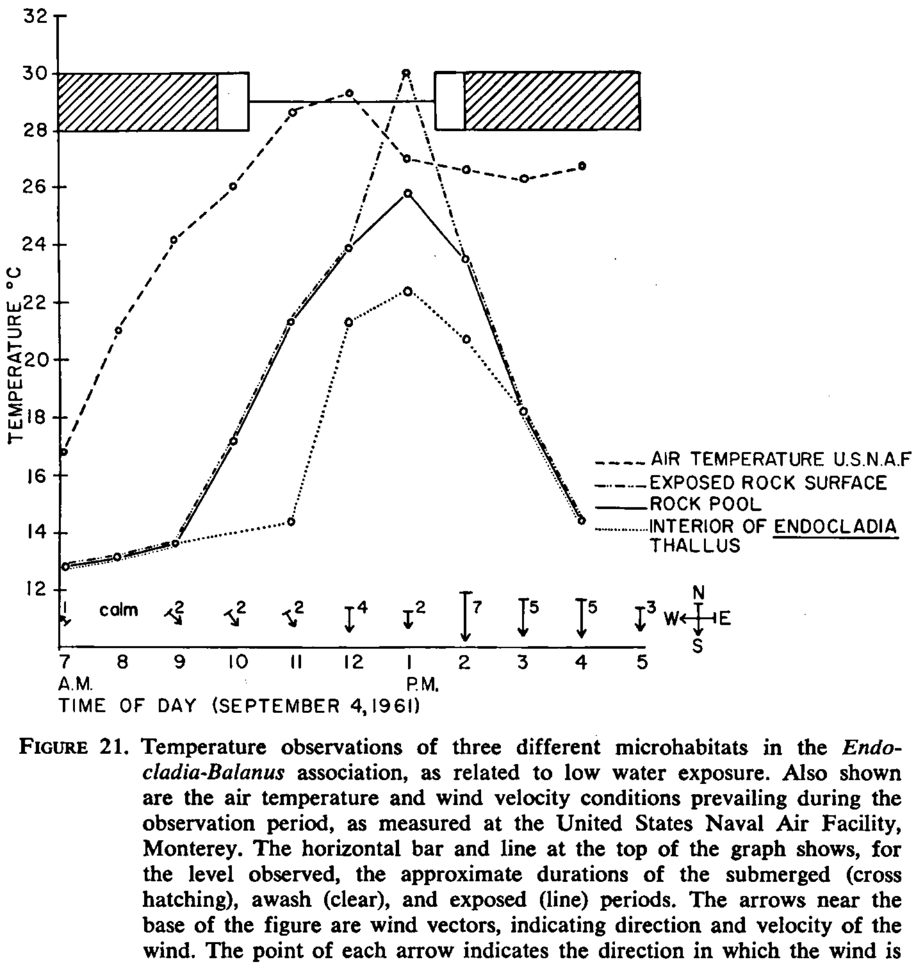


FIGURE 21. Temperature observations of three different microhabitats in the *Endocladia-Balanus* association, as related to low water exposure. Also shown are the air temperature and wind velocity conditions prevailing during the observation period, as measured at the United States Naval Air Facility, Monterey. The horizontal bar and line at the top of the graph shows, for the level observed, the approximate durations of the submerged (cross hatching), awash (clear), and exposed (line) periods. The arrows near the base of the figure are wind vectors, indicating direction and velocity of the wind. The point of each arrow indicates the direction in which the wind is blowing, and the number by each arrow shows wind speed in knots.

The amount of precipitation falling on the Monterey Peninsula is not great (fig. 23). The average annual rainfall for the 11.5 year period, February 1948—July 1959, was 13.95 in or 354.3 mm. The seasonal pattern is marked, with the greatest precipitation, amounting to over 2.5 in a month, falling in December and January, then decreasing gradually to less than 0.5 in in May. Very little rainfall comes during the summer months; the average monthly amount for the 11.5 year period never exceeded 0.1 in in June, July, and August. However, during this period the intertidal atmosphere is often supersaturated with fog droplets. The average monthly precipitation steadily increases in the fall from 0.1 in in September to 1.3 in in November.

An examination of the weather records for extreme weather conditions prevailing over low water periods revealed that while 1961 was an unusual

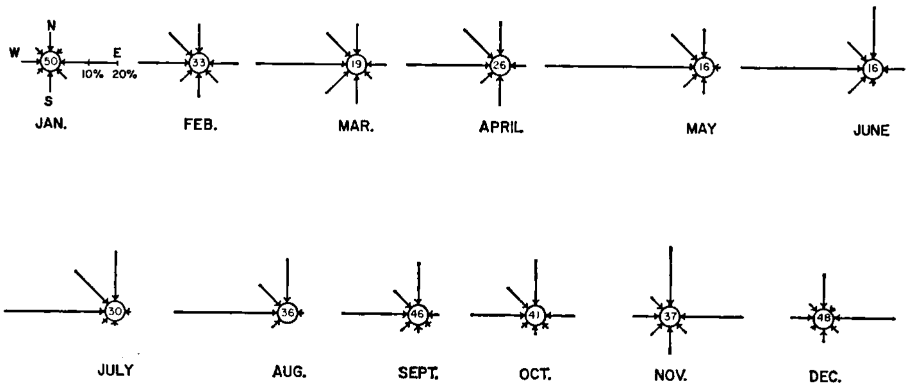


FIGURE 22. Average monthly wind directions in 1961 for the United States Naval Air Facility, Monterey, California. These "wind roses", for each month of the year, show the average wind distribution in terms of the direction from which it blew and its duration as a percentage of the total time. The number at the center of the rose denotes the percentage of total time during which the wind had a velocity of less than three knots.

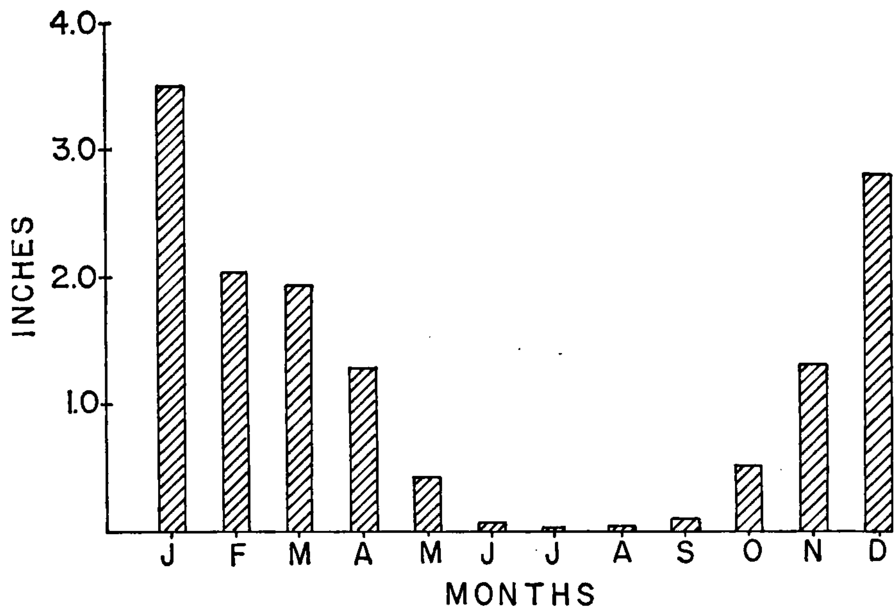
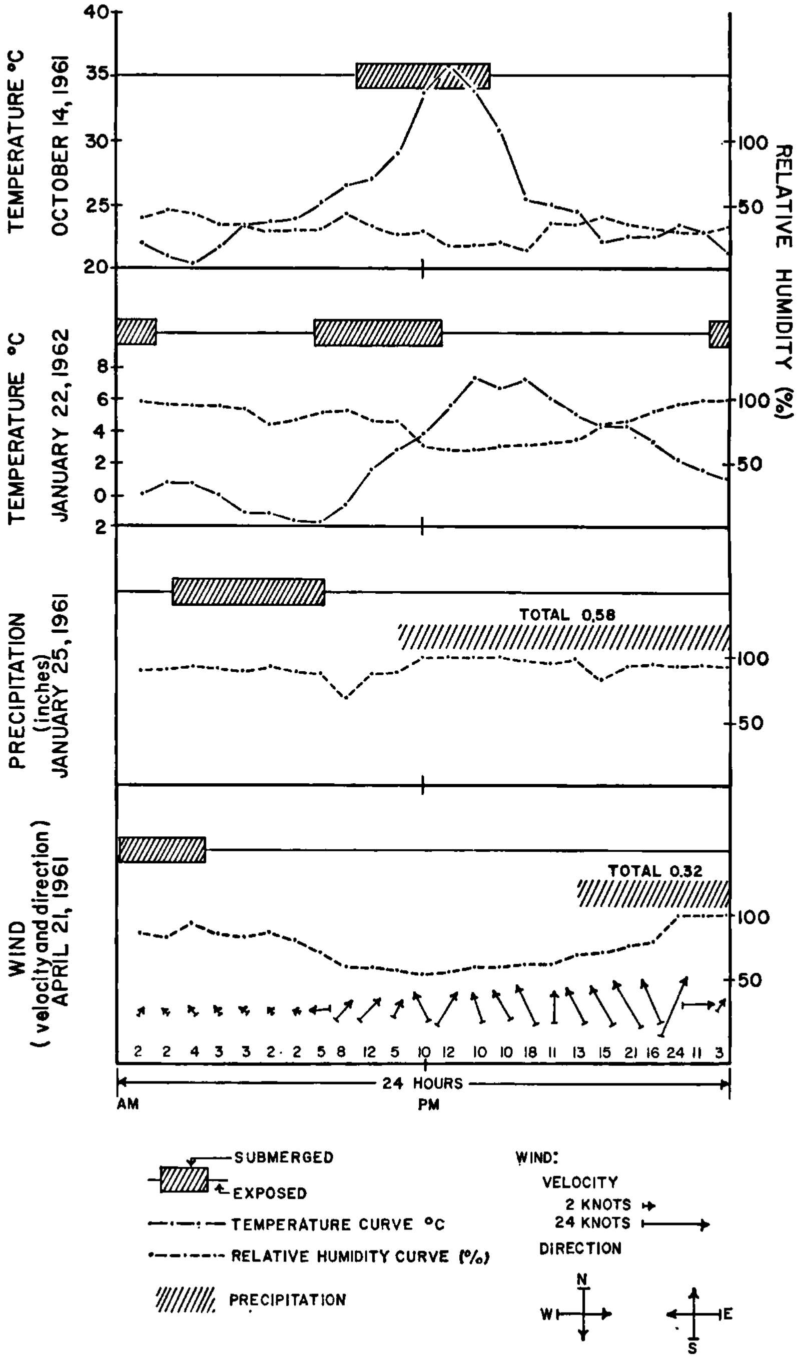


FIGURE 23. Average monthly precipitation at the United States Naval Air Facility, Monterey, California (February, 1948—July, 1959).


TEMPERATURE °C
OCTOBER 14, 1961
TEMPERATURE °C
JANUARY 22, 1962
PRECIPITATION (inches)
JANUARY 25, 1961
WIND (velocity and direction)
APRIL 21, 1961
RELATIVE HUMIDITY (%)
40
35
30
25
20
8
6
4
2
0
2
100
50
TOTAL 0.58
TOTAL 0.32
2 2 4 3 3 2 2 5 8 12 5 10 12 10 10 18 11 13 15 21 16 24 11 3
24 HOURS
AM
PM
SUBMERGED
EXPOSED
TEMPERATURE CURVE °C
RELATIVE HUMIDITY CURVE (%)
PRECIPITATION
WIND:
VELOCITY
2 KNOTS
24 KNOTS
DIRECTION
N
W
E
S

year with regard to temperature maxima, not all of these high temperatures exerted their full effects on the *Endocladia-Balanus* association. In contrast to the relatively high temperature of 30.1° C recorded in the association during the tidal exposure of September 4, 1961 (fig. 21), the higher temperature of 35.9° C on October 14, 1961, did not directly strike this belt because high water occurred in the late morning and early afternoon (fig. 24, top). Other high temperatures in the late morning or afternoon during the latter part of September and all of October, including the high temperature of 34.9° C on October 15, 1961, were not received directly by the association because of the high water cover during the mid-day period.

With respect to extreme minimum temperatures, on at least two occasions in 1962, the mercury dropped to below 0.0° C. At 5:00 A.M. on January 22, 1962, the temperature at the United States Naval Air Facility was -1.3° C; it reached a minimum of -1.8° C at 8:00 A.M. and did not rise above freezing until 10:00 A.M. This below-freezing weather coincided with a low water period for nearly four hours (fig. 24). Another below-freezing period was observed on February 27, 1962, and the following temperatures recorded: -0.8° C (2:00 A.M.), -0.3° C (6:00 A.M.), and -1.2° C (7:00 A.M.). Fresh-water puddles at the Hopkins Marine Station were frozen over at 7:00 A.M. The center of the *Endocladia-Balanus* association became exposed at about 5:20 A.M., and remained exposed throughout the remainder of the day. On this occasion, then, the organisms in the assemblage were subject to the early morning, below-freezing temperatures for approximately two hours.

With an average annual precipitation near 14 in, and this occurring essentially over a six-month span, the *Endocladia-Balanus* zone rarely receives more than one inch of rain during a given low-tide exposure. On January 25, 1961, 0.58 in was precipitated over a 13-hour stretch, and 0.32 in of rain fell in six hours on April 21, 1961 (fig. 24). Both rains occurred during periods of low water, and during the latter observation the southerly winds reached a velocity of 24 knots, one knot short of the maximum for the year. No deleterious effects on the organisms of the *Endocladia-Balanus* zone were noted.

GISLÉN (1943) has commented in general terms on the kind of weather intertidal organisms would experience in the different seasons of the year.

FIGURE 24. Occurrence of some extreme weather conditions as observed at the United States Naval Air Facility in relation to 24-hour periods of submergence and exposure in the *Endocladia-Balanus* association (+ 3.8 ft) at the Hopkins Marine Station. The horizontal line and bar at the top of each graph show the time of exposure and submergence, respectively. The relative humidity is shown as a broken line for each of the four observations, and is read with reference to the scale near the right hand margin. The base of each wind vector indicates the direction from which the wind is blowing, and the speed in knots is noted alongside. Other symbols are explained in the key.

On the basis of previous and present observations, one can predict that the association on the Monterey Peninsula is exposed to the following seasonal regime:

(a) Low temperature and precipitation. November, December, January, and February are the months of the year most likely to experience the lowest temperatures and the greatest amount of rainfall. During this season the single daily submergence occurs mostly during the early hours of the morning, thus tending to decrease the periods of exposure to low early morning temperatures.

(b) Moderate temperature and high wind velocity. March, April, May, and June frequently have well-developed westerly winds with moderate temperatures, which become higher toward the summer. The single daily submergence in the early hours of the morning, characteristic of the winter, persists into March and early April. At this time, in the afternoon hours especially, the organisms in the *Endocladia-Balanus* assemblage are subject to pronounced drying action. In late April, May, and June a single daily submergence occurs mostly in the late hours of the afternoon and during the evening.

(c) Moderate temperature and foggy mornings. July and August are comparatively cool summer months on the Monterey Peninsula. This is due to the moisture-laden fog banks which frequently blanket the region during the mid-summer morning hours. The association in this season is wetted by the daily, high water tide during the evening and late hours of the afternoon, as in the late spring.

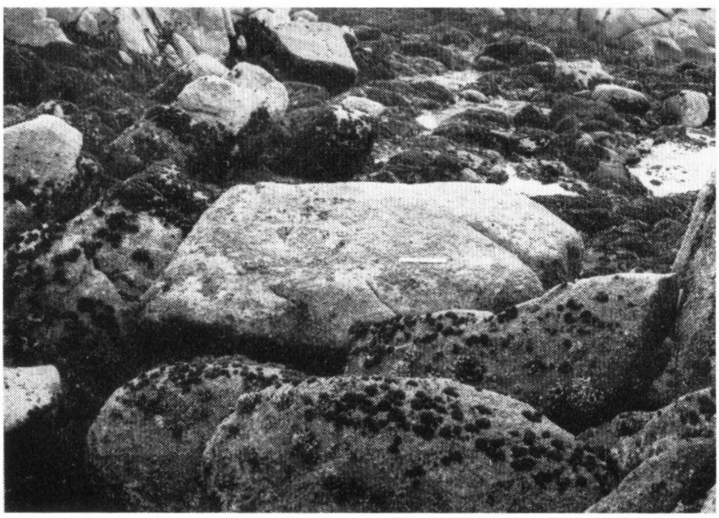


FIGURE 25. View of boulder overturned by high ground swells on February 9, 1960, Hopkins Marine Station (February 3, 1962). A 30 cm rule is resting on the surface.

(d) High temperatures and reduced wind velocity. September and October are generally warm to hot months with little wind. In early September the *Endocladia-Balanus* level is bathed by the single daily submergence in the evening and late afternoon; this then changes to a single daily wetting in the early afternoon by late September and on through October. Thus, early September is the time of year a prolonged exposure period is likely to occur in coincidence with high temperatures.

In the present study, some selected atmospheric extremes, mostly recorded at a weather station three and one half miles removed from the actual study area, have been examined in relation to the periods of intertidal exposure. While these data give a fair over-all impression of the meteorological conditions to which the organisms of the *Endocladia-Balanus* belt are exposed, real studies of the microclimate of the belt, involving the use of *in situ* weather-recording instruments, must await future work.

Under the conditions observed all of the *Endocladia-Balanus* associates apparently were well adjusted. Generally, no death or damage was noted, except for occasional detached portions of barnacles and *Endocladia* washed onto the shoreline. Even during heavy storm-surf no apparent change was detected on the more stable rock surfaces though high ground swells occasionally overturn large boulders bearing well-developed carpets of *Endocladia* and *Balanus* (fig. 25).

SAMPLING METHODS AND PROGRAM

The composition and structure of the association was determined from quadrat sampling, supplemented with qualitative collecting and field observations. The area covered by each of the quadrat samples was 400 cm^2, and the appearance and dimensions of the sampling frame are shown in fig. 26. The frame, designed for sampling on rough, irregular rock surfaces, was constructed of finished and carefully squared pine, the siding permanently joined while supported with wood braces. Four rectangular blocks of foam rubber were joined to the base of the wooden frame with neoprene rubber cement.

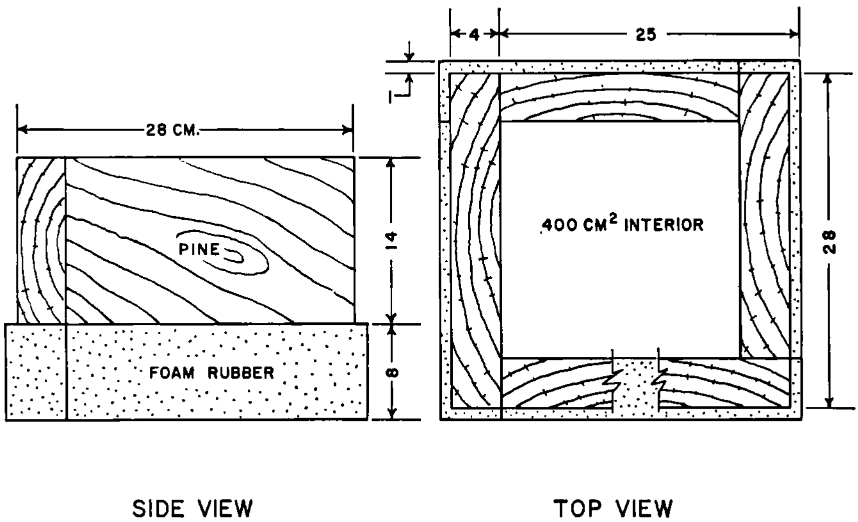


FIGURE 26. Diagram of the 400 cm^2 quadrat sampling frame.

When collecting a quadrat the box was pressed firmly against the substrate, compressing the foam rubber against the rock to form a tight gasket. A wooden square slightly less than 400 cm^2 was then worked through the top of the box to the surface of the area being sampled. The foam rubber siding was then carefully tucked in, to just meet the edges of the square. With the rubber base now properly aligned and pressed firmly against the substrate, the square was withdrawn, leaving the frame pressed in place. One liter of hot sea water (60—70° C, carried in a Dewar flask), was then poured evenly over the area within the sampling frame; in this manner all of the more motile organisms were killed and prevented from escaping. The time required for complete drainage of the hot water from the frame was usually about one minute. At this time the square was again introduced to mark the exact spot and the quadrat box was lifted from the rock. The square was now replaced by a wooden frame of 400 cm^2 and all of the larger algal species and visible microfauna were collected first. A 20 $\times$ 20 cm piece of one-inch mesh, galvanized hardware screen was superimposed on the frame to facilitate counting the barnacles. After the barnacle census, the remaining organisms were collected and preserved in 95% ethyl alcohol. Where possible contiguous barnacle sheets were chiseled from the rock surface in mass, to prevent the loss of the minute organisms living in close association with them. The preservative was selected because it is not noxious when samples need to be sorted for prolonged periods. Also, by the addition of the wet material making up the sample the concentration of the alcohol was reduced to about 70%.

The quadrat samples taken are listed in chronological sequence in table V. Excluding August, at least one quadrat sample was secured for each of the 12 months in a year during the three-year period of study. In all, an area of 6,400 cm^2 of the *Endocladia-Balanus* association was sampled quantitatively.

The particular quadrat sites selected are scattered more or less at random in the study area directly in front of the Hopkins Marine Station. In each case a typical formation dominated by *E. muricata* and *B. glandula* was selected on a rock surface lacking gross irregularities which would have made accurate sampling impossible. Qualitative sampling was carried out where the association appeared in fissures and on overhanging surfaces.

Qualitative collections of the more frequently occurring species were made in every month from May, 1959 to December, 1961. A surveillance of the seasonal occurrence, structure and reproductive state of certain populations was made possible by these samples.

TABLE V. Chronological tabulation of the quadrat samples collected in the study area, with their designation, relative height within the association and absolute height above mean lower low water.

Date	Designation of quadrat	Relative height of quadrat with respect to *E.-B.* association	Absolute height of center of quadrat (ft above mean lower low water)
Jan. 8, 1959	L_1	Lower margin	3.8
Feb. 3, 1959	L_2	Lower margin	3.6
Mar. 19, 1959	I	Center	4.9
May 11, 1959	II	Center	4.6
July 10, 1959	III	Center	4.4
Sept. 4, 1959	IV	Center	4.7
Nov. 13, 1959	V	Center	4.7
Jan. 13, 1960	VI	Center	4.3
Mar. 12, 1960	VII	Center	5.6
April 15, 1960	VIII	Center	4.9
June 15, 1960	IX	Center	5.0
Sept. 23, 1961	X	Center	3.9
Oct. 21, 1961	XI	Center	4.9
Nov. 18, 1961	H_1	Upper margin	5.8
Dec. 17, 1961	H_2	Upper margin	5.7
Dec. 20, 1961	XII	Center	3.6

QUALITATIVE COMPOSITION OF THE ASSOCIATION

List of species present

In any detailed community study, the ecologist needs to know what species are present. However, a really complete listing of the species of a community of organisms is usually neither practical nor very meaningful. If such a listing were compiled, to parallel existing conditions the ecologist would be forced to delete and add species constantly, for organisms move in and out of communities according to the time of day or season of the year. Different species replace one another geographically and are sometimes introduced from remote environments. On a greater time scale, all living systems evolve, and the biotic component of the ecosystem represents an ever-changing species assemblage. The species list here presented must be read with these important reservations in mind.

The cooperation of a considerable group of specialists was required to identify the species inhabiting the *Endocladia-Balanus* association. These specialists are listed below, and are credited with identifications in the species list.

Dr. Isabella A. Abbott, Hopkins Marine Station of Standford University, Pacific Grove, California. Marine algae.

Dr. Edward W. Baker, United States National Museum, Washington 25, D. C. Acarina.

Dr. J. L. Barnard, Institute of Marine BioResearch, Solvang, California. Amphipoda.

Dr. Cyril Berkeley, Pacific Biological Station, Nanaimo, British Columbia. Polychaetous annelids.

Dr. E. L. Bousfield, National Museum of Canada, Ottawa, Canada. Amphipoda.

Dr. I. E. Cornwall, 1951 Argyle Ave., Victoria, B. C., Canada. Cirripedia.

Dr. Francis Drouet, Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania. Marine blue-green algae.

Mr. Michael Ghiselin, Hopkins Marine Station of Stanford University, Pacific Grove, California. Opisthobranchia.

Dr. A. Myra Keen, Department of Geology, Stanford University, Stanford, California. Pelecypoda.

Mr. John Lawrence, Department of Entomology and Parasitology, University of California, Berkeley 4, California. Insecta.

Mr. James McLean, Department of Biology, Stanford University, Stanford, California. Mollusca.

Mr. A. T. Newberry, Hopkins Marine Station of Stanford University, Pacific Grove, California. Aves.

Dr. I. M. Newell, Division of Life Sciences, University of California at Riverside, Riverside, California. Halacaridae.

Miss Joan Steinberg, California Academy of Sciences, San Francisco, California. Opisthobranchia.

Dr. Alan Stone, United States National Museum, Washington 25, D. C. Insecta.

Dr. R. L. Usinger, Department of Entomology and Parasitology, University of California, Berkeley 4, California. Insecta.

Dr. Willis W. Wirth, United States National Museum, Washington 25, D. C. Insecta.

The following species list includes the names and authors of the species found, the authority responsible for the specific determination, and a literature reference for the species. Where no specialist or reference is listed, the species is usually well known and covered in such general references as RICKETTS & CALVIN (1962) and LIGHT et al. (1957), and responsibility for the identification rests with the writer. Annotations are included only for species not dealt with under separate autecologies later in this study. Even though all bacteria, protozoa, and most parasites were excluded from the list, the total number of species occurring in the association was 93. Full data on the presence and numbers of these species in all of the quadrat samples taken are included in Appendix I.

These species may also be divided roughly into those which are truly residents of the *Endocladia-Balanus* zone, remaining there day and night and at all phases of the tide, and those which are transients, moving in and out with tidal, daily, and seasonal change. The former species, the residents, are adequately sampled by the quadrat technique outlined earlier, and are treated in the next two sections that follow. The transient species, not adequately sampled with the quadrat frame at low tide, will be dealt with separately in a final section of the present topic.

Division Myxophyceae

Coccoid blue-greens. Several unidentified species were abundantly represented.

Coccochloris stagnina Sprengel. Determined by I. A. Abbott (DROUET & DAILY, 1956; UMEZAKI, 1961). Resident. In March, 1962, this was the most abundant blue-green alga encrusting the granitic rock surface.

Entophysalis conferta Drouet & Daily. Determined by I. A. Abbott (DROUET & DAILY, 1956; UMEZAKI, 1961). Resident. The blades of *Endocladia muricata* are densely matted with this species.

Entophysalis deusta Drouet & Daily. Determined by F. Drouet (DROUET & DAILY, 1956; UMEZAKI, 1961). Resident. A perforating blue-green, commonly found on the test of *Balanus glandula* where it causes pitting.

Lyngbya sp. Determined by I. A. Abbott (DROUET & DAILY, 1956). Resident. Epiphytic on *Endocladia muricata.*

Oscillatoria nigro-viridis Thwaites. Determined by F. Drouet (DROUET & DAILY, 1956; UMEZAKI, 1961). Resident. This species forms dark, slimy patches over the substrate, often covering, but apparently not harming, barnacles. These patches were well developed in the fall and winter of 1961—62. The patches are often circular, and can attain a diameter of up to 20 cm.

Oscillatoria sp. Determined by I. A. Abbott (DROUET & DAILY, 1956). Resident. Epiphytic on *Endocladia muricata.*

Plectonema terebrans Bornet & Flahault. Determined by F. Drouet (DROUET & DAILY, 1956; UMEZAKI, 1961). Resident. Found perforating the test of *B. glandula.*

Division Chrysophyta

Navicula sp. (CUPP, 1943). Resident. The sessile diatoms were most abundantly represented by this genus. They were most frequently found as scattered individuals on the granite surface and on the blades of *Endocladia.*

Other unidentified diatoms. Resident. Relatively few forms were sparsely present.

Division Chlorophyta

Pseudoulvella applanata Setchell & Gardner. Determined by I. A. Abbott (SMITH, 1944). Resident. The most abundant microscopic green alga, omnipresent. It grows diffusely on the rock substrate as well as on the shells of *Balanus glandula. Littorina* spp. and *Acmaea* spp.

Cladophora sp. Determined by I. A. Abbott (SMITH, 1944). Resident.

Division Rhodophyta

Endocladia muricata (Postels & Ruprecht) J. G. Agardh. Resident.

Gigartina agardhii Setchell & Gardner. Determined by I. A. Abbott (SMITH, 1944). Resident.

Gelidium coulteri Harvey. Determined by I. A. Abbott (SMITH, 1944). Resident.

Porphyra schizophylla Hollenberg. Determined by I. A. Abbott (SMITH, 1944). Resident. Small specimens of this alga are often found growing as epiphytes on *Endocladia muricata*.

Rhodoglossum affine (Harvey) Kylin. Determined by I. A. Abbott (SMITH, 1944). Resident.

Division Phaeophyta

Hapalospongidion gelatinosum Saunders. Determined by I. A. Abbott (SMITH, 1944). Resident. This form was found at the lower boundary of the *Endocladia-Balanus* association and below, forming a rusty-colored crust over the substrate.

Pelvetiopsis limitata (Setchell) Gardner. Determined by I. A. Abbott (SMITH, 1944). Resident.

Division Angiospermae

Phyllospadix scouleri Hook. Only the seedling of this species was found.

Phylum Coelenterata

Class Hydrozoa

Abietinaria sp. Resident. This hydroid and the following species were found growing on the holdfast region of *E. muricata*.

Sertularia sp. Resident.

Class Anthozoa

Anthopleura elegantissima (Brandt, 1835). Resident. This sea anemone was infrequently found at the *Endocladia-Balanus* level in small pools, wet cracks or other damp situations left exposed by the receding tide.

Phylum Platyhelminthes

Order Polycladida

Notoplana sp. probably *N. acticola* (Boone, 1929). Resident.

Phylum Nemertea

Class Enopla

Emplectonema gracile (Johnston, 1837). Resident.

Nemertopsis gracilis Coe, 1904. Resident. Since the two longitudinal stripes along the length of the dorsum are bridged anteriorly, this species probably represents the variety *bullocki*. This variety was first described from Montara, San Mateo County, California.

Phylum Nematoda

Undetermined nematodes. Resident. Many of these worms were found among the holdfast branchlets of *E. muricata* and within the live bivalve mollusk, *Lasaea cistula*. A few were observed in the algal film encrusting the rock surface

Phylum Annelida

Class Oligochaeta

One undetermined species. Resident. Occasionally one or two of these very small worms were found living in the interstices of the shell of *B. glandula*.

Class Polychaeta

Syllis (Typosyllis) vittata Grube. Determined by C. Berkeley (BERKELEY & BERKELEY, 1938; FAUVEL, 1923). Resident.

Syllis (Typosyllis) armillaris (Müller, 1771). Determined by C. Berkeley (BERKELEY & BERKELEY, 1938; FAUVEL, 1923; HARTMAN, 1959). Resident.

Syllis spenceri Berkeley & Berkeley, 1938. Determined by C. Berkeley (BERKELEY & BERKELEY, 1938; FAUVEL, 1923; HARTMAN, 1959). Resident.

Perinereis monterea (Chamberlin, 1918). Verified by C. Berkeley. Resident.

Nereis grubei (Kinberg, 1866). Verified by C. Berkeley. Resident.

Dexiospira spirillum (Linnaeus, 1758). Resident. These were found in increasing abundance toward the lower boundary of the association.

Phragmatopoma californica (Fewkes, 1889). Resident. These also were found in greatest abundance at the lower level.

Phylum Bryozoa

Suborder Cyclostomata

Filicrisia franciscana (Robertson, 1910). Resident. This species resembles very closely *F. geniculata.*

Phylum Mollusca

Class Amphineura

Cyanoplax dentiens (Gould, 1846). Verified by J. McLean. Resident.

Class Pelecypoda

Hiatella arctica (Linnaeus, 1767). Verified by J. McLean. Resident.

Lasaea cistula Keen, 1938. Resident.

Mytilus edulis Linnaeus, 1758. Resident.

Mytilus californianus Conrad, 1837. Resident. The two species of *Mytilus* are difficult to distinguish when very small; among those individuals large enough to be identified, *Mytilus californianus* was by far the more common.

Musculus sp.[1]) Determined to genus by A. M. Keen. Resident.

Class Gastropoda

Acmaea paradigitalis Fritchman, 1960. (Fritchman, 1960). Resident.

Acmaea digitalis Eschscholtz, 1833. Resident.

Acmaea scabra (Gould, 1846). Resident.

Acmaea pelta Eschscholtz, 1833 (= *A. cassis).* Resident.

Acmaea limatula Carpenter, 1864. Resident.

Ocenebra circumtexta Stearns, 1871. Verified by J. McLean. Resident.

Littorina scutulata Gould, 1849. Resident.

Littorina planaxis Philippi, 1847. Resident.

Acanthina spirata (de Blainville, 1832). Transient.

Thais emarginata (Deshayes, 1839). Transient.

Tegula funebralis (Adams, 1854). Transient.

Barleeia oldroydi Bartsch. Verified by J. McLean (SMITH & GORDON, 1948). Resident.

Tricolia pulloides (Carpenter). Determined by J. McLean (SMITH & GORDON, 1948). Resident.

Runcina sp. Determined by J. Steinberg and M. Ghiselin. An undescribed species. Resident. This very minute (1—2 mm long), orange opisthobranch was infrequently found in exposed situations, in association with *E. muricata.* Mr. Ghiselin has recently remarked that they appear to be more abundant around the tubes of *Phragmatopoma californica* (personal communication).

Phylum Arthropoda

Class Ostracoda

Unidentified spp. Resident. Great numbers of these organisms cling to the blades of *E. muricata.*

[1]) To be described soon by the author in The Veliger.

Class Copepoda

Harpacticoid copepods. Resident. These were found abundantly, clinging to the blades of *E. muricata.*

Class Cirripedia

Balanus glandula Darwin, 1854. Resident.

Chthamalus dalli Pilsbry, 1916. Verified by I. E. Cornwall. Resident.

Chthamalus microtretus Cornwall, 1937. Verified by I. E. Cornwall (Cornwall, 1937). Resident.

Tetraclita squamosa rubescens Darwin, 1854. Resident.

Mitella polymerus (Sowerby, 1833). Resident.

Order Isopoda

„*Dynamenella*" *glabra* (Richardson, 1899). According to Light et al. (1957) the generic name of this species is in doubt. Resident.

Excirolana chiltoni (Richardson, 1905). Resident.

Hemioniscus balani (Spence Bate). Resident. Parasitic in *C. dalli.*

Order Tanidacea

Unidentified species. Resident. This was found only twice throughout the study.

Order Amphipoda

Allorchestes ptilocerus Derzh. Determined by E. L. Bousfield in collaboration with J. L. Barnard. Resident.

Hyale sp. Determined by E. L. Bousfield in collaboration with J. L. Barnard. An undescribed species. Resident.

Pontogeneia sp. Determined by E. L. Bousfield in collaboration with J. L. Barnard. An undescribed species. The telson in this form is shallowly notched as opposed to the deeply cleft telson of other described species in the genus. Resident.

Order Decapoda

Pachygrapsus crassipes Randall, 1839. Apparently the juveniles are residents and the adults transients.

Pagurus samuelis (Stimpson, 1857). Transient.

Class Insecta

Diaulota densissima Casey, 1894. Determined by J. Lawrence in collaboration with R. L. Usinger (Usinger et al., 1956). Resident.

Limonia marmorata (Osten Sacken). Determined by A. Stone. Larva resident, adult transient.

Undetermined tipulid larva. Determined to the family Tipulidae by A. Stone. Larva resident, adult transient.

Undetermined ephydrid larva. Determined to the family Ephydridae by W. W. Wirth. Larva resident, adult transient.

Order Acarina

Suborder Tromibidiformes

Rhombognathus sp. Determined by I. M. Newell. Probably an undescribed species. Resident. This species is usually less than 0.5 mm in length. Sometimes as many as 5—10 individuals were found living in the various spaces provided by the tests of *B. glandula.*

Agauopsis sp. Determined by I. M. Newell. Probably an undescribed species. Resident.

Pronematus sp. Determined by E. W. Baker (Baker & Wharton, 1952). Resident. The occurrence of this mite in the *Endocladia-Balanus* association was unexpected in that *P. ubiquitous* normally lives on fig trees in California (Baker & Wharton, 1952). The *Pronematus* sp. found in this investigation is less than 0.5 mm in length, and was frequently encountered in the spaces provided by the tests of *B. glandula.*

Suborder Mesostigmata

An undetermined species. Determined to suborder by E. W. Baker (Baker & Wharton, 1952). Resident.

An undetermined parasitid species. Determined to the family Parasitidae by E. W. Baker (BAKER & WHARTON, 1952). Resident. Under 0.5 mm in length, this species was rarely seen. BAKER & WHARTON (1952) have observed that free-living members of this group are found typically in rotting logs and litter.

Suborder Sarcoptiformes

Suidasia sp. Determined by E. W. Baker (BAKER & WHARTON, 1952). Resident.

Hyadesia sp. Determined by E. W. Baker (BAKER & WHARTON, 1952). An undescribed species. Transient. A small red mite that scurries over high intertidal rocks. The genus is found in the supralittoral zone in many parts of the world.[1]

Ameronothrus sp. Determined by E. W. Baker (BAKER & WHARTON, 1952). Resident. This jet-black form was found living in the air pockets between the basal plate of *Balanus glandula* and the underlying granite rock. Typically, the genus is found in the intertidal zone. Young are produced viviparously.

Phylum Tardigrada

An undetermined species. Resident. This form was found on occasion in the algal film covering the granitic rock.

Phylum Chordata

Class Aves

Arenaria melanocephala (Vigors). Black Turnstone, Transient.

Larus heermanni Cassin. Heermann's Gull. Transient.

Larus californicus Lawrence. California Gull. Transient.

Larus occidentalis Audubon. Western Gull. Determined by A. T. Newberry (Checklist of North American Birds, 1957). Transient.

Crocethia alba (Pallas). Sanderling. Determined by A. T. Newberry (Check-list of North American Birds, 1957). Transient. This and the following three species of birds came in and out of the association only very incidentally.

Catoptrophorus semipalmatus (Gmelin). Willet. Determined by A. T. Newberry (Check-list of North American Birds, 1957). Transient.

Haematopus bachmani Audubon. Black Oystercatcher. Transient.

Euphagus cyanocephalus (Wagler). Brewers Blackbird. Transient.

Occurrence of resident species at different levels in the association

Ricketts (unpublished MS) and others have stressed the importance of the relative periods of submersion and exposure as factors influencing the vertical distribution of intertidal organisms. These students observed that the distributions of many organisms was correlated with certain critical levels that experienced abrupt changes in the duration of periods of cover and exposure. To gain an impression of how the organisms in the *Endocladia-Balanus* association are affected by different periods of exposure, the biotic composition of the two upper (H_1 and H_2) and two lower (L_1 and L_2) quadrat samples was compared with the composition of the 12 samples collected from the center of the assemblage. The periods for which the high, center, and low quadrats experience exposure to the atmosphere have already been presented (table II).

[1] This form was described recently as *Hyadesia glynni* Manson, 1963. Unfortunately some confusion has arisen with respect to the habitat niche of this species (Manson, 1963); the author has never observed *Hyadesia* to move below the water line.

SPECIES	PERCENT OF QUADRATS AT EACH LEVEL IN WHICH THE SPECIES WAS PRESENT		
	LOW	MIDDLE	HIGH
Littorina planaxis		83	100
*Diaulota densissima		100	100
*Mesostigmata, Fam.?		92	50
Porphyra schizophylla		42	0
*Suidasia sp.	0	100	100
*Oligochaete	0	75	50
*Tipulidae	50	100	100
Hyale sp.	100	75	100
Chthamalus microtretus	100	92	100
Endocladia muricata	100	100	100
Lasaea cistula	100	100	100
Littorina scutulata	100	100	100
Acmaea digitalis	100	100	100
Acmaea scabra	100	100	100
Balanus glandula	100	100	100
Chthamalus dalli	100	100	100
*Agauopsis sp.	100	100	100
Musculus sp.	100	92	50
Pachygrapsus crassipes (juv.)	50	50	0
Nemertopsis gracilis	50	100	
Perinereis monterea	0	66	
Acanthina spirata	0	42	
Syllis spenceri	100	100	
Syllis armillaris	100	100	
Filicrisia franciscana	100	100	
Dynamenella glabra	100	100	
Acmaea pelta	100	92	
Mytilus californianus	100	92	
Gigartina agardhii	100	83	
Emplectonema gracile	100	83	
Syllis vittata	100	83	
Notoplana acticola	50	33	
Nereis grubei	100	58	
Barleeia oldroydi	100	58	
Cyanoplax dentiens	100	58	
Thais emarginata	100	50	
Tricolia rubrilineata	100	50	
Allorchestes ptilocerus	100	50	
Tegula funebralis	100	42	
Mitella polymerus	50	8	
Pontogeneia sp.	100	16	
Phragmatopoma californica	100	8	
Hiatella arctica	100	8	
Ocenebra circumtexta	100	0	
Tetraclita rubescens	100		
Dexiospira spirillum	50		
Leptasterias pusilla	50		

OCCURRENCE OF MARINE AND TERRESTRIAL SPECIES AT EACH LEVEL	NO.	%	NO.	%	NO.	%
SPECIES OF MARINE ORIGIN	42	95	38	88	14	72
SPECIES OF TERRESTRIAL ORIGIN	2	5	5	12	5	28

FIGURE 27. Occurrence of 47 species in the low, middle, and high quadrat samples from the *Endocladia-Balanus* association. The percentage of the total quadrats for each of the three levels in which a species is present, even as a single individual, is indicated just above each of the distributions. For example, of the two quadrats collected at the high level, *Littorina planaxis* was present in both (100%), and of the 12 quadrats from the middle level it was found in 10 (83%). The entire vertical range is not shown for any of these species, but upper or lower boundaries, where these occur, are

The vertical distributions of 47 of the more common species, as they extend through the zone studied, are shown in fig. 27. Note that no one species was restricted to the center of the association, but rather each had a range extending below, above, or in both directions from the center. In most cases the frequency of occurrence in the quadrat samples is a good indication of the level most characteristic of the species under consideration. The two gastropods, *Barleeia* and *Tricolia*, for example, each present in 100% of the quadrats at the low level, were found in greatest abundance at and below this level, whereas they were much less abundant at higher levels, and occurred in only 58 and 50%, respectively, of the middle quadrats. It must be noted that these distributions were established from samples collected at low water. In the case of some of the more motile animals, e.g. *Acanthina spirata, Thais emarginata*, and *Tegula funebralis* the vertical position occupied at any one time is dependent on the height of the tide and time of day (cf. below).

No juvenile *Pachygrapsus crassipes* were collected at the highest level; however, the adults were frequently encountered in the splash zone. The young forms, when found, were always among the thalli of *E. muricata.* Apparently these plants serve as a kind of nursery grounds for the recently-settled, post-megalops stage, immediately adjacent to the comparatively high and barren haunts of the adult.

A sharp break is noticeable in the number of different species occupying each of the three levels. The numbers of species characteristic for the low and middle quadrats were 42 and 38, respectively, dropping to 14 for the samples collected at the high level. No soft-bodied polychaetes or nemerteans extended upward beyond the height of the middle quadrats. Only one echinoderm specimen, *Leptasterias pusilla*, was recorded from the quadrat samples, and this from the low level of + 3.6 ft.

Finally, note that in going from the low to the high level samples the percentage of species present which had a terrestrial origin (mostly insects and mites) increased from 5% to 28% (fig. 27, bottom).

indicated by arrow heads. Broken lines extending beyond the lowest and highest levels portray the uncertainty of entire ranges. The broken-line segment of a distribution under a particular level signifies that even though a species was taken there, its more characteristic habitat is the level designated by the solid line. Also, a broken line is shown for some species not collected from the quadrats at the level indicated (the frequency in this case is zero), but known to be found there frequently. For example, the oligochaete, though not collected in the two low quadrat samples was found at a low level on several occasions. It was most frequently found in the center of the association, 140 specimens in all, but encountered only once at the high level. The species are arranged in the order of their vertical distribution — from most terrestrial to most marine, as indicated by these data. The species which are terrestrial in origin are indicated by an asterisk in front of the name.

	L_1	L_2	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	H_1	H_2
L_1		23 60.5	25 65.7	22 57.8	24 63.2	22 57.8	24 63.2	24 63.2	21 55.3	23 60.5	26 68.4	24 63.2	21 55.3	21 55.3	12 31.6	12 31.6
L_2			24 63.2	20 52.6	22 57.8	21 55.3	23 60.5	22 57.8	20 52.6	21 55.3	25 65.7	23 60.5	20 52.6	20 52.6	11 29.0	11 29.0
I				29 76.3	31 81.4	27 71.0	30 78.9	29 76.3	25 65.7	29 76.3	34 89.4	31 81.4	25 65.7	25 65.7	16 42.1	16 42.1
II					30 78.9	27 71.0	28 73.7	28 73.7	26 68.4	26 68.4	30 78.9	28 73.7	25 65.7	24 63.2	16 42.1	16 42.1
III						28 73.7	29 76.3	29 76.3	26 68.4	30 78.9	33 86.8	30 78.9	26 68.4	24 63.2	17 44.8	17 44.8
IV							27 71.0	27 71.0	26 68.4	27 71.0	29 76.3	27 71.0	25 65.7	24 63.2	17 44.8	16 42.1
V								28 73.7	25 65.7	29 76.3	32 84.2	31 81.6	25 65.7	24 63.2	16 42.1	16 42.1
VI									26 68.4	29 76.3	31 81.6	28 73.7	24 63.2	25 65.7	16 42.1	16 42.1
VII										26 68.4	27 71.0	25 65.7	26 68.4	25 65.7	17 44.8	17 44.8
VIII											31 81.6	28 73.7	26 68.4	24 63.2	16 42.1	16 42.1
IX												33 86.8	27 71.0	26 68.4	17 44.8	17 44.8
X													25 65.7	24 63.2	17 44.8	17 44.8
XI														25 65.7	16 42.1	16 42.1
XII															15 39.5	16 42.1
H_1																15 39.5
H_2																

= 0–33.3 % SPECIES HELD IN COMMON

=33.4–66.6 % " " " "

=66.7–100 % " " " "

FIGURE 28. Percentage of the 38 species most characteristic of the center of the *Endocladia-Balanus* association which are held in common by all possible pairs of quadrats. The two figures shown in each of the squares above the diagonal give the number of species, out of the 38 being considered, which occur in both of the two quadrats under comparison (upper figure), and the percent of the 38 species which occur in both of these two quadrats (lower figure).

Consistency of species composition among resident species of the association

An instructive form of analysis has recently become increasingly popular for demonstrating the degree of similarity between the species components of an array of samples (SANDERS, 1960; WIESER, 1960). This technique is employed here in the trellis diagram (fig. 28) which indicates quantitatively,

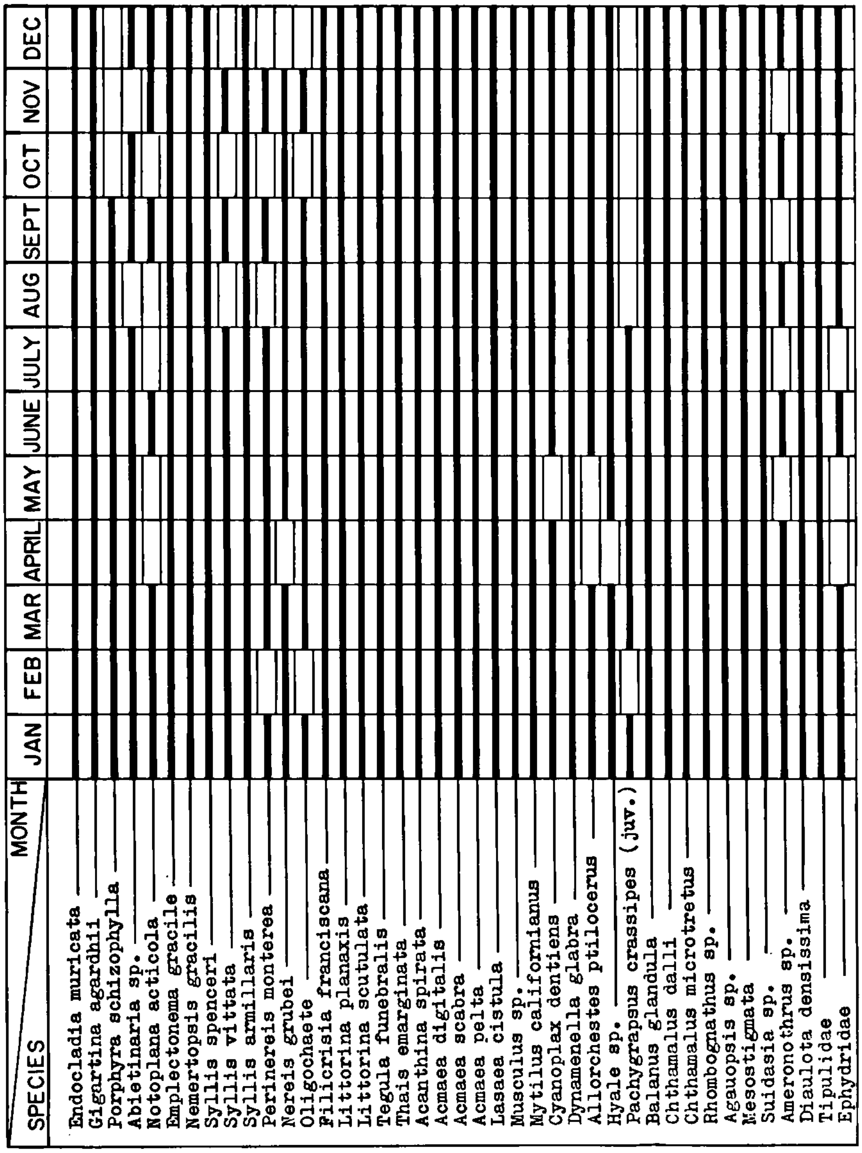


FIGURE 29. Qualitative seasonal occurrence of 41 characteristic species in the center of the *Endocladia-Balanus* association for the three-year period of study, 1959—61. If an organism was not detected on at least one occasion in a particular month for three years, it is designated as absent by a break in the solid bar. This information was collated from the quadrats, qualitative sampling, field observations, and photographs.

the degree of similarity in species composition among the 16 quadrats. All of the possible combinations, in pairs, of the low, middle, and high quadrats are compared with respect to the occurrence of 38 species characteristic of the center of the association. The species selected for this comparison are listed in fig. 29. *Tegula, Thais,* and *Acanthina,* though characteristic of the association during the high-water phase, were excluded from this analysis because of their near absence at low water when the quadrat samples were collected. Species which occurred only rarely or in very small numbers (see Appendix I) are also omitted from the analysis.

The trellis diagram shows that the affinity between quadrats I through XII is most strongly developed. The percentage of species held in common between any two of these samples very often exceeded 65%. Quadrat XII, even though located in the center of the association, shows the least typical species composition of the 12 samples taken at this level. This quadrat, however, was situated at the lowest absolute level of the middle series; its center was only + 3.6 ft above MLLW. The degree of affinity in species composition decreases markedly when either the low or high-level samples are compared with those taken in the center of the association. The greatest dissimilarity is evident in the high and low-level samples when compared among themselves.

Data obtained by quadrat sampling shows that, for the organisms present in significant numbers, the species composition of the assemblage undergoes little variation with the seasons. Figure 29 illustrates this stability of the association through the year. Twenty eight species, or 68% of the species listed in the figure, were present in every month of the year. The number of organisms absent for three or more months of the year was only eight, or 20% of the total considered. None of the species absent for periods of two or three consecutive months was ever abundantly represented in a quadrat sample; of these forms, *Allorchestes ptilocerus* was taken in greatest numbers, 21 individuals in March, 1959. It is thus likely that the absence of some of these less common forms in the tabulation could represent a sampling error. This is possibly not the case with juveniles of *Pachygrapsus crassipes,* which were absent for a five-month period extending from August through December. Here, while the numbers were always quite small (Appendix I), absence of young crabs during these months may be significant, for BOOLOOTIAN et al. (1959) observed that the adult females in 1957 and 1958 at the Hopkins Marine Station were ovigerous in April, May, June, and July. Off-season breeding was reported by HIATT (1948), but apparently occurs only sporadically among certain individuals.

Transient species in the *Endocladia-Balanus* association

It is clear at this point that the *Endocladia-Balanus* zone contains a resident association of organisms whose species composition, as determined

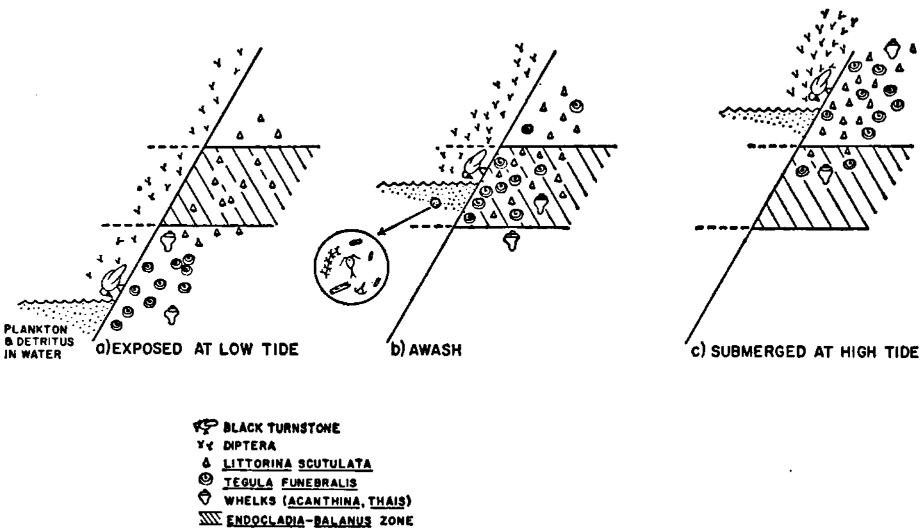


FIGURE 30. Movement of some transient species into, through, and above the *Endocladia-Balanus* level during a rising tide.

by quadrat sampling at low tide, is relatively constant in space and time. However, superimposed on this relatively stable background of species, is an ever-changing biotic component, which changes with the phases of the tide, the time of day, and the season of the year. This component consists of organisms which are not adequately sampled in the quadrat collections, and must be studied by other means.

If the *Endocladia-Balanus* level is observed at an advancing tide during the daylight hours in the spring, it is often possible to witness the following events, illustrated diagrammatically in fig. 30. In the association itself most of the marine animals appear relatively torpid at low water (fig. 30-a). Diptera of the families Tipulidae and Ephydridae, actively move about both in the air and on the substrate. Searching around and in the apertures of *Balanus glandula* one sees the staphylinid beetle, *Diaulota densissima* and occasionally a small red mite, *Hyadesia* sp., the latter scurrying rapidly in and out of view. *Littorina scutulata* is inactive; many individuals are hidden from view in the empty tests of *B. glandula* or in the holdfasts of *E. muricata.* A few *Tegula funebralis* and *Acanthina spirata* or *Thais emarginata* are present, moving slowly upward with the water line. Occasionally two or three Black Turnstones may fly or jump to the rising tide line from a nearby region.

When wave splashing begins to wet the *Endocladia-Balanus* level many of the marine species become active (fig. 30-b). Barnacles begin to sweep the water, crustaceans move about more actively, snails and limpets commence their browsing activities, and the transient species move into the belt from the lower levels. These are represented by the advancing front of *T. fune-*

bralis some whelks, and an occasional *Pagurus samuelis*, moving upward near the water line of the flooding tide. *D. densissima* moves to the undersides of *B. glandula* and the adults of the Diptera move higher up, out of reach of the sea. The red mite, *Hyadesia* sp., disappears. Black Turnstones often spend considerable time in the association when the tide is at this level. The rising water brings into the *Endocladia-Balanus* zone such phytoplankters as *Ceratium, Chaetoceros, Rhizosolenia, Coscinodiscus* or *Biddulphia*, for example, as well as zooplankters like *Oikopleura*, nauplius larvae and copepods. Characteristically, the water is also heavily charged with organic detritus—broken up plant fragments, exuvia, etc. Both living organisms and detritus may serve as food for certain of the resident species.

As the tide rises higher, say to + 4.5 ft, some species characteristic of the belt at low water begin to move upward with the transients (fig. 30-c). There is a conspicuous response in *Littorina scutulata,* which in some localities moves completely out of the association to a higher level. WIESER (1952) reported on the extensive movements made by *Littorina obtusata* in phase with the rising and falling tide. He also reviewed the general nature of this tendency of certain species to occupy different levels according to the height of the tide, and proposed the term "dynamics of vertical distribution" for the changes taking place.

During the high tide period, then, the abundance of whelks and *Tegula funebralis* is high. Fewer *Littorina scutulata* are present and there is a complete absence of birds and aerial insects. Plankton and detritus are available to filter feeders mainly at high water. No fishes were ever observed to invade the association at high water.

If a similar tidal pattern is observed at night some striking differences appear. The Black Turnstones and gulls are absent altogether from the association; in the study area many of them are roosting on a large rock outcropping nearby. *Hyadesia* sp. and *Diaulota densissima* are not to be seen moving about on the rock surfaces. In fact, *D. densissima* is observed in greatest abundance during hot, sunny days. A very noticeable difference during the dark hours is the increased abundance of *Tegula funebralis*, which

TABLE VI. The occurrence and relative abundance of some motile animals in the *Endocladia-Balanus* association in relation to the phase of the tide and time of day.

Species	Low Water		High Water	
	Day	Night	Day	Night
Hyadesia sp.	few	none	none	none
Diaulota densissima	many	ncne (hidden)	ncne (hidden)	none (hidden)
Diptera (aerial)	many	many	none	none
Black Turnstone	few	none	none	none
Gulls	many	none	none	none
Pagurus samuelis	none	none	few	few
Thais emarginata	few	few	few	many
Acanthina spirata	few	few	few	many
Tegula funebralis	few	few	few	many

moves up with the advancing tide line. Diptera are also common on the rocks at night. These observations are summarized in table VI.

In addition to diurnal and tidal changes in the transient fauna of the *Endocladia-Balanus* zone, one may note seasonal changes as well. Except for non-breeding residents, most of the Black Turnstone population is absent from the Monterey Bay area in the late spring and summer (BENT, 1929). During this period the birds are breeding along the southwestern coastline of Alaska (AOU Check-list, 1957). The seasonal occurrence of the three most commonly encountered gulls was given by CRINNELL & MILLER (1944), and is summarized in fig. 31. The Western Gull is present throughout the

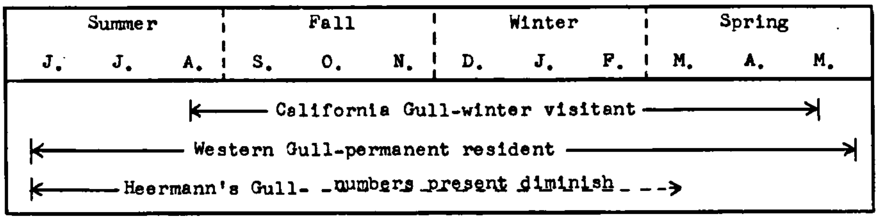


FIGURE 31. Seasonal occurrence of gulls most frequently encountered in the *Endocladia-Balanus* association in the Monterey Bay.

year. The California Gull, like the Black Turnstone, is absent during the summer months. Most abundant in the summer and fall is Heermann's Gull, which may sometimes be seen by the hundreds on the rocks in the study area. The numbers of this species usually begin to decline in the late fall, until by the early spring it is absent.

In summary, then, the *Endocladia-Balanus* association is characterized by a consistently present assemblage of benthic organisms; these residents are periodically joined by relatively small numbers of transient species, the particular transients varying somewhat with the phase of the tide, the time of day, and the season of the year.

Comparison of the biotic composition of the *Endocladia-Balanus* association with that of other associations in similar habitats

It is of interest now to compare the faunal and floral composition of this association with that of associations at similar intertidal levels elsewhere. In the present context only the qualitative floral and faunal similarities are considered. The *Balanus-Littorina* biome studied by SHELFORD et al. (1935) in the Puget Sound region included the following species which were found in the present study: *Balanus glandula, Littorina scutulata, Acmaea digitalis, Thais emarginata, Mytilus californianus,* and *Chthamalus dalli.* Shelford and co-workers recognized within this biome the *Balanus-Mytilus californianus* and the *Balanus-Mytilus edulis* associations. The first association was divided into four faciations for the west coast of Vancouver Island, and all of the above-named species were found within these faciations, often with overlapping vertical distributions. The width of the belt occupied by the association was 14 ft. *Littorina scutulata, Balanus glandula,* and *Mytilus californianus* were listed as dominant animal species.

From 1936 to 1938, RIGG & MILLER also studied the *Balanus-Mytilus californianus* association of Shelford in the environs of the Strait of Juan de Fuca. They divided the broad belt occupied by this association into three zones: splash, upper intertidal, and lower intertidal. The splash zone is equivalent to Shelford's *Littorina-glandula* and *Littorina-cariosus* faciations, between + 8.0 and + 14.0 ft above sea level. The upper intertidal zone extends down to + 4.0 ft, and the lower intertidal zone to + 1.0 ft. The investigators found that the organisms in the upper intertidal belt were exposed for more than half the time; the average exposure time in the center of the *Endocladia-Balanus* association is 72%.

Endocladia muricata and *Gigartina* sp. were found by Rigg & Miller to be distributed vertically between about + 6.0 and + 9.0 ft. This level overlaps both the splash and upper intertidal zones. Some of the invertebrates found here were *L. scutulata, A. digitalis, T. emarginata,* and *M. californianus. Balanus glandula* was more often found in the upper level of the splash zone, whereas *B. cariosus* was associated with *E. muricata.* With respect to (a) the time spent submerged and exposed, (b) the dominant species present, and (c) the manner in which they are vertically distributed, it appears that this more northern + 6.0 to + 9.0 ft level is the equivalent of the *Endocladia-Balanus* belt at Pacific Grove. The photographs of Rigg & Miller demonstrate the same outward appearance as the assemblage investigated in the present study.

MOKYEVSKY's (1960a) studies of littoral organisms in the Sea of Japan demonstrated notable similarities to the eastern Pacific assemblage described above. Of the three horizons investigated he observed in the highest, 1.8 to 2.5 meters above the "zero summer tidal level", a narrow band (minimum width five to six cm) of the red alga *Gloiopeltis capillaris.* This was described as a characteristic species in the high littoral zone of practically all of the north-western shores of the Pacific Ocean. *Gloiopeltis* is also a member of the Endocladiaceae, has a highly branching tuft-like thallus, and is short, usually between 1 to 4 cm in height (KYLIN, 1956). The observations discussed here were made largely in the vicinity of Peter the Great Bay.

Characteristic animals in the *Gloiopeltis* belt were: Gastropoda- *Acmaea testudinalis, Littorina sitchana subtenebrosa;* Cirripedia- *Chthamalus dalli*; Isopoda- *Dynamenella glabra;* Amphipoda- *Allorchestes malleolus, Hyale bassargini*; Diptera- Syrphidae, Tipulidae. *Chthamalus dalli, A. testudinalis* and larvae of the Syrphidae occurred consistently in abundance. Only the dipteran larvae were reported to live in the alga. *Dynamenella glabra* and *Hyale bassargini* are associated with colonies of *Chthamalus,* the latter species often found in the empty cups of the barnacle. Compared with the *Endocladia-Balanus* assemblage, two species (*C. dalli, D. glabra*), four genera (*Acmaea, Littorina, Allorchestes, Hyale*), and one family (Tipulidae) of the *Gloiopeltis* belt are the same.

Two species and four genera of the mid and sublittoral levels corresponded to the fauna of the eastern Pacific, viz. Nemertea- *Emplectonema*; Gastropoda- *Thais*; Pelecypoda- *Musculus, Mytilus edulis*; Polychaeta- *Syllis (Typosyllis) armillaris bilineata*; Cirripedia- *Balanus*; Amphipoda- *Pontogeneia. Balanus* was present only as a single dead specimen of *B. cariosus.*

The attention devoted to the high intertidal zone by English ecologists has been considerable. In certain localities the structure and interrelationships of associations here have been worked out in some detail (e.g. COLMAN, 1940; GLYNNE-WILLIAMS & HOBART, 1952; MORTON, 1954), and it is possible to make some rather critical comparisons with the *Endocladia-Balanus* association.

COLMAN (1940) studied a region on the English shores at Church Reef, and reported on the microfauna contained within several species of algae and the lichen, *Pygmaea pumila* (= *Lichina pygmaea*). From Colman's description of the vertical distribution of *Pygmaea,* and the abundance in it of certain genera of animals found also in my own study, it appears that this plant is an ecological counterpart of *Endocladia muricata. Pygmaea pumila* grows in tufts about two cm in height. This is less than half the height of *E. muricata,* which under favorable conditions can grow from four to six cm. The vertical distribution of *Pygmaea* is given as "....between high water springs and mean sea-level or a little lower". The extreme vertical limits of distribution of *Endocladia* extend from just above the lowest of the higher low waters to just below the highest of the higher high waters (high water springs). *Pygmaea* thus lives slightly higher up on the shore than *Endocladia.* By comparing Colman's effective vertical distribution of *Pygmaea* with an exposure curve for the same general area presented by MORTON (1954), this lichen is found to live under conditions of exposure ranging from 58% of the time to complete atmospheric exposure in the highest level at Church Reef in Wembury. The minimum and maximum exposure figures for *Endocladia* at Pacific Grove were calculated to be 16% and 84%, respectively. However, the tufts of *E. muricata,* in association with *Balanus glandula,* were just above mean sea level, and below the mean higher high waters — within the same intertidal distributional limits as *Pygmaea.* Like *Endocladia, Pygmaea* grows well in very exposed situations. Colman found that the fauna living in association with *Pygmaea* was not particularly rich in numbers of species. All of the major groups of organisms found in *Pygmaea* are also characteristic of *Endocladia*: Nematoda, Oligochaeta, Cirripedia, Isopoda, Amphipoda, Insecta, Acarina, Pelecypoda, and Gastropoda. *Geranomyia unicolor,* a tipulid larva, was often abundantly encountered in the lichen tuft. Nemerteans and polychaetes were always plentiful in the tufts of *Endocladia,* but were never found in the lichen, although reported in some algae. Also, harpacticoid copepods and ostracods are present in great numbers along the blades of *Endocladia,* but were reported as abundant by

Colman only for the algal species. Nematodes, while present, were not particularly numerous in either of these plants.

Many of the genera, too, are held in common. Of the 12 found by Colman, 58% are also a part of the *Endocladia-Balanus* association. These are: Cirripedia- *Chthamalus, Balanus*; Amphipoda- *Hyale*; Acarina- *Rhombognathus*; Pelecypoda- *Mytilus, Lasaea*; Gastropoda- *Littorina*. Apparently *Mytilus edulis* is the only species found in common. *Lasaea rubra* and the isopod, *Campecopea hirsuta*, made up in numbers more than 90% of the animals found. Four species of insects were found, and of these two dipteran larvae were most plentifully represented.

All of these animals were taken from whole plant tufts, and for this reason it must be noted that some of the species living exposed on the rocks or among a dense barnacle cluster were not included in the tabulation. However, MORTON (1954) studied the fauna inhabiting, and living in the immediate vicinity of, the empty tests of *Chthamalus stellatus*. Morton found that this fauna consisted of both "terrestrial" and "marine elements". The most common marine species, in the order of their abundance, were *Lasaea rubra, Campecopea hirsuta, Littorina neritoides*, and *L. rudis*. The terrestrial species included *Anurida maritima* (Collembola), *Micralymma marinum* (Coleoptera), *Bdella interrupta* (Acarina), *Neobisium maritimum* (Pseudoscorpionida), and *Otina otis* (pulmonate gastropod). Springtails, pseudoscorpians and pulmonate gastropods, while apparently a characteristic part of this assemblage in England, were never observed in the *Endocladia-Balanus* association on the Monterey Peninsula.

FISCHER-PIETTE (1940) has discussed the occurrence of *Lasaea rubra* in tufts of two species of *Pygmaea* (referred to as *Lichina pygmaea* and *L. confinis*) on French shores, and has noted that a species of *Gelidium*, living in the upper intertidal zone in Australia, contains high numbers of *Lasaea australis*. A Balanoid Zone has been described by T. A. STEPHENSON (1949) for many of the rocky shores throughout the world, but his studies of the association have not been in sufficiently fine detail to make close comparisons possible.

AUTECOLOGICAL INFORMATION ON SELECTED SPECIES

Up to this point the location of the *Endocladia-Balanus* association and the environmental conditions impinging on it have been examined in some detail, and the species composition of the assemblage has been considered in relation to time of the day and phase of the tide. It now appears desirable to present some autecological information concerning the more common and characteristic species of the association. Subsequent to these considerations a synthesis of the various components will be made, in an effort to gain insight into some of the interactions of the entire assemblage.

Scope and methods of study

Many of the genera considered are cosmopolitan, and have been studied by a number of investigators in various countries. For this reason the literature is often diverse and voluminous for a single genus. No attempt has been made to review completely the literature for each of the genera examined; instead, only the papers containing pertinent ecological information on Pacific coast forms are cited. For each species, where feasible, the following things were investigated: (a) habitat niche, (b) activity patterns, (c) organic matter content of the body, (d) seasonal occurrence, (e) population structure, (f) reproductive activity, (g) feeding relationships, and (h) growth rates.

Habitat niche, as used here, is defined as the precise location or range of locations in which the representatives of a given species were found living in the *Endocladia-Balanus* association. For the most part the habitat niche of each species was determined from field observations. Occasionally barnacle sheets, *Endocladia* and *Gigartina* thalli, and even large sections of the granitic substratum were examined in the laboratory.

Activity pattern includes all of the various gross movements made by a given species in its daily existence. Field studies were undertaken to observe these activities in the assemblage.

Dry weight measurements were made of all the species taken in each of the quadrat samples (Appendix II). These weights were obtained from alcohol-preserved specimens (except in the cases of *E. muricata* and *G. agardhii*, where fresh samples were used) by first drying at 60° C, and then at 105° C, until a constant weight was attained. Such dry weight determinations give a rough idea of the organic matter content of each species. However, many animal species contain certain parts that play little if any role in the energy aspects of community food relations. For example, the calcium carbonate in the shells of gastropods, pelecypods, and cirripeds, although often ingested by predators, cannot serve as a source of food. Many marine ecologists have worked with organisms large enough to dissect, and have stressed the importance of separating shell from soft body tissues to better equate the organic matter contents, as determined by dry weight measurements, of diverse groups of organisms (THORSON, 1957). The majority of the animals dealt with in the present study were so small that such separation of soft and hard parts would have been difficult. Also, the great number of size-classes in many species made it impractical to adopt this method.

To compensate for this difficulty, a second estimate of the organic matter content of the different species was obtained by the use of micro-Kjeldahl analyses for total nitrogen (CONWAY, 1947). Such analyses should give more accurate measures of the organic matter content in the various organisms. The rationale behind this assumption, and some of the advantages are as follows. (a) On a dry weight basis it has been found that generally the protoplasm of plant and animal cells contains about 75% protein (GIESE, 1962). A quantitative measure of the nitrogen content should provide a fair approximation of the protein content. (b) The nitrogen content is relatively easy to determine using Conway's micro-diffusion modification of the Kjeldahl method. (c) It was found that for many species there is no significant variation in the ratio of nitrogen content to dry weight with size-classes and seasons (to be amplified later). Also, the various statistical tests carried out on the relationship between body weight and nitrogen content demand a reasonably normal distribution of these variates, and where this relationship was investigated (as in *L. scutulata*) the assumption of normality seems well justified. A tabulation of the nitrogen contents of the more common *Endocladia-Balanus* associates is given in Appendix III.

Two sources of error must be contended with in adopting the procedures noted above. First, the conchiolin (scleroprotein) of molluscan shells and the chitin (acetylglucosamine) of arthropod cuticles contain some nitrogen that is measured, but which may not represent organic matter that can be used as a source of energy and materials by the animals ingesting these substances. VINOGRADOV (1953) has observed that the amount of conchiolin in mollusk shells may vary from a trace to 5%, and marine mollusks have more than brackish or fresh-water species. Scleroproteins are highly resistant to enzyme action. Chitin, according to VINOGRADOV (1953), is one of the principle structural elements of the exoskeleton in Crustacea and insects, and contains about 6% nitrogen. NICOL (1960) noted that a chitinase is known only from certain terrestrial pulmonates and arthropods.

A second source of error relates to the analytical technique used. TER MEULEN (1930) presented some evidence that the Kjeldahl procedure does not detect all of the nitrogen in organisms. He showed that with the Kjeldahl technique the percent yield of nitrogen for a variety of organic substances was often in the range of 5—10% less than that shown when the hydrogenation method was used. Since the real nature of the digestion reactions is little understood (KIRK, 1950) it is difficult to determine just which nitrogen residues of a protein are released. However, it is desirable to determine, along with the samples, the percent recovery of a known substance. In one typical analysis of five samples of DL threonine a recovery of $98.7 \pm 1.0\%$ ($P < 0.05$) was obtained.

The occurrence of particular species through the year was determined by the quantitative and qualitative sampling program outlined earlier. The seasonal occurrence or absence of organisms is of importance in ecological studies, for it can affect greatly the species composition of a community. Further, for each species the number of individuals per unit of environment, and their sizes and weights are also of importance in understanding the structure of the natural population. These characteristics have been examined in detail for some of the species more abundantly present in the association. Since special sampling procedures were used for the different species studied, these are best taken up separately.

Reproductive activity in this study was of particular interest in connection with the manner in which it affects the extent and frequency of recruitment. Also, among the species composing the *Endocladia-Balanus* association, the young are introduced into the adult population in a variety of forms and at different degrees of development. This aspect of reproduction, as well, was investigated. The methods used are considered under the sections devoted to individual species, to follow.

An analysis of the feeding activities and relationships of the species in the assemblage involved direct observation in the association and in the laboratory, and an examination of gut contents. Field observations were carried out at all phases of the tide and at different times of the day. Numerous isolated feeding experiments were made with many of the smaller species which were difficult to observe under natural conditions. Finally, an attempt was made to check the gut contents of specimens killed while actually feeding. For the typically marine species, collections were made at high water, and the animals immediately preserved in 70% ethyl alcohol. The body tissues were dehydrated through hour-long immersions in a series of successively more concentrated ethyl alcohol solutions (from 70 to 100%), and cleared by soaking for a two-day period in Cedarwood oil. After this treatment the gut could be easily located and dissected out. Animals feeding most actively at low water were collected at this time, and then immediately dissected and the gut examined.

Growth rates of some of the more abundant species were determined by a variety of techniques, which are discussed separately under the appropriate autecological sections.

Rhodophyta

Endocladia muricata (Postels & Ruprecht) J. G. Agardh, 1847

This alga is a member of the order Cryptonemiales, in the division Rhodophyta. It is the most common and conspicuous of the macroscopic algae found in the association, and is most easily recognized by the bushy appearance of its branchlets, each bearing many minute spines with highly pigmented tips (fig. 32). *Endocladia* is abundant in the upper intertidal zone, especially where the wave action is moderate to rough.

On the surface of the branches of *Endocladia* it is possible under high magnification (430 ×) to observe dense clusters of blue-green algae. These filamentous patches are distributed over the entire thallus, and the most

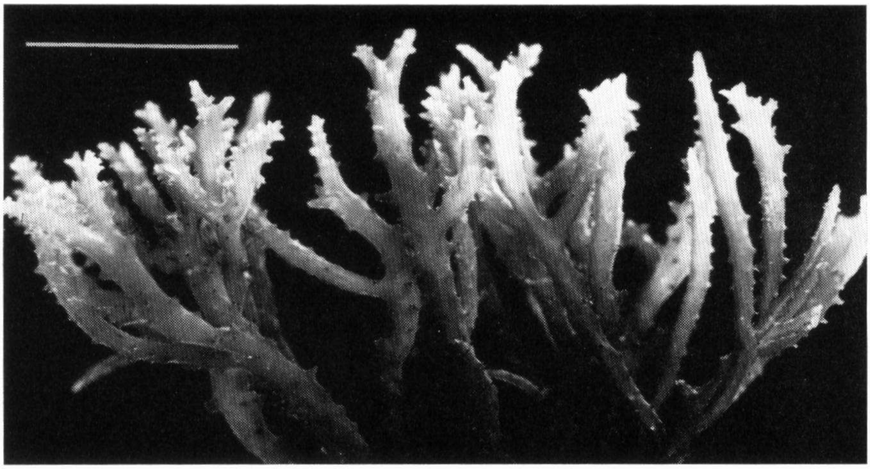


FIGURE 32. Close-up view of the upper-most portion of one thallus of *Endocladia muricata* (February 14, 1962). The scale represents 5 mm.

common blue-greens forming them are *Entophysalis conferta, Lyngbya* sp., and *Oscillatoria* sp. Because these epiphytes are so commonly and characteristically found on *Endocladia* it has become routine practice among some algologists to collect *Endocladia* for myxophycean material.

Since *Endocladia muricata* is an abundant species it was practical to carry out nitrogen analyses at different times of the year to determine the nitrogen level on a seasonal basis. Because the organisms are subject to the weather conditions of the atmosphere about 72% of the time, the nitrogen levels were examined with reference to the terrestrial seasons.

The nitrogen content of *E. muricata* (plus attached microscopic epiphytes) was determined in three samples from each of four different months, representative of the four seasons in the year (fig. 33). The mean nitrogen contents in July, October, January, and April were 3.6, 3.2, 3.0, and 2.6% of the dry weight, respectively. Since in the analysis of variance the calculated F ratio is greater than the tabulated value ($P < 0.05$), the hypothesis that the means are the same is rejected. The observed F ratio is 13.0, and the tabulated value, $F_{0.05}$ (3,8) = 4.07.

Now that a difference in the means has been established on a seasonal basis, it is important to learn where this difference lies. While a variety of methods are available for discriminating between means, the choice of any one of these depends on the relative importance of Type I and II errors (FEDERER, 1955). TUKEY's (1949) multiple range technique has a relatively small Type I error, and was selected for separating the means where a significant F test was observed. In this case, though, Tukey's test does not allow a separation of the means at the 5% level of statistical significance, even though significant inter-sample variation exists. Seasonally, the nitrogen levels in the autumn and winter are reasonably close, lowest in the spring and highest during the summer. Thus, the nitrogen content in this species is partitioned accordingly: January and October, 3.1% (group mean of these two months); April, 2.6%; July, 3.6%. The occurrence of the highest nitrogen levels in the summer is somewhat surprising, for VINOGRADOV (1953) indicates that for several species of northern hemisphere algae the maximum nitrogen level is reached in the winter and early spring, and the minimum in the summer and autumn.

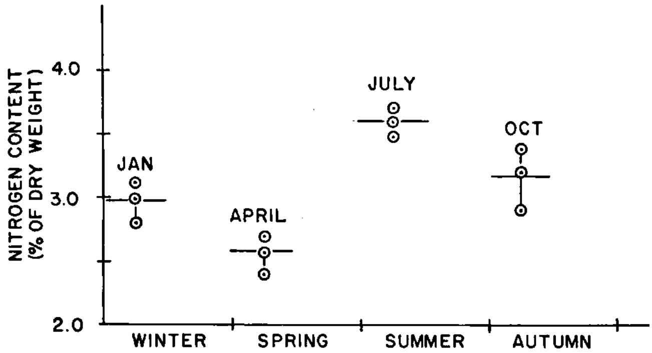


FIGURE 33. Nitrogen content of *E. muricata* at different seasons of the year. Each value represents the determination from a thallus of a different plant. The horizontal line in each series represents the mean nitrogen level for that particular month; dots represent values obtained on individual samples.

The life cycle and anatomy of the reproductive structures of *E. muricata* were described in 1928 by KYLIN. He showed that separate male and female gametophytes produce non-motile sex cells (spermatia) and carpogonia, respectively. Fertilization gives rise to carpospores which in turn germinate into free, sessile tetrasporophytes indistinguishable from gametophytes on the basis of gross appearance. Eventually, meiotic divisions in the tetrasporophyte give rise to haploid tetraspores which are released, presumably forming equal numbers of male and female gametophytic thalli. These major life cycle events are demonstrated schematically in fig. 34. Dr. I. A. Abbott (personal communication) has observed that the gametophytes are most abundant in the spring, thus the low nitrogen level in the spring appears to be related to the predominance of haploid plants at that time.

To learn the degree of seasonal variation in the standing crop, and to measure the net production, five relatively uniform rock surfaces were selected as study sites and observed over a period of 14 months. Care was taken to choose localities where plants were regularly distributed over the rock face. At each site, a study plot 100 cm wide and 65 to 92 cm high (depending on the extent of vertical growth in the particular plot) was selected and marked. Each plot was then subdivided into 12 vertical strips, each 8.3 cm wide and running from top to bottom of the plot. One strip, selected at random, was cropped from each plot each month from April 1959 to March 1960. An attempt was made to pick only the thallus, leaving the

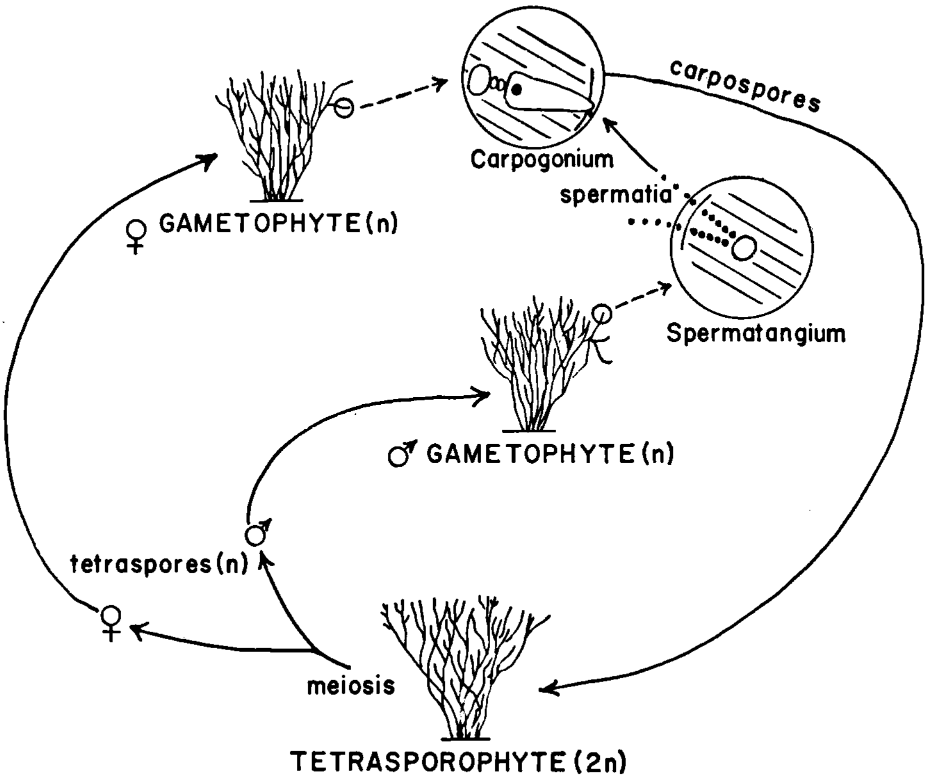


FIGURE 34. Major events in the life cycle of *E. muricata*, as adapted from KYLIN (1928).

holdfasts so as not to cause permanent damage, but this was difficult because barnacles serving as a substrate for the alga would often tear or crumble from the rock. Harvest data are tabulated in Appendix IV.

The initial harvests of the strips in study areas I, II, and III were selected as representative in order to examine the seasonal variation in standing crop. The combined dry-weight harvests of the three strips, collected in each of the 12 months in the year, are shown in table VII. Although the rock surfaces were selected and partitioned on the basis of what appeared to be nearly comparable and homogeneous carpets of thalli, a considerable range in weights was found in the combined standing crops within the same season. In the autumn, for example, the difference in weight between the two months of October and December was 86 g, or 67.7% of the maximum in October. However, the hypothesis of equal means was rejected at the 5% level, indicating the observed seasonal differences are probably significant. The calculated F ratio was 5.9, as opposed to the tabulated value, $F_{0.05}$ (3,8) = 4.07. The greatest standing crop of *Endocladia* was observed in the spring and summer seasons, which are characterized by warmer temperatures, increased daylength and upwelling along the coast of deep, nutrient-rich water.

The season of winter storms, from November through March, includes almost all of the low figure months.

TABLE VII. Seasonal variation of *E. muricata* (dry weight) for study areas I, II, and III. Each monthly figure represents combined data from three field samples.

Month		Standing crop biomass g/ 2,034 cm²	g/m²	Seasonal average g/m²
April,	1959	44.9	221	SPRING 189
May,	„	35.7	176	
June,	„	34.8	171	
July,	„	31.0	152	SUMMER 128
Aug.,	„	29.7	146	
Sept.,	„	17.4	85	
Oct.,	„	25.9	127	AUTUMN 87
Nov.,	„	19.0	93	
Dec.,	„	8.3	41	
Jan.,	1960	24.0	118	WINTER 79
Feb.	„	12.6	62	
Mar.,	„	11.7	58	

Subsequent to the initial cropping each month, all of the vertical sample strips were again harvested in April, May, and June of 1960. Net production was determined from regrowth into the denuded strips (Appendix IV, right hand column). The "harvest" method of determining net production has been described by E. P. ODUM (1959, pp. 80—81). The figures obtained in the present case do not quite represent net production, but net production minus some undetermined losses of regrowing *Endocladia* due to scouring by waves and to the feeding activities of certain animals. Figure 35 is a scatter diagram relating the second harvest weights to the total time available for regrowth. The maximum net production measured was about 36 g/m²/month, or 1.2 g/m²/day. Appendix IV shows that most of the maximum and near-maximum net production figures were attained where significant time during the spring season was available for regrowth. This is well-illustrated by the four maximum values falling on the diagonal in fig. 35: for the two lower values (2 g/m² in one month, and 74 g/m² in three months) the entire period for regrowth fell in the spring season; for the two higher values (149 g/m² in five months, and 184 g/m² in six months), respectively, 60% and 50% of the time for regrowth fell in the spring season. Many of the minimal net production observations, points close to or actually on the abscissa, are in part explained by damage to, or removal of, *Endocladia* holdfasts during the initial cropping of the sample strips.

In conjunction with the above estimations of net production, short-term experiments were carried out to measure the rate of photosynthesis under natural daylight conditions. The oxygen technique was employed, the liberated gas being determined by the standard Winkler procedure. The photosynthetic rates were determined on three occasions in overcast weather during the late morning hours, on samples ranging in fresh wet weight from 9.3 to 15.0 g (table VIII). Transparent large-mouth bottles containing the alga immersed in sea water were rotated at a constant rate for 15-minute intervals, to insure uniform exposure and gaseous diffusion. The tabulation shows the steps by which the original, fresh weight algal samples are adjusted so that the net production of both the harvest and oxygen techniques may be directly compared.

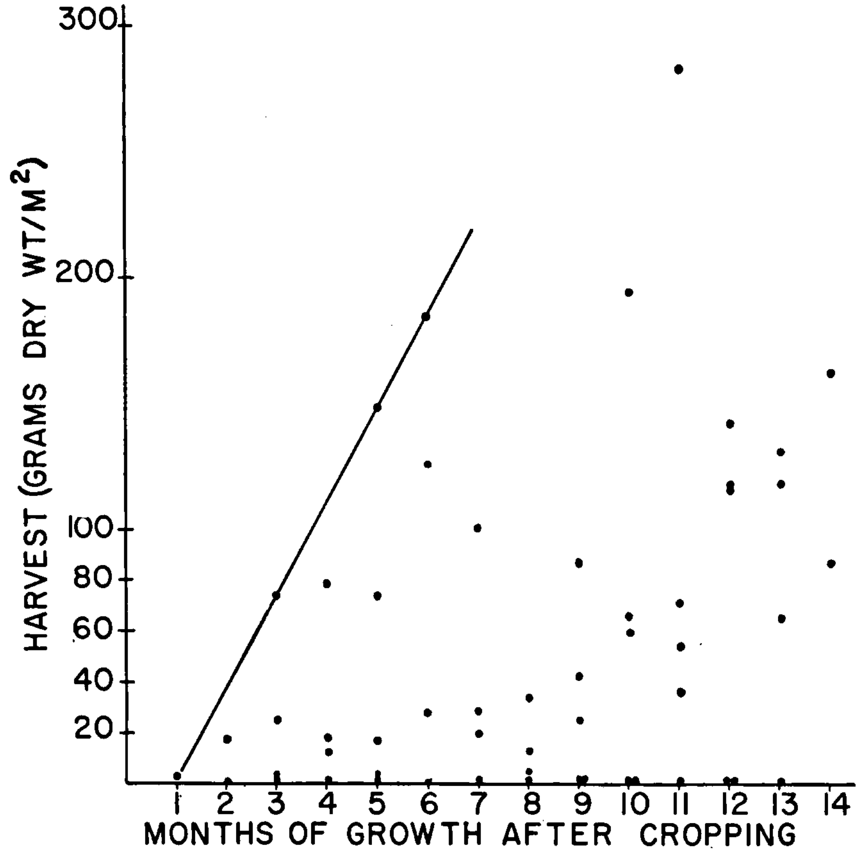


FIGURE 35. Regrowth of *E. muricata* on cropped sample strips, April 1959—June 1960. Original data in Appendix IV. Diagonal line simply indicates maximum net production measured by this method.

To change fresh weights to dry weights it is necessary to know the quantity of water held by fresh thalli. The mean dry weight of *Endocladia*, as a percentage of the fresh weight, determined for five samples from different times of the year, was 29.9 ± 2.8%. The carbon fixed for each ml of O_2 liberated is 0.536 mg, and in knowing the quantity of carbon on a dry weight basis, it is possible to calculate the production of organic matter.

TABLE VIII. Net production of *E. muricata* measured for 15-minute intervals during overcast, late morning hours, 1959.

Units	Aug. 20	Aug. 26	Aug. 28	Adjustments & assumptions
Fresh wt. of sample in g	9.3	15.0	15.0	Blotted with paper towel to remove excess water.
Ml O_2/g fresh wt./hr.	0.6	0.7	0.6	———
Ml O_2/g dry wt./hr.	2.0	2.3	2.0	Dry wt. is 29.9% of fresh wt.
Mg carbon/g dry wt./hr.	1.1	1.2	1.1	0.536 mg carbon fixed/ml O_2 released.
Mg organic matter/g dry wt./hr.	3.9	4.3	3.9	Carbon content is 28.32% of organic matter.
Mg organic matter/g dry wt./day	9.1	10.5	9.1	3.4 hr. photosynthesis/24 hr. Respiration = 0.20 mg carbon/g/hr.
G organic matter/ m^2/day	1.1	1.3	1.1	Average study site has 121 g *Endocladia*/m^2.

The carbon content of the red alga, *Rhodomela* sp., the only species in this group listed by VINOGRADOV (1953), is 28.32% of the dry weight. This figure is used as an approximation for converting carbon to organic matter in *Endocladia.* On a long-term basis, where this alga occurs in the association studied, it is submerged 14% of the time (3.4 hrs) during the daylight hours. Haberman & Blinks (unpublished data) found that the respiratory rate in *Endocladia* is on the order of 0.20 mg carbon/g dry wt./hr. Since the quantity of carbon fixed is a net level, going on for 3.4 hrs in the day, respiration alone was assumed to progress at the rate of 20.6 hrs (24.0 minus 3.4)/day.

The net gain in organic matter as determined by this technique agrees with the harvest observations. The maximum net production observed by harvesting was 1.2 g/m^2/day, and the average, as determined by the oxygen method, was also 1.2 g/m^2/day.

Agreement of these two methods is not so good when a photosynthetic quotient of 1.25 is assumed, as recommended by RYTHER (1956) for phytoplankton populations. In this case the mean net production of *Endocladia* is 0.8 g/m^2/day, or only 67% of the best yields obtained from the regrowth measurements conducted in the field.

When subject to exposure during windy and clear weather, the thalli of *E. muricata* take on a hardened and desiccated consistency. To test the photosynthetic activity of the alga during prolonged atmospheric exposure, eight 15-g samples were allowed to desiccate for one, two, three, and up to a maximum of eight hours under daylight conditions. This period covers the maximum time the alga is exposed to drying during the daylight hours. At the termination of each exposure interval the sample was immersed for 15 minutes in sea water and its O_2 evolution or consumption measured (fig. 36). The loss in weight of the samples during exposure (fig. 36) amounted to about 35% of the original fresh weight after six hours. This weight was maintained throughout the remainder of the experiment. A heavy overcast at 9:00 A.M. gradually dissipated into a clear sky around midday; this lasted until 4:00 P.M. when again the sun was obscured by an advancing fog bank.

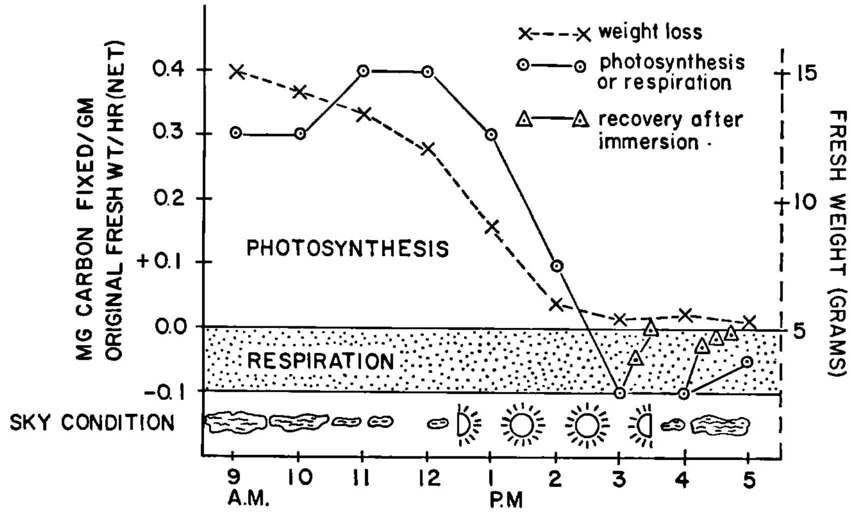


FIGURE 36. Photosynthetic activity and weight loss of *E. muricata* during exposure to the atmosphere for a period of eight hours, August 26, 1959. The relative extent of sky cover is indicated pictorially in the lower portion of the figure.

Photosynthetic activity was highest at 11:00 A.M. and 12:00 noon, after two and three hours of drying and a maximum weight loss of 20%. A sharp drop in weight and in photosynthetic rate occurred concomitantly between the three and six-hour periods of exposure. Respiration exceeded photosynthesis when the fresh weight of the desiccating samples fell below 40% of the initial wet weight. However, two samples exposed for six and seven hours and reimmersed in seawater, recovered to the compensation level in 30 and 45 minutes, respectively.

NORTHCRAFT (1946) observed no recolonization of *E. muricata* on denuded rocks (holdfasts completely removed) after 27 months, and stated that the reason may be related ". . . . to the fact that it grows slowly as has been shown by BAKER (1909) for algae growing high in the intertidal zone along the coast of England". In four sample strips harvested during the present study, the net production was such that the initial *Endocladia* crop was surpassed by regrowth. In six months, from December 1959 to June 1960, the new crop on a sample strip in study site IV exceeded the initial standing crop by 35% on a weight basis. Several of the holdfasts in the sample strips were observed to regenerate new thalli. From the rate of net production measured, it appears that the establishment of spores may be more important than the rate of growth in recolonization of *Endocladia*.

Gigartina agardhii Setchell & Gardner, 1933

Gigartina agardhii, a red alga in the order Gigartinales, was present throughout the year, and at times formed a large fraction of the plant component of the *Endocladia-Balanus* association. However, its occurrence at the intertidal level studied was on the whole more irregular than that of *E. muricata.* The two thalli of *G. agardhii* pictured in fig. 5 show that the branches are less dense and more flattened than those of *E. muricata.* An abundant microfauna was not supported by this alga.

Doty (1946) set the vertical distribution of this alga at Mussel Point (Hopkins Marine Station) +1 to +3 ft, as compared with the higher position of *E. muricata,* +3 to +4 ft. *Gigartina agardhii* was absent from three quadrats, and contributed samples of less than 50 mg each in three others.

The nitrogen content was determined in samples taken at four different times during the year and is shown in fig. 37. Analyses were performed on pieces from three different thalli for each of the four months examined. The mean nitrogen content in June, September, January, and April was 2.6, 2.6, 3.4, and 2.1% of the dry weight, respectively. The hypothesis that

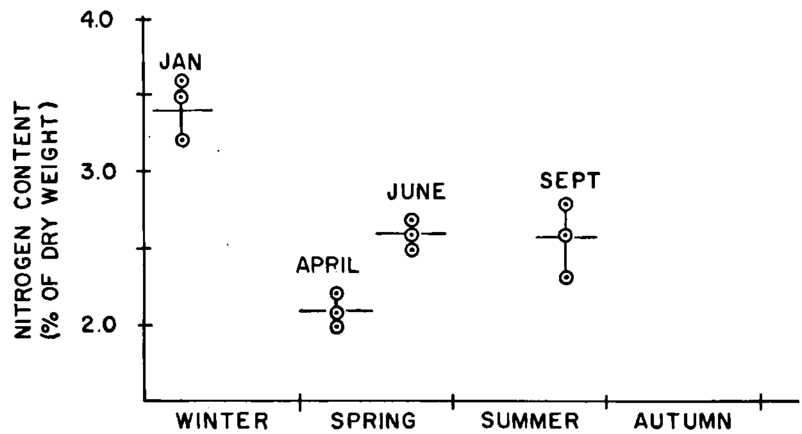


Figure 37. Nitrogen content of *G. agardhii* at different seasons of the year. The horizontal line in each series represents the mean nitrogen level for that particular month; dots represent values obtained on individual samples.

the means are not different is rejected at the 0.05 level of significance. The calculated F ratio is 12.4 and the tabulated value, $F_{0.05}$ (3,8) = 4.07. Tukey's test shows that the means can be separated into two groups ($P <$ 0.05), viz. January and April-June-September. The mean nitrogen level in the winter is 3.4%, and in the spring and summer seasons 2.4% (the group mean for the three months examined). The autumn nitrogen level will also be treated as 2.4%, even though analyses were not carried out in this season. The highest nitrogen content occurred in the one winter month investigated, January. This followed the trend pointed out by VINOGRADOV (1953) for other Rhodophyta; a higher nitrogen level tends to occur during the winter, with lower values in the summer.

Platyhelminthes

Notoplana acticola (Boone, 1929)

Although often more abundant in other habitats, for example under stones at a lower intertidal level, the polyclad worm *N. acticola* was occasionally present in the empty tests of *Balanus glandula* or within spaces in the holdfasts of *Endocladia muricata*. At low water the animals were relatively inactive, but when wetted by the rising tide they were observed to move about quite actively in the association.

The mean nitrogen content of a combined sample of two, nonpreserved specimens was 13.9% of the dry weight.

This polyclad species was found in only five of the 16 quadrat samples collected. A single specimen occurred in each of four quadrats (L_2, I, IX, and X), and three individuals were present in Quadrat V (November 13, 1959). No *N. acticola* were present at the upper border of the association. Minimum and maximum dry weight biomasses of 0.9 and 22.0 mg were observed in Quadrats X (September 23, 1961) and V, respectively.

Seasonally, *N. acticola* was absent in April, May, July, August, and October, over the three years of observation. The rather sparse distribution of the species in the *Endocladia-Balanus* association [seven individuals per 16 quadrats (6,400 cm^2), or about 11 worms/m^2], coupled with the small area covered by each quadrat sample, could well explain its absence in the samples taken during the several months indicated.

Typically, polyclads are carnivores, feeding on living, moribund or dead animal tissues (HYMAN, 1951). *Notoplana acticola* was observed feeding on only one occasion. On March 29, 1960, one *N. acticola*, about two cm in length, was found engulfing a limpet, *Acmaea digitalis*, during the daylight hours of the early morning in a shady location, where the rock surface was wet from recent wave washing. The cleanly detached shell, about one cm in length, was lying beside the feeding worm. The extruded pharynx surrounded half of the limpet's body. When the limpet was extracted from the feeding worm its tissues showed signs of digestive dissolution.

Five specimens of *N. acticola* were starved for one week, but refused a variety of foods when offered during the day or overnight: amphipods, syllids, nemerteans, mites, *Lasaea cistula*, and tissue fragments of *Balanus glandula*. However, from HYMAN's (1951) remark that "....polyclads often devour bit by bit live sessile, helpless animals such as oysters, barnacles, ascidians, and the like", it appears possible that *Balanus* and *Chthamalus* spp. are eaten by *N. acticola* in the *Endocladia-Balanus* assemblage.

Nemertea

The two species of nemertean worms found in the assemblage, *Emplecto-*

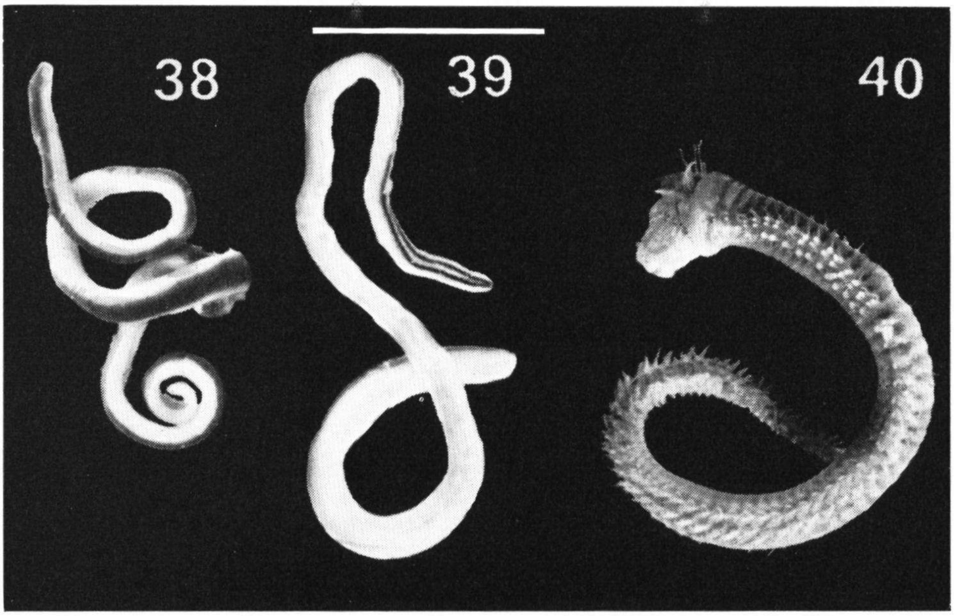


FIGURE 38. *Emplectonema gracile* (Jaunary 26, 1962).

FIGURE 39. *Nemertopsis gracilis* (February 15, 1962).

FIGURE 40. *Nereis grubei* (January 30, 1962). Worm removed from mucoid tube The scale in all three cases represents 1 cm.

nema gracile and *Nemertopsis gracilis,* are members of the family Emplectonematidae, suborder Monostylifera. Monostyliferan nemerteans have an armed proboscis with a single stylet (HYMAN, 1951). The two species can be distinguished externally by the color and pattern of pigmentation on the dorsum. *Emplectonema gracile* (fig. 38) has a dark dorsal surface which is green or blue-green in life. *Nemertopsis gracilis* is characterized by a pale dorsal surface bearing two longitudinal chocolate-brown lines which extend along the entire length of the body (fig. 39). The specimens shown in these photographs are greatly contracted; a worm four to five cm long when contracted often extends out to at least 20 or 30 cm when crawling undisturbed over a flat surface.

Emplectonema gracile (Johnston, 1837)

At low water *E. gracile* was commonly found in the larger spaces often present in the holdfasts of *E. muricata,* in the empty cups of dead *B. glandula* or in the cavities frequently formed between continuous sheets of these barnacles and the underlying substrate. The worms became active when wetted by the rising tide, and were seen moving over the bare rock surface most abundantly at night.

The mean nitrogen content of three, freshly-collected specimens was 8.3 ± 0.7% of the dry weight. The worms analyzed ranged in dry weight from 3.2 to 11.8 mg.

Emplectonema gracile was present in the two low-level quadrats, and in all of the center samples except Quadrats VI (January 13, 1960) and VII (March 12, 1960), but was absent from both quadrats taken at the upper margin of the association. The mean occurrence of the worm in the low and center quadrats, respectively, was 3.0 and 4.6 individuals/quadrat. Where present in the center quadrat samples, it ranged in abundance from a single specimen each in Quadrats IV (September 4, 1959) and IX (June 15, 1960) to a maximum of 13 specimens in Quadrat XII (December 20, 1961). The mean dry weight biomass of *E. gracile*, in the center of the association, was 22.3 mg/quadrat, or 558 mg/m^2. While not present or abundantly represented in all quadrats, qualitative sampling showed that this species was present in all 12 months of the year.

No ingested food remains were found in the guts of 10 specimens examined. These worms were collected at high water, six during the daylight hours and four at night. However, field observations suggest that the worm is a relatively unselective carnivore. Frequently when quadrat samples were being collected, as many as two or three individuals would move onto the quadrat site from adjacent areas and ingest the soft tissues of damaged barnacles. Also, at high water two specimens were found probing with their heads into the apertures of *B. glandula.* One specimen was observed feeding on the eggs of *Thais emarginata* on July 25, 1959; the head was entirely within the egg case. On March 4, 1962, one *E. gracile* was observed in rapid pursuit of a *Nereis grubei* of equal size. The nemertean struck out twice with its proboscis at the fleeing polychaete, but was unsuccessful in its capture.

Nemertopsis gracilis Coe, 1904

Although commonly found in the holdfasts of *Endocladia muricata, N. gracilis* was more frequently encountered in the empty tests of *Balanus glandula,* where sometimes as many as 10 intertwined individuals formed a compact mass. The species was most active at high water during the night. At this time the worms were frequently observed crawling over the rock substrate and the tests of *B. glandula.*

The combined nitrogen content of two, freshly-collected specimens was 11.4% of the dry weight.

Of the two nemertean species this one was more often found in greater abundance. It was present in every center quadrat sample, absent in one low-level sample (Quadrat L_2, February 3, 1959) and absent in both high-level quadrats. At the center level a maximum of 55 specimens was collected in Quadrat II (May 11, 1959), and a minimum of one specimen occurred in

Quadrat IV (September 4, 1959). The mean number of *N. gracilis* in the center of the assemblage was 16.5 individuals/quadrat. At the same level these worms had a mean dry weight biomass of 24.1 mg/quadrat, or 602 mg/m^2. While *N. gracilis* was absent from three quadrats, qualitative sampling demonstrated its presence in the central portion of the association at all seasons.

The guts of 10 specimens were examined immediately after collecting, but only on one occasion was any ingested material found. One individual, collected on December 14, 1961, during the high tide at night, contained one fragment of a *Lasaea cistula* shell. Both living individuals and macerated fragments of small syllid polychaetes, barnacles, amphipods, *Lasaea, N. gracilis*, and mites, were offered during the day and night to three healthy *N. gracilis* previously starved for one week. The nermerteans did not eat any of these presumed foods.

Annelida

Annelid worms form a conspicuous component in the *Endocladia-Balanus* association, and the Syllidae, in terms of numbers, biomass, and frequency of occurrence outranked all of the other polychaete groups. The genus *Syllis*, as defined by FAUVEL (1923), is represented by three species: *S. spenceri*, *S. vittata,* and *S. armillaris.* Two nereid polychaetes occurred in quadrat samples with fair consistency, while one very minute oligochaete was characteristically present.

The genus *Syllis*, of the subfamily Syllinae, is characterized as follows: (a) parapodia with ventral cirri, (b) palps separated, (c) tentacles and dorsal cirri moniliform, and (d) proboscis without a trepan, and armed with a single, large, anteriorly-placed tooth. The three species of syllids found in the present study can be identified with the following key, slightly modified from FAUVEL (1923).

1a. Two to three dorsal-most setae from each mid-body bundle with end of shaft long and oblique; body color cream, and dorsum with distinctive chocolate-brown pattern .... *Syllis spenceri.*
1b. Setae otherwise; body color purple or violet .... 2.
2a. Dorsal cirri long; with more than 20 articles .... *Syllis vittata.*
2b. Dorsal cirri short; with less than 20 articles; dorsum with transverse pink bands .... *Syllis armillaris.*

Syllis spenceri Berkeley & Berkeley, 1938

Syllis spenceri was described by BERKELEY in 1938 from a series of specimens collected in Departure Bay, near Vancouver, British Columbia. Berkeley has remarked (personal communication) that it is a relatively rare form, found on only two or three other occasions since its original description. A specimen is shown in the photograph in fig. 42, the unique pattern of pigmentation on the dorsum being especially evident. Empty

Balanus glandula tests, the interstices and spaces formed between sheets of these barnacles and the underlying substratum, and the holdfasts of *Endocladia muricata* provided shelter for *S. spenceri*. Only rarely was an individual ever found on an exposed surface.

Nitrogen analyses were performed on alcohol-preserved specimens; the results are tabulated in table IX. In the analysis of variance for unequal size groups a calculated F ratio of 8.1 was obtained, as opposed to the tabulated value, $F_{0.05}$ (2,12) = 3.88. On this basis the null hypothesis of equal means was rejected ($P < 0.05$).

The mean nitrogen level in October is about 22% lower than in April and January. The April and January means can be pooled and treated as one

TABLE IX. Nitrogen content of *S. spenceri*.

Collection date	No. of worms in sample	Dry wt. of sample (mg)	Mean nitrogen content (% of dry wt.)
Apr. 1960	7	16.8	13.4 ± 1.3
Oct. 1960	3	9.8	10.4 ± 0.4
Jan. 1961	5	17.5	13.5 ± 1.0

sample; this gives a mean nitrogen content for these two seasons of 13.4%. With this new value it is possible to make a two-sample comparison between the 13.4 and 10.4% levels. A T test shows that the hypothesis of equal means must be rejected ($P < 0.05$). The nitrogen content in October, then, appears to be significantly lower. No analyses were performed on specimens collected during the summer months.

Syllis spenceri was present in all of the quadrat collections except the two taken at the upper-most level. It had a mean occurrence in the low and center samples of 10.5 and 39.1 individuals/quadrat, respectively. Excluding Quadrat IV (September 4, 1959), which yielded a single specimen of *S. spenceri*, all the center quadrats contained at least 17 individuals each. The highest number recorded was 82 individuals in Quadrat VII (March 12, 1960). The center quadrats contained a mean dry weight biomass for this species of 62.3 mg, equivalent to 1,560 mg/m^2. In conclusion, this species was abundantly represented everywhere in the center of the association in every month during the three years of investigations.

Information on food habits is sparse. Of five specimens examined internally, the gut of one contained blue-green algal cells and other unidentified plant material. When a quadrat sample was being collected on July 10, 1959, three *S. spenceri* were observed to move onto the soft tissues of dead *B. glandula*. They fed on this material for about 30 minutes. These two observations suggest that *S. spenceri* is omnivorous.

Syllis vittata Grube, 1840

The dorsum of *S. vittata*, devoid of any conspicuous color pattern (fig. 41), is uniformly some shade of purple. The body color and the prominent white cirri make this species easy to distinguish from *S. spenceri*. Berkeley has remarked (personal communication) that this species has never before been reported outside of European waters. HARTMAN, in her "Catalogue of the Polychaetous Annelids of the World" (1959), lists the species as occurring only in the Mediterranean (though this compilation does not intend to describe the known ranges of distribution). The specimens examined agree in every essential with FAUVEL's (1923) diagnosis: the setal blades are pectinate and bidentate in the young, becoming unidentate in the adults; the cirri are uniformly white; and three violet bands are present on the dorsum of the anterior segments.

Syllis vittata was found living in the holdfasts of *E. muricata* at the *Endocladia-Balanus* level. However, it was also encountered lower in the intertidal zone, living in association with other species of algae.

The combined nitrogen content of five, freshly-collected specimens was 11.8% of the dry weight.

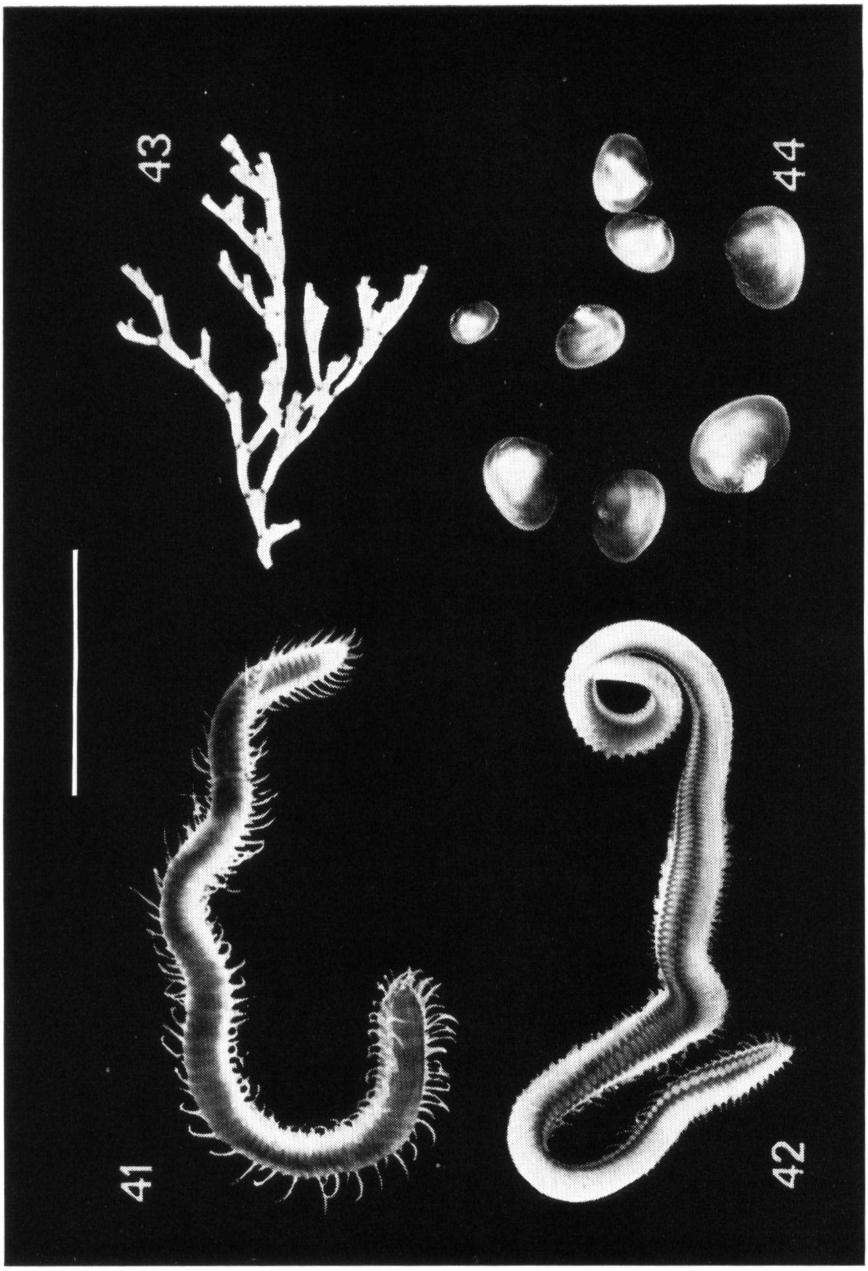
Syllis vittata was present in the low quadrats, and in the center quadrats excluding samples XI (October 21, 1961) and XII (December 20, 1961), but was absent from the upper margin of the association. The mean number of individuals per quadrat at the low and center levels was 15.5 and 9.2, respectively. Where present in the center samples, it ranged in abundance from a single specimen each in Quadrats II (May 11, 1959) and VII (March 12, 1960), to a maximum number of 29 individuals in Quadrat I (March 19, 1959). Also, in the center samples it demonstrated a mean dry weight biomass of 4.8 mg/quadrat, or 120 mg/m^2. *Syllis vittata* was not present in either the quantitative or qualitative samples taken in August, October, and December.

The guts of three specimens contained blue-green algal cells in abundance, and unidentified brown fragments, probably of algal origin. Specimens starved for one week refused such animal foods as mites, smaller syllids, and barnacle tissues.

Syllis armillaris (Müller, 1771)

Syllis armillaris was characterized by FAUVEL (1923) as follows: (a) dorsal cirri short, fusiform, and of less than 20 articles, (b) setal blades unidentate, (c) body uniformly violet with transverse pink bands on the dorsum. Some of the larger individuals showed these characters, but the unequivocal identification of specimens less than 10 mm in length was often difficult. The interstices in the tests of *B. glandula* and the holdfasts of *E. muricata* were the sites most commonly frequented by the young individuals. Adults were found at the study level in the tufts of *E. muricata* only.

The species was present in all of the quantitative collections, excluding the two quadrats taken at the uppermost level. The mean number per sample, in the low and center quadrats was 4.5 and 56.9 individuals, respectively. In the center samples the syllid ranged in abundance from a single specimen in Quadrat VII (March 12, 1960) to a maximum of 140 individuals in Quadrat


41
42
43
44

II (May 11, 1959). Most of these specimens were small, as indicated by a mean dry weight biomass for the 12 center quadrats of 4.3 mg, an average of 0.075 mg/individual. Worms weighing as much as two and three mg were not very often encountered here. The individuals taken at the lower margin of the association were somewhat larger, with a mean dry weight of 0.322 mg. It seems likely that the adult population has its center of distribution at a still lower intertidal level.

Nereis grubei (Kinberg, 1866)

Nereis grubei, shown in fig. 40, is a green polychaete with a diamond-shaped arrangement of large conical teeth on area VI of the proboscis (LIGHT et al., 1957). This species was occasionally present in the spaces between barnacles and in the holdfasts of *E. muricata.* It constructs a mucoid tube which is firmly attached to the substrate. REISH (1954) studied these worms at San Pedro, California, and found great numbers of them associated with the green alga, *Cladophora trichotoma.* He also showed that *N. grubei* lives in association with a variety of other marine plants (though he does not report it in *E. muricata*), in beds of *Mytilus californianus* and on *Limnoria*-infected pilings.

Nereis grubei was present in the low quadrat samples and in seven of the center collections. The mean number of individuals per quadrat at the low and center levels was 5.0 and 1.4, respectively. A mean dry weight biomass of 1.2 mg/quadrat, or 30 mg/m^2 was observed in the center of the *Endocladia-Balanus* association. The quantitative and qualitative samples showed the worm to be present in all months except April and December; in view of the low numbers of individuals taken in other samples, absence in these months is not considered significant. In the population of *N. grubei* studied by Reish in southern California, individuals were observed to be present and to reproduce throughout the year.

The gut contents of four specimens revealed a rather diversified diet. The alimentary canal in two specimens was tightly packed with fragments of

FIGURE 41. *Syllis vittata* (February 15, 1962). Three faint bands can be seen immediately posterior to the pigmented eye spots. Close examination of the posterior quarter of the specimen will reveal two pigmented eye spots adjacent to a transverse white band marking an incipient fracture zone where an epitoke will detach from the parent.

FIGURE 42. *Syllis spenceri* (February 14, 1962).

FIGURE 43. A sprig of *Filicrisia franciscana* (February 14, 1962).

FIGURE 44. *Lasaea cistula* (February 14, 1962). Five young clams can be seen through the valve in the specimen in the upper left corner.
The scale in all four cases represents 5 mm.

E. muricata. One specimen contained a valve of *Lasaea cistula,* a fragment of *Gigartina* sp., many shells, rocks, and masses of unidentified organic detritus. One other worm contained a single valve of *L. cistula.* REISH (1954) likewise observed that the diet of *N. grubei* is quite varied, consisting of both plant and animal materials, and organic detritus.

Reish also measured the weight increment of 10 specimens regularly fed in the laboratory. He found that growth was highly variable among different individuals. The wet weight gain in one specimen was 36.3 mg in 16 weeks; then a loss in weight occurred when the worm became sexually mature and spawned.

Perinereis monterea (Chamberlin, 1918)

The body color of *P. monterea* is brown, and the two transverse patches of paragnaths on area VI of the proboscis (LIGHT et al., 1957) make it a readily distinguished form. This species lives in mucous tubes which are often attached to the tests of *B. glandula* or in the concavities of large holdfasts of *E. muricata.*

One alcohol-preserved specimen, weighing 18.3 mg when dried, contained 13.4% nitrogen.

Perinereis monterea was present only in eight of the mid-level quadrats. Where present it ranged in abundance from a single specimen each in Quadrats IX (June 15, 1960) and X (September 23, 1961), to a maximum of six individuals in Quadrat I (March 19, 1959). A mean occurrence of 1.9 individuals/mid-level quadrat was observed, and the species had a mean dry weight biomass of 12.1 mg/quadrat, or 302 mg/m^2. It was not collected in February, August, October or December.

The gut of a single specimen contained one fragment of *E. muricata.*

Bryozoa

Filicrisia franciscana (Robertson, 1910)

The bryozoan *F. franciscana* (fig. 43) was found as small sprigs growing out from around the bases of *E. muricata.*

A combined sample of several different preserved colonies with a total dry weight of 34.8 mg contained 0.7% nitrogen. This low nitrogen content of the colony as a whole reflects the presence of the well-developed calcareous skeleton whose weight contributes greatly to the dry weight of the animal.

Sprigs of *F. franciscana* were present in all of the low and center quadrat samples, but were absent from quadrats taken at the upper margin of the association. The mean dry weight biomass of this species at the low and center levels was 12.4 and 6.9 mg/quadrat, or 310 and 170 mg/m^2, respectively. In the center quadrats, dry weight biomass ranged from 0.1 mg in Quadrat IV (September 4, 1959) to 34.8 mg in Quadrat VI (January 13, 1960). Every month sampled over the three-year period was characterized by the presence of this form.

Studies of gut contents were not carried out, but it is probable that, like most other bryozoans, *F. franciscana* is a ciliary filter feeder which ingests a wide variety of minute organisms and particles of organic detritus.

Mollusca-Pelecypoda
Lasaea cistula Keen, 1938.

The tiny bivalve, *L. cistula*, is a member of the family Erycinidae in the order Heterodonta. Species belonging to this family are typically nestlers in habit and hermaphroditic, often brooding their young inside the mantle cavity. In 1938 KEEN pointed out the distinctness of the two northeastern Pacific species of *Lasaea* from the European *L. rubra*, and described them as *L. cistula* and *L. subviridis*. The genus is cosmopolitan, and the two local species are distributed together for about 600 to 700 miles along the west coast of North America. Of the two species, only *L. cistula* (fig. 44) was found in the *Endocladia-Balanus* association.

In the intertidal zone in the study area, *L. cistula* was confined sharply to the level of the *Endocladia-Balanus* association, usually as a nestler in the interstices of *Balanus glandula*, and in the holdfasts of *Endocladia muricata* and *Gigartina agardhii*. Occasionally, some individuals were found attached by byssus threads to the exposed rock surface.

Lasaea cistula has been found living in association with at least three other species of organisms. KEEN (1938) has found it in the bases of *Postelsia palmaeformis* in central California. HAAS (1942) emphasized its intimate association on the shell or byssus threads of *Brachidontes multiformis*, south of Point Conception, and on *Mytilus californianus* to the north. He stated that *L. cistula* living in dead *Donax* shells or in the empty cups of *Balanus glandula*, apparently in an aberrant situation, really conformed to the more common habitat on closer inspection, for the byssus threads of *B. multiformis* could be found attached to these objects. He also remarked that both species were collected at Pacific Grove from "kelp holdfasts". *Lasaea subviridis* was found by KEEN (1938) in September 1936, and on several occasions by the author from 1959 to 1961, in the byssus threads of *Mytilus californianus* at Rosarito Beach, between Tijuana and Ensenada, Baja California.

The nitrogen content of this species was investigated in relation to body size and season; nitrogen determinations were carried out on both preserved and fresh material, to determine differences attributable to preservation procedures.

It was found that *L. cistula* could be divided conveniently into 12 size-classes. These classes are listed with their corresponding limits, which indicate for each class the range of the greatest shell length, as measured with an ocular micrometer.

The nitrogen content was analyzed in eight different classes, to determine its quantity in clams of varying size (fig. 45). The eight size-classes analyzed,

Class	Limits (mm)
0.5	0.35—0.65
0.8	0.66—0.94
1.1	0.95—1.25
1.4	1.26—1.54
1.7	1.55—1.85
2.0	1.86—2.14
2.3	2.15—2.45
2.6	2.46—2.74
2.9	2.75—3.05
3.2	3.06—3.34
3.5	3.35—3.65
3.8	3.66—3.94

and the number of individuals in each were: 0.8 mm (40 individuals), 1.1 (40), 1.4 (20), 1.7 (10), 2.0 (10), 2.3 (10), 2.6 (10), and 2.9 (1). On the basis of a calculated *T* value of 28.8, as opposed to the tabulated value, $T_{0.05}$ (6) = 2.45, it is concluded that a linear relationship exists between the dry weight (X) of the various size-classes and their nitrogen content

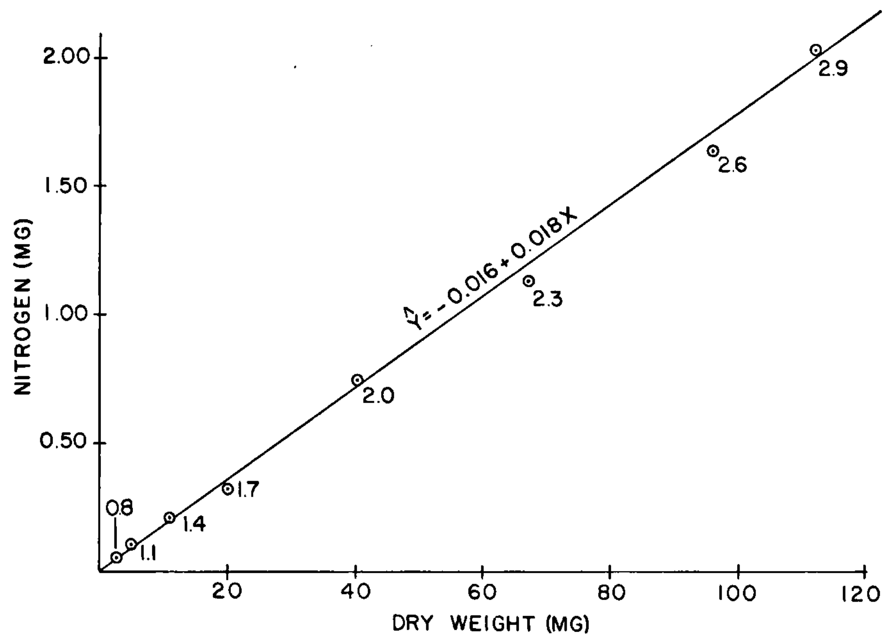


FIGURE 45. Nitrogen content versus dry weight of intact animal including shell in eight different size-classes of freshly-collected *L. cistula* (February 18, 1961). The numbers of specimens in the various size-classes are adjusted so that each value is representative of 40 individuals. The size-class of each determination is indicated beside its particular value.

($\hat{Y}$) ($P < 0.05$). The prediction equation for this linear relationship is: $\hat{Y} = -0.016 + 0.018\,X$.

To determine whether the nitrogen content of *L. cistula* showed a seasonal variation, nitrogen analyses were performed on seven size-classes each, in April, July, October, and January (fig. 46). The mean values for nitrogen content in these different months, in the order given, were 1.4%, 1.7%, 1.6%, and 1.6%. The analysis of variance shows that the means are not the same ($P < 0.05$). A calculated F ratio of 6.0 was obtained, as opposed to the tabulated value, $F_{0.05}$ (3,24) = 3.01.

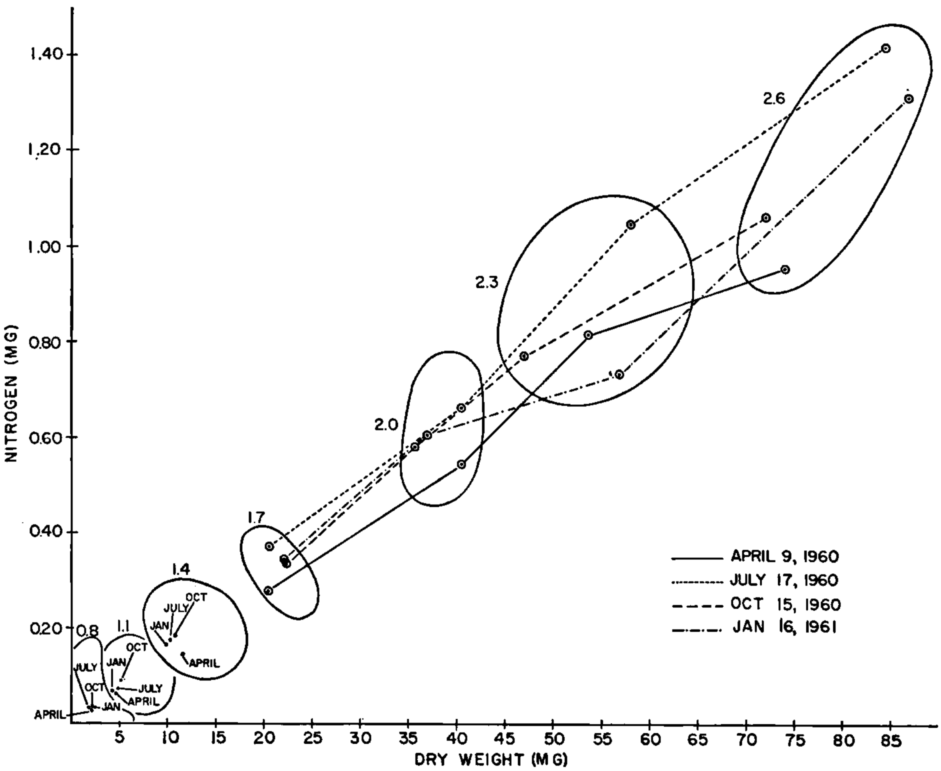


FIGURE 46. Nitrogen content versus dry weight in preserved *L. cistula* in four different months, representative of the four seasons in the year. The various nitrogen values are adjusted so that each is representative of 40 individuals. The seven size-classes are encircled for easier recognition.

According to Tukey's test the 1.4% nitrogen level in April is significantly lower than in October, January or July ($P < 0.05$). Thus, the nitrogen level for the species is treated as 1.4% in the spring and 1.6% in the summer, autumn, and winter. The 1.6% level represents the group mean for the October, January, and July samples.

Preserved biological specimens often come to weigh less than similar, freshly-collected forms (THORSON, 1957). To learn the extent by which ethyl alcohol affects the nitrogen content in *L. cistula*, a comparison was made between the percent nitrogen content of specimens in equal size-classes in preserved and freshly-collected samples (table X). This comparison shows that the percent nitrogen content of fresh specimens in six classes is 0.1 to 0.4% higher than in preserved specimens. The percent nitrogen levels were the same in the 1.4 and 2.9 mm size-classes. The mean percent nitrogen contents of the preserved and fresh samples were 1.6 and 1.8%,

TABLE X. A comparison of the percent nitrogen content in preserved and fresh collections of *L. cistula*. These values were calculated from the percent nitrogen composition as adjusted for 40 individuals.

Sample	Size-Classes							
	0.8	1.1	1.4	1.7	2.0	2.3	2.6	2.9
Preserved Oct. 15, 1960	1.6	1.7	1.7	1.5	1.6	1.6	1.5	1.8
Fresh Feb. 18, 1961	2.0	1.8	1.7	1.6	1.8	1.7	1.7	1.8

respectively. A *T* test demonstrates that the difference in the nitrogen levels between these two groups is statistically significant ($P < 0.05$). The observed *T* is 3.2, and the tabulated value, $T_{0.05}$ (14) = 2.14. From these data it is assumed that preserved *L. cistula* have a nitrogen content averaging some 0.2% of the dry weight less than that of nonpreserved specimens.

In summary, then, these analyses indicate: (a) a linear relationship between size and nitrogen content, (b) a relative drop in nitrogen level in the spring, and (c) a higher nitrogen content in fresh than in preserved material.

The great abundance of *L. cistula* is a distinctive feature of the *Endocladia-Balanus* assemblage. An estimation of the absolute numbers of individuals per quadrat was extrapolated from the number counted in a weighed fraction taken from the quadrat sample. *Lasaea cistula* sorted from any particular quadrat sample were thoroughly mixed and poured evenly, one layer deep, over a flat surface. A watch glass two cm in diameter was placed on top of a continuous layer of clams and carefully rotated until the rim made complete contact with the flat surface. In this manner fractions were obtained from the quadrat samples which could be counted easily. The number of individual clams present in these fractions ranged from 237 to 632. After a count was made, both the subsample and the remainder of the *Lasaea* from the same quadrat were dried to a constant weight, and the total number of clams determined by a simple proportion. Replicate estimations of the number of individuals present in the same sample yielded values differing by only 1.8% (e.g., values of 10, 900 and 11, 100 *Lasaea* for Quadrat II).

Lasaea cistula was present in all of the quadrat samples. The mean number of individuals per quadrat, at the low, center, and high levels, was 155, 6,200, and 440, respectively. In the center samples the numbers ranged from 1,100 in Quadrat XII (December 20, 1961) to 11,100 individuals in Quadrat II

(May 11, 1959). *Lasaea cistula* was abundant at all seasons. Indeed, the only change detected in the numerical occurrence of this species was associated with vertical position in the intertidal belt; there was a sharp decline in the mean number of *L. cistula* per quadrat at the upper and lower levels of the assemblage.

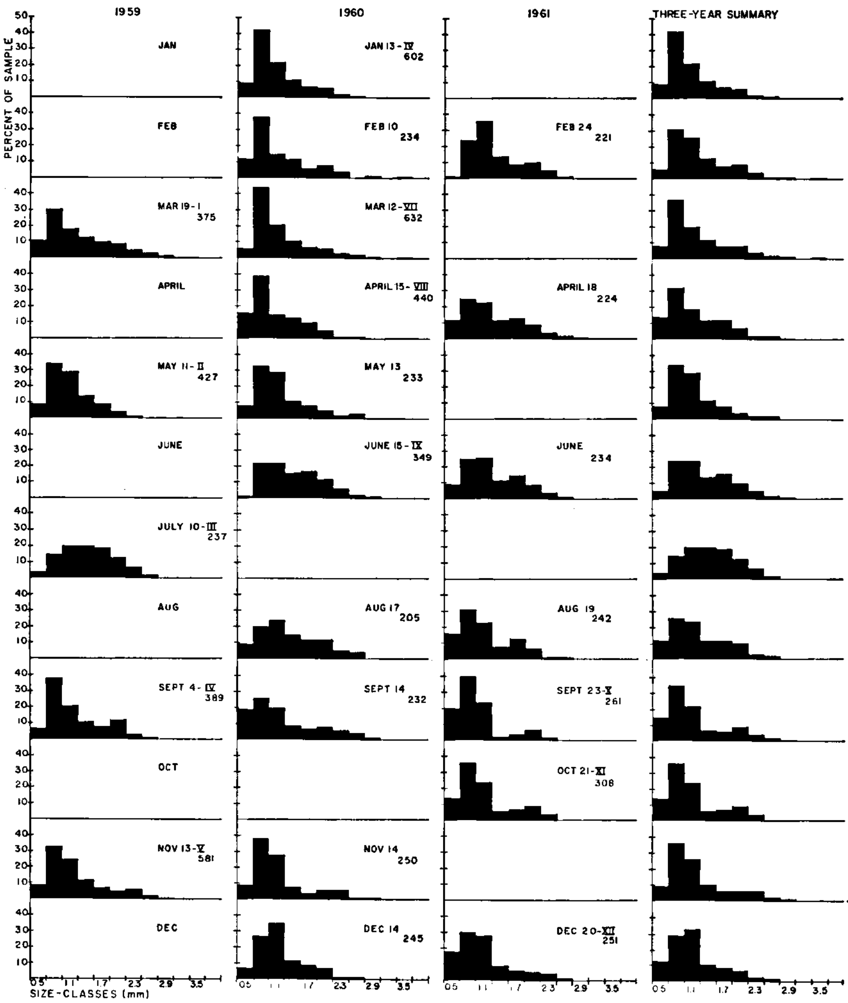


FIGURE 47. Size-class frequency distributions of *L. cistula* (March 1959—December 1961). The first three columns show these distributions in 1959, 1960, and 1961; column four represents a summary of the frequency distributions for the three-year period. Where the same month was sampled more than once, the summary distribution represents the mean for that particular month over the three years. Collection date and number of individuals measured in each sample are indicated, as well as the numbers of the quadrat samples.

The mean dry weight biomass of the species in the low, center, and high quadrats was 71.7, 2,096.8, and 144.4 mg/quadrat, or 1,790, 52,420, and 3,610 mg/m^2. At the center level the weight ranged from 362.7 mg in Quadrat XII to 3,601.9 mg in Quadrat IX (June 15, 1960).

The population structure of *L. cistula* was examined in size-class frequency distributions for 22 collections taken during the period March 1959 to December 1961. The samples were drawn from both quadrat and qualitative collections. Subsamples from the quadrat collections were secured as outlined earlier. The *L. cistula* from the qualitative collections were sampled in the following way. Fragments of *B. glandula* and *E. muricata* were selected at random from a thoroughly mixed qualitative sample of biota from the *Endocladia-Balanus* zone. All of the *L. cistula* adhering to these pieces were then sorted out until at least 200 specimens were obtained. The number of clams in such subsamples ranged from 205 to 250 individuals. The greatest shell length of each of the specimens in each sample was then measured with a calibrated ocular micrometer. The results are shown in fig. 47.

It is observed from the frequency distributions that the smallest free-living clams belonged to the 0.5 mm class, and often the samples contained close to 10% of these forms. The 0.8 and 1.1 mm size-classes most frequently dominated the populations. Usually the percentage steadily declined in the larger classes until less than 5% of the sample contained individuals larger than 2.46 mm. The two largest *L. cistula* measured, from the total of 7,172 examined, were 3.38 and 3.50 mm in shell length. These specimens were collected in the February and March, 1960 samples.

During the summer months, from June through August, a tendency was evident for a greater proportion of the 0.8 mm size-class to spread out into the 1.1 and 1.4 mm groups. Secondary modes in the larger size-classes are not very well developed. The most obvious sequence shown by these is the 1.7 mm class of April 1961, which moved to the 2.0 mm class in September and October 1961. The scattered and discontinuous occurrence of secondary modes does not permit an estimate of the growth rate for the species. For the remainder of the year a positively skewed distribution is most characteristic, suggestive of a high mortality rate and a constant addition of young clams to the adult population.

The number of *L. cistula* in Quadrat II (11,100) was the highest estimated in any of the quantitative samples. However, the dry weight of this sample (2,777.2 mg) was exceeded by the dry weights of two other samples containing smaller numbers of individuals (see Appendices I and II). This is explained by the form of the size-frequency distributions in these samples. In Quadrat II, the combined frequencies of the three smallest size-classes, 0.5—1.1 mm, make up 74% of the entire distribution, thus accounting for the large numbers of individuals. When the population size and weight relations of any particular sample are examined, it is also necessary to consider the shape of the size-class frequency distribution.

The eggs in this species are large and yolky, and are retained in the parental mantle cavity up to the juvenile stage of development. The frequency with which the hermaphroditic adults were found brooding young over the three-year period was determined by direct observation. Twenty large specimens were selected and examined in each of 31 months, from March 1959 to December 1961. The valves of each clam were parted, thus exposing the gills. The young, here defined as recognizable eggs or small clams, were teased away from the gills, counted, and measured. Occasionally a yolk-like substance was found on the ctenidia of some clams; because of the uncertain nature of this material, the few individuals with it were recorded as not brooding young. Out of 620 adults examined, 110 bore young. The young in each monthly sample included both cleaving eggs and small clams (young with calcareous valves) in roughly equal numbers. Results of the survey are shown in fig. 48.

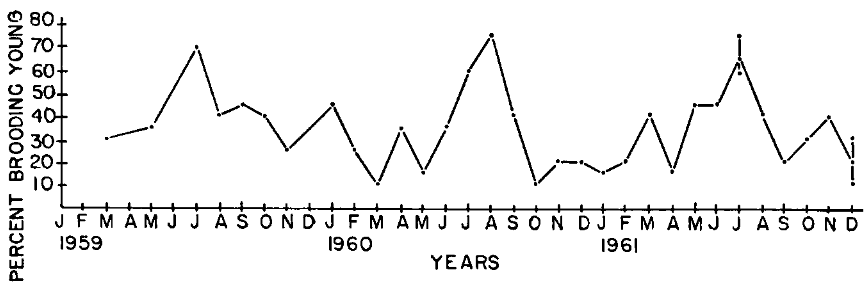


FIGURE 48. Percent of *L. cistula* brooding young during the three-year period, March 1959—December 1961. Three replicate samples each, in July and December 1961, are joined by vertical lines.

The data show the existence of an annual cyclic variation in the percent of adults brooding young. Although at least 10% of the adults in every sample bore young, this percentage rose during the summer months. The pattern is somewhat irregular, but the occurrence of young in at least 60% of the larger *L. cistula* in either July or August is apparent. Also, in each year one other peak of at least 30% was present; in 1959 a secondary peak occurred in September, in 1960 in January and again in April, and in 1961 in March and November. Samples of 20 specimens are small, but three replicate determinations each in July and December of 1961 showed that frequencies of the same order of magnitude are consistent. In these two months the greatest deviation away from the middle value did not exceed 10% in either direction.

The highest percentages of *L. cistula* carry young during the summer months when sea water temperatures in the inshore waters are relatively high (fig. 49). The average, three-year pattern of brooding in *L. cistula* shows a peak of 64% in July. For the same three-year period, the monthly mean inshore sea temperature reached a high of 14.6° C in August.

The largest young measured while still in the parent ranged from 0.53 to 0.65 mm in shell length, overlapping the size limits of the smallest size-class of clams found living outside the parents. Generally, it was found that

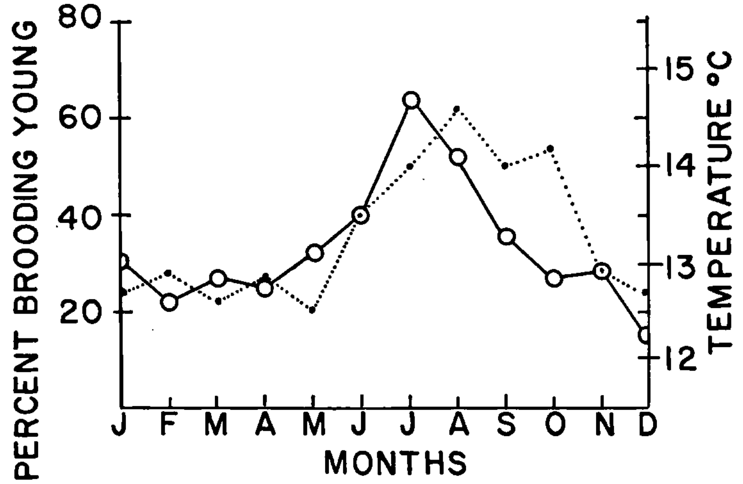


FIGURE 49. Three year monthly means of the percent of adult *L. cistula* brooding young (solid line), and inshore sea water temperatures at Pacific Grove, California (broken line), for the years 1959—1961.

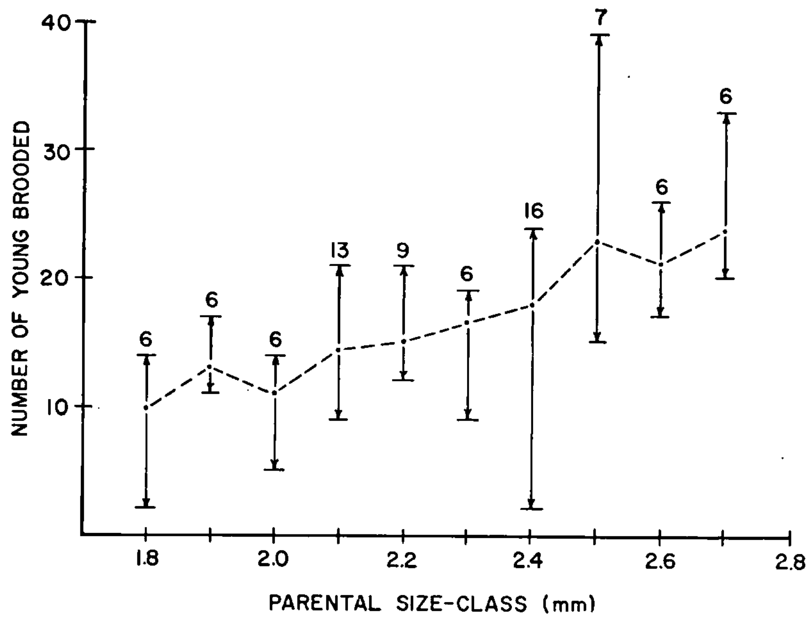


FIGURE 50. Number of young contained in those *L. cistula* found to be brooding, versus parental size. The 81 individuals examined came from various samples collected over the three-year period of study. The broken diagonal line connects the mean number of young brooded in individual parents of each size-class. The minimum and maximum number of young brooded in any single adult in each class is represented by the length of the vertical bar, and the number of specimens examined in each size-class by the figure directly above the maximum number brooded.

larger individual adults tend to produce more young than smaller ones (fig. 50). The mean number of young brooded per specimen ranged from 9.7 in the 1.8 mm size-class to 23.7 in the 2.7 mm size-class. The greatest number of young brooded by a single adult was 39, in an individual in the 2.5 mm size-class. Only two young were found in one individual in the 2.4 mm size-class; however, these two young were in the 0.5 mm size-class (the smallest size-class of the free-living clams), and it seems probable that some young had been released from this adult before it was collected.

The size of the smallest individuals brooding young is not known, but very few specimens examined in the 0.5—1.1 mm size-classes contained any young.

The stomachs of three specimens contained many green algal cells and some unidentified organic detritus. Some specimens were found with nauplius larvae on the gills, but because of their large size they probably are not captured by the ciliary-mucoid feeding mechanism of the bivalve, nor ingested and used as food. BALLANTINE & MORTON (1956) investigated the digestive action of *L. rubra* on a variety of microorganisms, and found that certain golden-brown algae were easily digested, whereas diatoms and the armoured dinoflagellate, *Peridinium*, were not affected. These workers concluded that probably ". . . . organic detritus figures largely in its food budget".

Mytilus californianus Conrad, 1837

Under favorable circumstances this species forms extensive beds of many thousands of individuals, which may dominate certain intertidal levels. Spaces formed beneath these dense aggregations provide cover and protection for a variety of other forms. This rich assemblage, the so-called *Mytilus* community, has attracted the attention of numerous biologists on the Pacific coast. For example, several aspects of the natural history of *M. californianus* were investigated by STOHLER (1930), FOX (1936), WHEDON (1936), YOUNG (1941, 1945), and COE (1944, 1948); ecological succession in the association was observed for one year by HEWATT (1935); and MACGINITIE (1939) carried out studies on the *Mytilus* association composition and structure in different situations.

The *M. californianus* assemblage is best developed below the *Endocladia-Balanus* level, particularly in situations exposed to heavy seas. All of the specimens of *M. californianus* found at the study level were small (2—5 mm in shell length), and were taken most frequently attached to the basal branches of *E. muricata* (fig. 51).

The mean nitrogen content of three, freshly-dried specimens was 2.2 ± 0.08%. This level is calculated from the dry weight of the whole animal, including byssal threads, shell, and body.

The mean number of *M. californianus* present in the low and center samples was 225.0 and 132.3 individuals/quadrat, respectively. In the center samples the numbers ranged from zero in Quadrat III (July 10, 1959) to 521 individuals in Quadrat I (March 19, 1959). No specimens were present

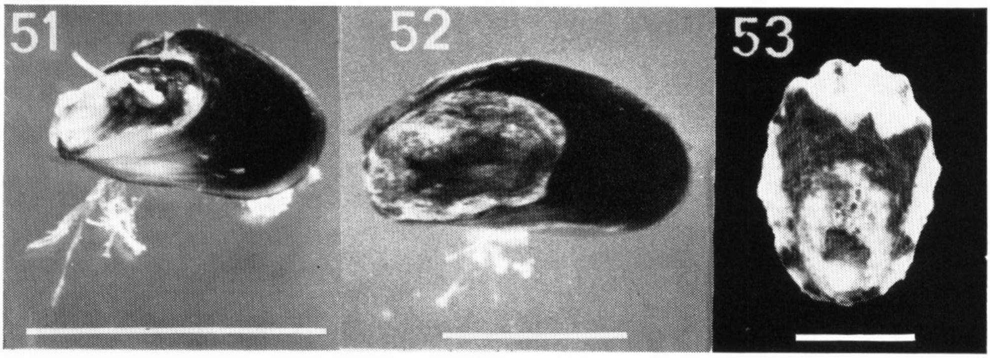


FIGURE 51. *Mytilus californianus* (February 15, 1962). The scale represents 5 mm.

FIGURE 52. *Musculus* sp. (February 14, 1962). The scale represents 2 mm.

FIGURE 53. *Acmaea digitalis* (January 26, 1962). The scale represents 5 mm.

at the upper margin of the assemblage. The mean dry weight biomass of the species in the low and center samples was 453.8 and 252.0 mg/quadrat, or 11,340 and 6,300 mg/m^2.

STOHLER (1930) studied *M. californianus* in the Monterey Bay area, and found that the production of gametes was highest in July and December. In the present study, the greatest absolute numbers of juvenile *M. californianus* were collected from the March and May quadrat samples in 1959; 521 and 495 individuals, respectively. Most of these specimens were under 2 mm in length, suggesting a heavy larval settlement in the late winter or early spring.

The stomachs of three specimens, collected at high water while feeding, contained the diatom, *Navicula* sp., the dinoflagellate, *Peridinium* sp., and unidentified plant fragments and other organic debris. COE (1948) remarked that the nutritional requirements of most bivalves (among those investigated) with a ciliary-mucoid method of feeding are satisfied by the intracellular digestion of small cells and particles, and the extracellular enzymatic breakdown of free starch and glycogen.

COE (1948) studied the growth rates of submerged *M. californianus* populations in La Jolla, California, and found that in one year the average length and dry weight attained was 56.1 mm and 25.5 g (body + shell), respectively. These measurements were more than doubled in the second year. He emphasized the high correlation between the most rapid growth rate, the abundance of diatoms and dinoflagellates, and the peak water temperatures and solar radiation levels, for a two-year period.

Musculus sp.

In the initial phase of the present study many minute ($\leq$ 1 mm), rusty-brown bivalves were tentatively identified as juvenile *Mytilus edulis*. However, in the laboratory on August 26, 1961, about 100 minute clams were seen crawling out from an adult specimen of *Musculus* sp. which measured approximately 3 mm in length. This observation revealed the true generic identity of these smallest clams. *Musculus* sp. (fig. 52) can be distinguished by its small size (rarely attaining an overall shell length of 4 mm) together with a keel-like dorsal shell margin and a ridge which extends obliquely from the posterior portion of the ventral shell margin anteriorly towards the beaks. The size and shell morphology of this species do not agree with those in any of the known forms in the eastern Pacific, Japan, or in the western Atlantic, and it appears that the population living in the *Endocladia-Balanus* association represents a new species of *Musculus* (KEEN, 1961, personal communication).

Musculus sp. was most commonly found attached to the basal branches of *Endocladia muricata* in exposed, wave-swept areas. Its distribution was very erratic; the species sometimes occurred by the hundreds in some thalli and was altogether absent from others only two to three feet away at the same level on the same rock.

A combined sample of 20 individuals, whose greatest shell length ranged from 0.7 to 3.4 mm, had a mean nitrogen content of 3.2% of the total dry weight, including shell and byssus.

Musculus sp. was present in the low, center, and high quadrat samples, with a mean occurrence at these levels of 450.5, 311.8, and 0.5 individuals/ quadrat, respectively. The irregular distribution of these forms is evident from the numbers observed in the 12 center quadrats. At this level the abundance per sample ranged from complete absence in Quadrat IV (September 4, 1959) to 2,382 in Quadrat X (September 23, 1961). It was represented by less than 10 individuals in each of four quadrat samples. In the center of the *Endocladia-Balanus* association *Musculus* sp. had a mean dry weight biomass of 73.3 mg/quadrat, or 1,830 mg/m². The species was abundant throughout the year.

In this form the young are brooded along the gills as in *Lasaea*. Two average-sized specimens (about 2 mm in length) contained 62 and 132 young, respectively. The eggs and newly-released juveniles in this species are less than half the size of those in *Lasaea*. Over the three-year period of study, some *Musculus* sp. were found brooding young in each of the 12 months of the year, except December (a single specimen examined in December did not contain young clams). It is certain that this brooding bivalve, like *L. cistula*, is a year-long breeder.

Plant fragments and unidentified organic detritus were found in the stomachs of three specimens killed while feeding at high water.

Mollusca-Gastropoda (Genus *Acmaea*)

The aspidobranch gastropods, *Acmaea digitalis*, *A. scabra*, and *A. pelta* were commonly present in the *Endocladia-Balanus* assemblage. All three of these limpets were recognized as eurytopic species by TEST (1945); *A. digitalis* and *A. scabra* often ranged for a considerable distance both above and below the study level. *Acmaea pelta,* too, demonstrated a broad vertical range in the intertidal zone, but at a somewhat lower horizon. Specimens of *Acmaea paradigitalis* and *A. limatula* were observed in the association only sporadically.

Acmaea digitalis Eschscholtz, 1833

Individuals of *A. digitalis* with a minimum shell length of about 2 mm were identified from a combination of four characters: (a) the extreme forward position of the apex of the shell, (b) the concave profile between apex and margin of the shell at the anterior end, (c) the convex profile of the shell from the apex to the posterior margin, when viewed from the side, (d) the three to four broad ribs on the upper surface, radiating posteriorly from the apex; these often produced a scalloped margin on the posterior border of the shell (fig. 53).

Average-sized specimens of *A. digitalis* (5—15 mm in shell length) were commonly found as single individuals clinging to the granitic substratum. In contrast with Shotwell's (1950) observations, in the present study the largest limpets of this species (20—25 mm) were found at higher levels, often crowded together in rock depressions or fissures. The inside surface of the empty cups in *B. glandula,* or the exposed plates making up the walls of living barnacles, especially when overgrown with *E. muricata,* provided the habitat niche for the smallest individuals observed (1—5 mm). Yonge (1962) observed that *A. digitalis* employs water movements for cleansing purposes, and related this to its exposed position in the intertidal zone.

Some of the nitrogen analyses in *A. digitalis* were performed on fresh material, but most of the specimens available were preserved in alcohol. It is then important to know if a difference in the percent nitrogen con-

Table XI. A comparison of the percent nitrogen contents in fresh and preserved individuals of *A. digitalis* of nearly comparable size. Preserved specimens belong to the various collections indicated in the key. The various size-classes indicate the greatest shell length as measured with a 0.5 mm rule.

Shell length (mm)	3.5	4.0	4.5	5.0	6.0	7.0	7.5	8.0	9.0	9.5	15.0
% N in preserved specimens	—	2.1○	2.0×	2.0○	1.9×	—	2.6•	2.0+	2.5•	1.8+	2.0•
% N in fresh specimens (Feb. 18, 1961)	2.5	—	—	1.8 2.1	2.2	1.8	—	1.9	1.9 2.3	—	1.9

Key: ○ April 9, 1960; × July 17, 1960; + Oct. 15, 1960; • Jan. 16, 1961.

tent exists between fresh and preserved animals. This was checked in *A. digitalis* by comparing the percent nitrogen levels of freshly-collected and preserved individuals covering a broad and very similar size range (table XI). A *T* test performed on the pooled means within each group gives a calculated T-statistic of 0.77, in contrast to the tabulated value, $T_{0 \cdot 05}$ (16) = 2.12. Therefore, the hypothesis that the means are the same is accepted at the 5% level of significance ($P < 0.05$). Apparently the nitrogen composition is not altered in alcohol-preserved specimens of *A. digitalis*, suggesting the feasibility of using both types of material to determine the relation between weight and percent nitrogen.

To learn the relation between weight and nitrogen content in this species, a regression analysis was performed on 15 individuals ranging in dry weight from 2.4 to 395.1 mg (fig. 54). The hypothesis of linearity was accepted ($P < 0.05$); a calculated T ratio of 1,430 was observed, as compared to the

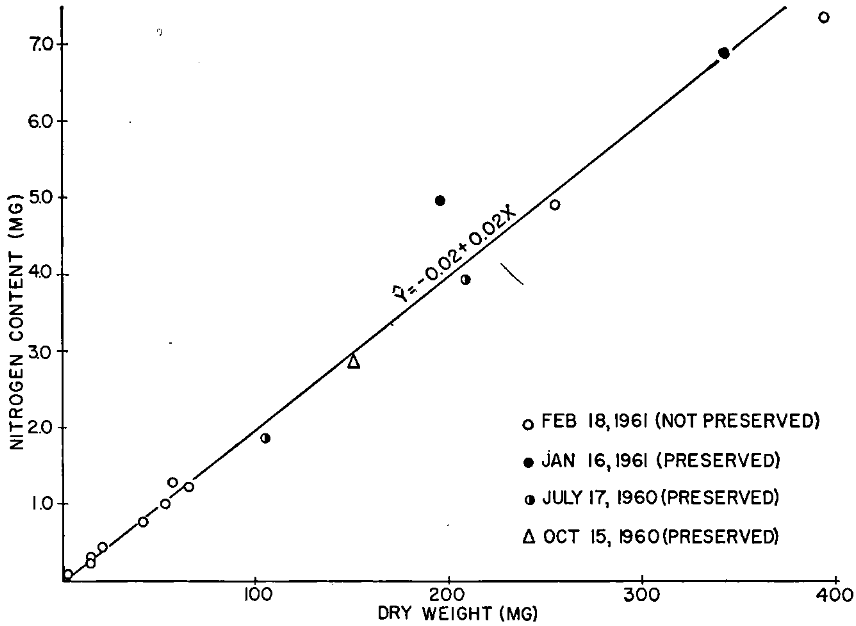


FIGURE 54. Linear relationship between nitrogen content and weight in *A. digitalis*. The four different symbols indicate the various collection dates whether the samples were preserved or fresh.

tabulated value, $T_{0 \cdot 05}(13)$ = 2.16. The prediction equation for the population is $\hat{Y} = -0.02 + 0.02\, X$, where ($\hat{Y}$) is mg nitrogen and (X) the dry weight of the whole limpet (body + shell). This species has a nitrogen content of approximately 2%, and most of the data are in close agreement with the predicted linear projection.

The percent nitrogen content of three individuals in each of four months was examined statistically to determine the degree of variability in the four seasons of the year (table XII). On the basis of the analysis of variance the hypothesis that the means are the same was rejected at the 5% level of significance. The calculated F ratio is 7.5, as compared with the tabulated value, $F_{0 \cdot 05}$ (3,8) = 4.06.

These means can be separated by TUKEY's (1949) multiple range test into a July-April-October group and a January sample ($P < 0.05$). The specimens collected in the winter demonstrated the highest mean nitrogen content, 2.5%. A group mean of 2.0% nitrogen was observed during the spring, summer, and autumn.

TABLE XII. Percent nitrogen content of *A. digitalis* in four different months of the year, April 1960—January 1961.

April		July		Oct.		Jan.	
Wt. (mg)	% N	Wt.	% N	Wt.	% N	Wt.	% N
76.9	1.9	209.1	1.9	150.3	1.9	196.0	2.5
10.4	2.0	18.0	1.9	40.6	2.0	54.9	2.5
4.2	2.1	7.2	2.0	16.6	2.4	37.1	2.6
$\overline{X}$ =	2.0		1.9		2.1		2.5

This species was taken at all levels in the assemblage with a mean occurrence of 1.5, 20.2, and 3.5 individuals/quadrat at the low, center, and upper levels. In the center samples it ranged in abundance from 2 in Quadrat IX (June 15, 1960) to 43 in Quadrat II (May 11, 1959). The mean dry weight biomass of the species, in the center of the belt, was 720.4 mg/quadrat, or 18,010 mg/m^2, with a range from 72.4 mg in Quadrat X (September 23, 1961) to 1,693.7 mg in Quadrat XI (October 21, 1961). The species was abundantly represented in the *Endocladia-Balanus* association at all seasons of the year.

The reproductive potential of *A. digitalis* was investigated over a 15-month period by FRITCHMAN (1961) at Moss Beach, San Mateo County, California. He presented strong evidence that the population of limpets in this locality spawned at least three times during 1951: in April, from the latter half of June into the first of July, and in December.

The stomach contents of three specimens, collected at high water while feeding, contained spherical, green algal cells in abundance. Most of this material was probably *Coccochloris stagnina* and *Pseudoulvella applanata.*

Acmaea scabra (Gould, 1846)

This species is most easily distinguished externally by the tuberculated appearance of the shell, as the specific name implies, and the irregularly scalloped margin (fig. 55). Internally, the pale skin of the head and lateral walls of the foot is peppered with tiny black specks.

All individuals observed at low water in the *Endocladia-Balanus* belt were clinging to the rock, their shell margins often fitting in closely with the irregularities of the underlying surface. When wetted by the rising tide they would raise their shells and begin foraging over the surface. Larger individuals of *A. scabra,* like those of *A. digitalis,* were more commonly encountered at a higher intertidal level — well up into Zone I of RICKETTS & CALVIN (1962). YONGE (1962) observed that the mantle cavity in this

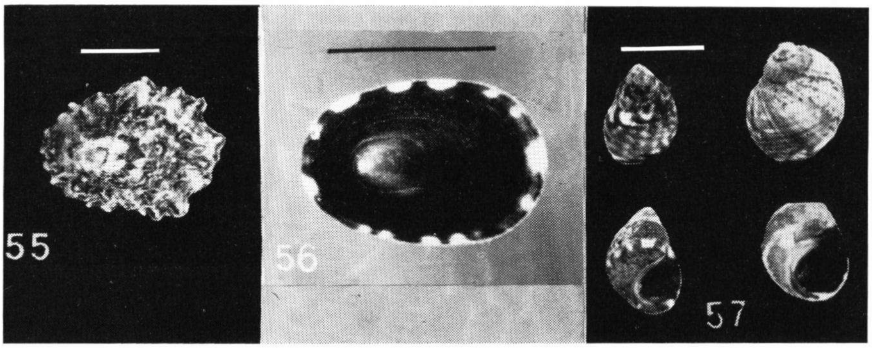


FIGURE 55. *Acmaea scabra* (January 26, 1962). The scale represents 5 mm.

FIGURE 56. *Acmaea pelta* (February 14, 1962). The scale represents 4 mm.

FIGURE 57. *Littorina scutulata*, left and *L. planaxis*, right (January 26, 1962). The scale represents 5 mm.

species, too, is kept clean mainly through the action of the strong water currents in this habitat.

The mean nitrogen content of three, freshly-collected individuals was 2.5 ± 0.24% of the dry weight.

Acmaea scabra was commonly present in the center of the study level, with a mean occurrence per quadrat of 24.2 individuals. Except in Quadrat V (November 13, 1959), which contained seven specimens, at least 10 individuals of *A. scabra* were taken in each of the center samples. The maximum number of individuals of this species tallied was 59, in Quadrat I (March 19, 1959). For the center samples the mean dry weight biomass per quadrat was 386.2 mg (or 9,655 mg/m^2), nearly half that recorded in *A. digitalis*. In the *Endocladia-Balanus* association individuals of *A. scabra* tended to be smaller than those of *A. digitalis*. A comparison of the weights of the two species illustrates this size difference. The mean individual dry weights of *A. scabra* and *A. digitalis*, from the center quadrat samples, were 15.9 and 35.7 mg, respectively. *Acmaea scabra* was present in every month over the three-year period of study.

A population of *A. scabra* living in association with *E. muricata* and *B. glandula* was studied by FRITCHMAN (1961) on the Rockaway Breakwater, San Mateo County, California. He observed three spawning periods per year in this species, viz. from late winter to early spring, early in the summer, and in the late fall. He remarked, though, that this particular population was not living under the optimal conditions for the species. Moreover, Fritchman pointed out (from an observation made at the Hopkins Marine Station) that populations occupying high levels in the summer may become reproductively inactive. A single spawning season was noted by HEWATT (1934) at the Hopkins Marine Station; ovigerous individuals appeared from late August to mid January. Also, small specimens 2—5 mm in shell length were found on the rocks during the winter months, and by the following July these had reached a length of 8—12 mm.

Green and blue-green algal cells were present in high numbers in the gut contents of three specimens collected while feeding at high water. The ingested plant cells were probably *Coccochloris stagnina* and *Pseudoulvella applanata.*

Acmaea pelta Eschscholtz, 1833

Acmaea pelta can usually be distinguished from *A. digitalis* and *A. scabra* by the smooth texture of the outer shell surface, with delicate black or brown and white spots (fig. 56). However, the color and pattern are highly variable, often rendering a positive identification of 1—2 mm forms difficult.

TEST (1945) remarked that ".... *A. pelta* is indeed so eurytopic that it is difficult to set limits to its niche. It is able to survive in all three intertidal zones, although it does not extend far into the high zone." This worker gave the intermediate intertidal zone as most characteristic for the species, and noted that the largest specimens occurred on the "large, immovable rocks of the reefs.... and on the surf-swept sea palm, *Postelsia*" [GRANT (TEST), 1938, quoted in RICKETTS & CALVIN, 1962]. Of the 13 species of *Acmaea* studied by YONGE (1962), *A. pelta* demonstrated the greatest ciliary reduction in the mantle cavity. Again, Yonge observed that the cleansing needs are satisfied by the highly turbulent waters where this species is often found. At low water in the *Endocladia-Balanus* association *A. pelta* was concealed in the empty tests of *B. glandula* or under tufts of *E. muricata,* but in the general study area it was more frequently encountered at lower levels and in more exposed situations. TEST (1945) noted that *A. pelta* probably could be found in the intertidal zone along the entire length of the California coast, and FRITCHMAN (1962) portrays its range as extending from California into the Aleutian Islands (60° N. latitude).

Of the three acmaeid species analyzed, *A. pelta* appeared to have the highest nitrogen content in terms of percent of dry weight, though data are sparse; one, freshly-collected specimen contained 3.2% nitrogen. This comparatively high level is probably due to the rather thin shell, which contributes less to the dry weight of the whole animal.

Acmaea pelta was absent in the two high quadrat samples, and had a mean occurrence of 9.0 individuals/quadrat in the 12 center collections and 20.5 at the two low-level sites. These figures make evident the higher concentration of the species at lower levels. This limpet was not taken in Quadrat X (September 23, 1961), was represented by less than 10 individuals in six other quadrats, and had a maximum occurrence in Quadrat II (May 11, 1959) of 22 individuals. Low-level and center quadrats had mean dry weight biomasses of 42.6 and 32.4 mg, respectively, equivalent to 1,060 and 810 mg/m^2. The mean dry weight of whole individuals of *A. pelta* taken in the center of the association was 3.6 mg. Although qualitative and quantitative sampling demonstrated its presence throughout the three-year study period, this limpet was the least abundant and smallest of the three characteristic acmaeid species.

FRITCHMAN (1961) found that *A. pelta,* living in association with *E. muricata* and *B. glandula* south of Rockaway Beach, San Mateo County, California, spawned 11 times over a period of 32 months. The spawnings occurred mainly in the fall, winter, and spring months.

The gut of one specimen collected at high water was packed with macerated fragments of unicellular algae.

Mollusca-Gastropoda (Genus *Littorina*)

Littorina scutulata and *L. planaxis,* the two species of periwinkles living in the upper portion of the intertidal zone along the California coast, are important members of the *Endocladia-Balanus* association. *Littorina planaxis* is a squat, robust form with a flattened and polished inner columellar lip. The shell color is often a dirty brown, while that of *L. scutulata* is usually darker in hue with a checkered pattern formed by many more or less evenly-spaced white blotches (fig. 57). These forms are quite easily distinguished when the height of the shell is greater than about 2 mm, but the identification of smaller specimens should be made with reference to a large series of each species.

Littorina scutulata Gould, 1849

Because of the vertical movements made by this species with the rising and falling tides, it is found living within a comparatively broad zone. *Littorina scutulata* tends to move upward with the advancing tide, sometimes from the lower border of the *Endocladia-Balanus* level into the splash zone. At this level the species is commonly present on the bare rock surface. At low water the greatest density is centered among thick patches of *B. glandula.* The smallest specimens were frequently found in the holdfasts of *E. muricata,* while larger forms tended to aggregate around or within the empty cups of *B. glandula.* Sometimes snails 1—2 mm in shell height were found in the sutures on the sides of solitary barnacles or in the interstices between closely growing barnacles. Experiments carried out by HEWATT (1934) demonstrated the negatively phototactic response of this species.

The nitrogen content was investigated with respect to: (a) size, (b) season, and (c) its level in preserved versus freshly-collected specimens. All statistical tests performed with data on the nitrogen contents in this study require that the relation between weight and nitrogen be normally distributed. As outlined in BENNETT & FRANKLIN (1954), a simple test of normality, with moderately large samples (n equal to or greater than 50), is to plot the data on probability paper, as a cumulative frequency polygon. If the observations show a reasonably straight-line function, then it is safe to assume that they approach normality. When treated in this manner, the 52 observations of *L. scutulata* (Appendix III), grouped into 13 classes ranging from 0.50—

0.59 to 1.70—1.79% nitrogen, give a nearly straight-line, demonstrating that the data most likely show a normal distribution.

The various sizes of *L. scutulata* encountered in this study were divided into the 10 size-classes shown below with their corresponding limits:

Class	Limits (mm)
1	0 — 1.4
2	1.5— 2.4
3	2.5— 3.4
4	3.5— 4.4
5	4.5— 5.4
6	5.5— 6.4
7	6.5— 7.4
8	7.5— 8.4
9	8.5— 9.4
10	9.5—10.4

Measurements of the greatest shell height were made with a rule showing 0.5 mm subdivisions. Nitrogen analyses were performed on 12, nonpreserved

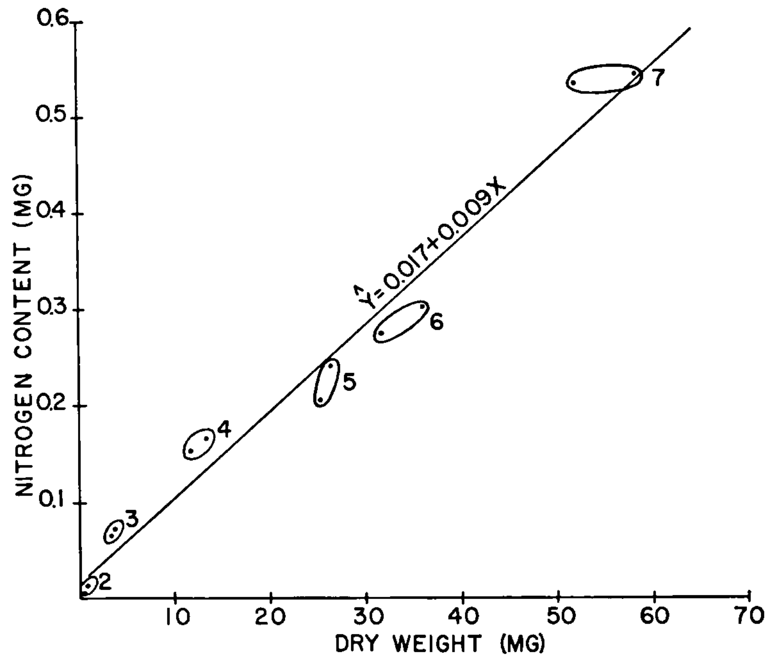


FIGURE 58. Linear relationship between dry weight and nitrogen content in freshly-collected *L. scutulata* (February 18, 1961). Specimens from size-classes 2 through 7 mm were analyzed, and the two individuals in each are encircled. The prediction equation and straight-line function are given, ($\hat{Y}$) indicating nitrogen content and (X) the dry weight.

specimens, in the 2—7 mm size-classes (fig. 58). Two individuals were selected from each size-class to show the extent of intra-class variability. Regression analysis shows a linear relationship between dry weight and nitrogen content. The hypothesis of a nonlinear relationship was rejected ($P < 0.05$) on the basis of a calculated T value of 19.6, as opposed to the tabulated value, $T_{0.05}$ (10) = 2.23. The straight-line function of this relationship is superimposed on the actual results obtained, and from the prediction equation ($\check{Y} = 0.017 + 0.009\ X$) it is possible to calculate the nitrogen content from the dry weight of any individual of the species. The two determinations in each size-class give an indication of the variability in specimens of equal size. For example, the greatest difference in the nitrogen content between two individuals in the same size-class was 0.04 mg or 17%, in the 5 mm size-class. The greatest dry weight difference between two individuals in the same class was apparent in the 7 mm size-class; this amounted to 6.4 mg or 11%.

To determine whether or not the nitrogen content of *L. scutulata* varied in the different seasons, an examination was made of the individual percent nitrogen values of six preserved specimens each, in April, July, October, and January (table XIII). The mean nitrogen content of each of these four samples was 0.89, 0.84, 0.92, and 0.83%, respectively. The analysis of variance shows that these means belong to the same population ($P < 0.05$). The null hypothesis was accepted on the basis of a calculated F ratio of 0.12, as opposed to the tabulated value, $F_{0.05}$ (6,20) = 2.60.

TABLE XIII. Percent nitrogen content and dry weight of *L. scutulata* in four different months of the year (April 1960—January 1961).

April		July		Oct.		Jan.	
Wt. (mg)	% N	Wt.	% N	Wt.	% N	Wt.	% N
46.8	0.72	23.7	0.75	65.7	0.66	57.9	0.68
36.9	0.60	21.6	0.76	34.2	0.78	57.0	0.62
19.1	0.85	8.9	0.88	33.4	0.74	54.9	0.78
7.7	0.86	8.7	0.76	23.6	0.81	38.9	0.79
3.0	1.26	6.2	0.82	6.4	1.22	19.5	0.91
1.6	1.06	2.2	1.09	5.4	1.28	8.0	1.20
$\bar{X}$ =	0.89		0.84		0.92		0.83

To determine the difference, if any, in nitrogen content between preserved and fresh material, 10 comparisons were made of the percent nitrogen in preserved and fresh specimens of comparable size groups (table XIV). Eight of the comparisons indicate that the nitrogen content is higher in fresh than in preserved specimens. Mean nitrogen contents of 0.9% and 1.2%, respectively, were calculated for the 10 preserved and 10 fresh specimens. These means appear to be significantly different ($P < 0.05$); the calculated T-statistic is 2.3, and the tabulated value, $T_{0.05}$ (18) = 2.10. Freshly collected *L. scutulata* show a nitrogen content averaging 0.3% of the dry body weight higher than alcohol-preserved specimens.

Littorina scutulata was present in every quadrat sample, with a mean occurrence of 13.0, 552.3, and 324.5 individuals/quadrat in the low, center, and high levels, respectively. In the center of the association a minimum of 95 individuals was present in Quadrat IX (June 15, 1960) and a maximum of 1,149 individuals in Quadrat IV (September 4, 1959). Also, more than 1,000 snails were present in each of Quadrats III (July 10, 1959) and XII (December 20, 1961). It is apparent from this enumeration, that at low water, *L. scutulata* is present in great numbers in the center of the *Endocladia-Balanus* assemblage. With the rising tide many of these snails move from the center of the association to a higher position in the intertidal belt. The species occurred in all samples taken at all seasons during the year. The mean dry weight biomasses of these littorines were 256.1, 3,604.4, and 1,389.4 mg/quadrat at the low, middle, and high levels, respectively. These correspond with values of 6.4, 90.1, and 34.7 gm/m^2.

Since this species was present in the association in high numbers throughout the year, it was possible to study the size-class frequency distribution in the population in the different seasons. The percent composition of the

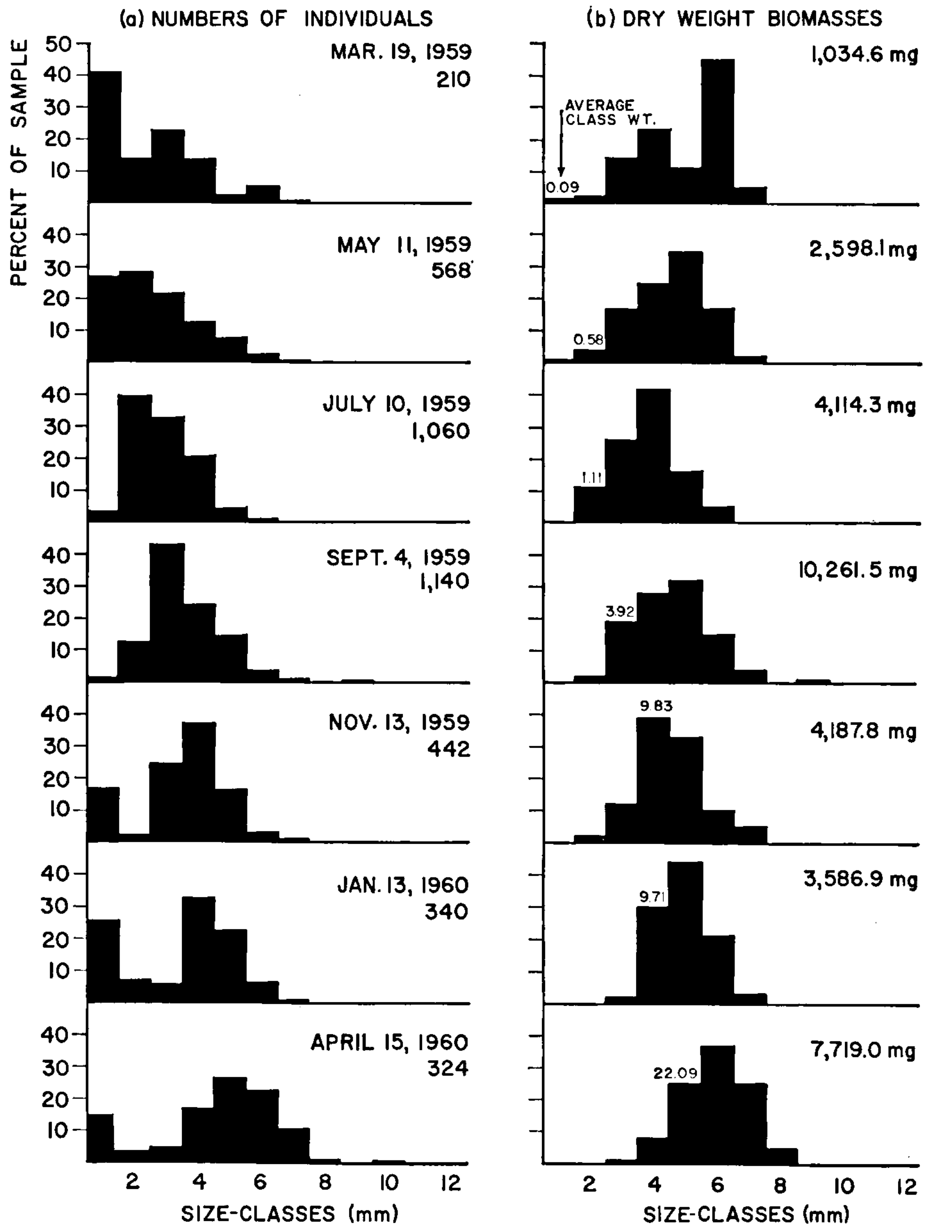
TABLE XIV. A comparison of the percent nitrogen contents in fresh and preserved individuals of *L. scutulata*. Preserved specimens belong to the two collections indicated by the symbols.

shell length (mm)	2	3	3	4	4	5	5	6	6	7
% N in preserved specimens	1.1*	1.1*	1.0°	0.8*	0.8*	0.9*	0.8°	0.8°	0.7°	0.8°
% N in fresh specimens (Feb. 18, 1961)	1.8	2.0	1.8	1.3	1.2	0.8	0.9	0.8	0.9	0.9

Key: ° March 10, 1960
* June 13, 1960

various size-classes present in each of seven quadrat samples is illustrated in fig. 59-a. Of the 12 frequency distributions examined in the center quadrats, only the seven presented in fig. 59-a show a temporal continuity. The similar form of these distributions over the 14 months suggests that they are composed of individuals from the same population. Some samples of *L. scutulata* collected on the same date, but in slightly different areas, for example from each of two rock outcroppings separated by 20 meters, or

FIGURE 59. (a) Size-class frequency distributions of the total population of *L. scutulata* from each of seven quadrat samples taken in the center of the *Endocladia-Balanus* association, shown in terms of percent of individuals in each size-class. For each sample are indicated the date of collection and the number of snails present. A bimonthly sequence is represented except for the quadrat sample collected in April 1960. (b) Corresponding dry weight biomasses for each size-class shown in (a), treated in terms of percent of total biomass for the species. The total dry weight of each sample is indicated. Also, the average weights of individuals are noted in the class corresponding to the modal class in the adjacent size frequency distribution in (a).


(a) NUMBERS OF INDIVIDUALS
(b) DRY WEIGHT BIOMASSES
PERCENT OF SAMPLE
MAR. 19, 1959
210
1,034.6 mg
AVERAGE CLASS WT.
0.09
MAY 11, 1959
568
2,598.1 mg
0.58
JULY 10, 1959
1,060
4,114.3 mg
1.11
SEPT. 4, 1959
1,140
10,261.5 mg
3.92
NOV. 13, 1959
442
4,187.8 mg
9.83
JAN. 13, 1960
340
3,586.9 mg
9.71
APRIL 15, 1960
324
7,719.0 mg
22.09
SIZE-CLASSES (mm)
SIZE-CLASSES (mm)

from slightly different intertidal levels, revealed strikingly different frequency distributions. NORTH (1954) observed similar differences in the size distribution of *L. scutulata* in three diverse environments, and noted that the difference in degree of exposure to wave action appears to be one of the influencing factors.

In March, 1959 the 1 mm size-class was very prominent, and was made up of slightly more than 40% of the 210 snails in the quadrat sample. A distinct mode was also present in the 3 mm size-class, amounting to 23% of the sample. By May the 2 mm size-class was the most prominent in the frequency distribution. A stepwise progression from the 2 mm size group in May 1959 to the 5 mm size group in April 1960 can be followed A 1 mm size-class was nearly absent in July and September, but again became established in November, January, and April.

The appearance in these frequency distributions of a high number of small snails in January, March, and May indicates active recruitment of young *L. scutulata* into the population over this period and perhaps beyond it, for Quadrat IX (not shown) collected on June 15, 1960, had a 1 mm size-class of 16%. Many small individuals were found by HEWATT (1934), especially in empty barnacle shells, during the late spring and summer. Four separate littorine egg masses were present in Quadrat H_2, collected on December 17, 1961 at the upper margin of the *Endocladia-Balanus* association. In addition, qualitative collections in October and November 1961 demonstrated the presence of this same type of egg. The egg masses collected in the high level quadrat sample were attached in the interstices on the outer walls of *B. glandula.* The transparent capsules contained eight, three, two, and one developing gastropods, each. The capsule with three snails also contained two empty pockets, representing vacated sites of development. All of the periwinkles within the capsules were at an advanced stage of development, with well-formed shells.

RICKETTS & CALVIN (1962) observed that the young of *L. scutulata* are found frequently at a lower intertidal level, notably on the rockweeds *Pelvetia* and *Fucus.* On the basis of four lines of evidence, the littorine egg masses found at the upper margin of the *Endocladia-Balanus* association are believed to be those of *L. scutulata.* First, the shell morphology of the developing snails is more similar to that of small, free-living *L. scutulata* than to that of *L. planaxis* young. Further, in the December quadrat sample, 543 specimens of *L. scutulata* of all sizes were present, down to the size of those in the egg capsules; only 46 specimens of *L. planaxis* were present, the smallest measuring 3.5 mm. Next, the egg capsules were found at the time of year when the size-frequency distributions of *L. scutulata* contain a high percentage of young forms. Finally, the few observations recorded by HEWATT (1938) indicate a pelagic larva for *L. planaxis,* rather than development in an attached egg mass (cf. *L. planaxis*).

The appearance of many small snails throughout most of the year, and egg masses from October to December suggests that *L. scutulata,* at the *Endocladia-Balanus* level, produces young in all seasons except for the summer months. While the reproductive peak of *Lasaea cistula* closely approximated the maximum shore temperatures for the year as recorded at the Hopkins Marine Station, the sample of *L. scutulata* contained the lowest fraction of young snails during this period.

With size-class frequency distributions such as those shown in fig. 59-a, it is possible to arrive at an estimate of rate of shell growth by tracing the modal progression with time. It is assumed that the snails making up the 1 mm size-class in March 1959 have grown to the 5 mm size-class position by April 1960. Since linear shell growth appears to be realized (fig. 60), the average increment in shell height for the 13-month period was 4 mm, or 0.3 mm/snail/month.

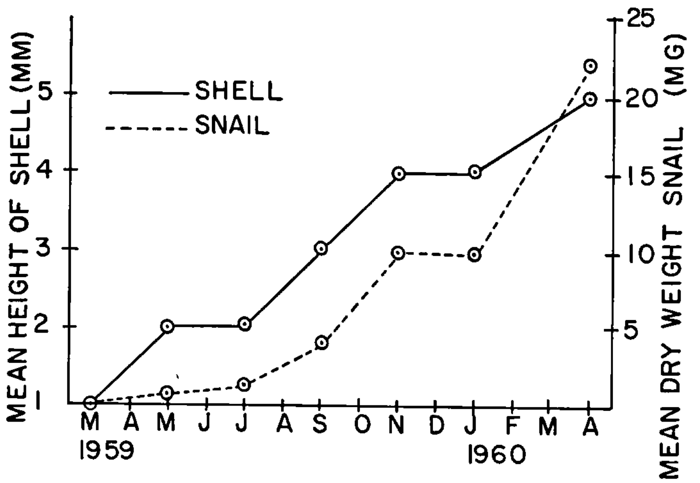


FIGURE 60. Increase in mean shell height and mean body weight of *L. scutulata* as interpreted from size-class frequency and size-class weight distributions.

Using this type of analysis it is also possible to estimate the average weight gain of the population. The same size-class distributions are indicated in fig. 59-b, but show, for each size-class, the dry weight biomasses rather than number of individuals. The mean weight of the individuals is indicated for each class which corresponds to a modal class in fig. 59-a. Both increase in mean weight and mean shell height are shown graphically in fig. 60. A decrease in growth rate is apparent in both shell height and total body weight (shell + snail) between November 1959 and January 1960. A decrease in the rate of weight gain over this same period was also observed in a laboratory population of the snail *Tegula funebralis* (cf. *T. funebralis*).

The stomachs of eight specimens contained mostly broken up and unidentified plant fragments, green and blue-green algal cells and a few specimens of the sessile diatom, *Navicula* sp. This organic material was mixed with a considerable quantity of small rock fragments, which are unavoidably ingested along with the food in the process of radular scraping. One tardigrade was also found among the stomach contents of one specimen.

Littorina planaxis Philippi, 1847

Although many small and medium-sized individuals of this species are found in the *Endocladia-Balanus* association, most of the larger adults live in the splash zone above it, where they may be found singly or in small aggregates often with the margin of the shell aperture firmly attached to the rock surface by a mucilaginous secretion. Specimens that are wetted by the rising tide begin moving about actively. HEWATT (1934) made the interesting observation that as monthly spring tides approach the animals migrate to higher levels, then back down again with the onset of intermediate and neap tides. In the *Endocladia-Balanus* association *L. planaxis* is commonly found in association with *L. scutulata* in the empty tests of *B. glandula* or more rarely as isolated individuals adhering to the granite substrate. Like *L. scutulata*, this littorine is also negatively phototactic (HEWATT, 1934).

The mean nitrogen content of three, freshly-collected snails was 1.0 ± 0.06% of the dry weight.

The mean number of *L. planaxis* in the 12 center quadrat samples was 135.3 individuals; it was absent from the quadrat samples taken low in the association, while the two quadrats at the upper-most border of the association each contained 46 individuals. The number present in the center samples was highly variable (Appendix I); a maximum of 808 was taken in Quadrat XI (October 21, 1961), while none were observed in Quadrats VI (January 13, 1960) and XII (December 20, 1961). Less than 13 specimens were present in each of five other quadrat samples. Qualitative and quantitative sampling confirmed its presence the year around.

A maximum dry weight biomass of 1,478.3 mg, equivalent to 37.0 g/m^2, was recorded in Quadrat H_2 (December 17, 1961). The mean dry weight biomasses per quadrat at the center and high levels were 418.1 and 1,310.8 mg, respectively, or 10.4 and 32.8 g/m^2. A striking difference was noted between these two levels in the mean dry weight per individual. For the 12 center quadrats this was 3.1 mg/individual, as opposed to 28.5 mg/individual at the upper margin of the association. NORTH (1954), in studying populations of *L. planaxis* in La Jolla, California, also observed a tendency for larger individuals to occupy higher levels in the upper intertidal zone.

RICKETTS & CALVIN (1962) note that, while reproduction in this species has not been studied, it is possible to find adults copulating at any time of the year, most frequently during the spring and summer months. They suggest that *L. planaxis* may deposit its eggs in an attached capsule. The observations of HEWATT (1938) contradict this suggestion. Of *L. planaxis* he says, "Great numbers of these periwinkles were copulating during the last week in March, 1932. One female discharged a mass of eggs in an aquarium April 17, 1932. Trochophores were found to be abundant in plankton samples taken May 13, 1932." MORTON (1960) points out that the modes of reproduction among species of *Littorina* are exceedingly diverse, and the present study throws no new light on the situation in *L. planaxis.*

The digestive tracts of three specimens contained essentially the same material found in *L. scutulata*: unidentified plant fragments, green and blue-green algal cells, and many inorganic particles scraped from the rock surface. *Navicula* sp. and tardigrades were not found in the specimens examined.

By periodically measuring marked individuals of *L. planaxis* in the field, over a span of a year and a quarter, NORTH (1954) found that the average growth increment of 26 specimens was 0.2 mm/month in shell height, or 0.6 mg/month in dry tissue weight.

Mollusca-other Gastropoda

Acanthina spirata (de Blainville, 1832)

HEWATT (1937) remarked that *Acanthina lapilloides* (= *A. spirata*) is always found in association with *Balanus glandula,* in situations not subject to heavy wave action. However, RICKETTS & CALVIN (1962) observed that it is characteristically present in the mussel beds where surf may be strong. In the study area it was observed as a transient and important member of the *Endocladia-Balanus* association.

Two, fresh, unpreserved specimens of *Acanthina* contained 0.92 and 0.84% nitrogen.

The numbers of individuals present in the quadrat collections represent the abundance of this form only during the low-water phase. At that time the individuals of *Acanthina* remaining in the association were relatively scarce and inactive. As noted earlier (fig. 30), this species moves up and down with the tide, and at low water most individuals are located well below the *Endocladia-Balanus* belt. At high water more *Acanthina* move up into the belt, and individuals commence to feed. The species was not found in the low or high samples, and was absent in seven of the quadrats taken from the center of the association. Where present in the center quadrats its numbers ranged from one to nine, and its mean occurrence in the 12 center quadrats was 1.4 individuals/quadrat. However, since the whelk grows to a comparatively large size, its biomass is not insignificant. In the center samples the mean dry weight biomass was 510.9 mg/quadrat (or 12.8 g/m^2) with a range, considering only samples with snails, from 163.1 to 2,925.9 mg/quadrat (= 4.1 to 73.2 g/m^2). *Acanthina* was present in the assemblage the year around, though it has been reported to migrate to lower levels during the spawning season (HEWATT, 1937).

Typically, the Muricidae are carnivorous gastropods, many of them boring into the shells of other gastropod species and bivalves (MORTON, 1960). In HEWATT's (1934, 1937) food web, illustrative of a protected region in the intertidal zone at Pacific Grove, *Acanthina* is shown to feed on *Tegula* *funebralis, Littorina scutulata*, and *Balanus glandula*. On several occasions in the present study *Acanthina* was observed feeding on *Chthamalus dalli* and *Balanus glandula*. An entrance was made into the barnacles through the opercular valves. HEWATT (1934) describes in detail how this predaceous snail employs the spine on the lip of its shell in gaining entrance to barnacles and *L. scutulata*. In this study specimens maintained in an aquarium fed on average-sized *Tegula funebralis* (12—14 mm, largest basal diameter). The live *Tegula* were held firmly by the foot of *Acanthina*, and in every instance a hole was drilled in the base of the shell just below the anal canal. Empty shells of *L. scutulata* and *L. cistula* were frequently found with similar holes, indicating that perhaps *Acanthina* also feeds in this manner on these species.

Thais emarginata (Deshayes, 1839)

Although reported by HEWATT (1937), and RICKETTS & CALVIN (1962) to be more plentiful on rock surfaces exposed to the full force of the sea, *Thais emarginata* was reasonably abundant in the semi-protected habitat of the *Endocladia-Balanus* assemblage at the Hopkins Marine Station.

The average nitrogen content of three, freshly-collected specimens of *T. emarginata* was greater than that of the other whelk, *A. spirata*, by a factor of approximately five-eighths. *Thais emarginata*, with a range in the whole dry weight of the body of 75.2 to 374.8 mg, contained 1.4 ± 0.12% nitrogen.

The specimens of *T. emarginata* taken in the quadrat collections represent only those remaining in the *Endocladia-Balanus* association during low-tide periods. Populations during these periods are deceptively small, for then most individuals, like those of *Acanthina*, are taking refuge in crevices or have moved down to lower and damper intertidal levels. The mean numbers of this form in the low and center samples from the association were 4.0 and 1.5 individuals/quadrat, respectively. However, the species was absent from six center quadrat collections and from the upper margin of the association. The individuals of *Thais* taken in the quadrat samples were relatively small. One of the larger whole specimens had a dry weight of 123.3 mg, and one of the smaller ones weighed 0.5 mg. The mean dry weight biomass of the species in the low and center samples was 262.4 and 38.8 mg/quadrat, respectively, equivalent to 6.6 and 1.0 g/m^2.

According to HEWATT (1934), whose observations were few, *T. emarginata* has a short spawning season, reaching peak activity in March. These animals lay flask-shaped capsules which contain 700—1,000 small eggs. After 15—20 days of development, and the feeding of some ciliated trochophore larvae on the remaining eggs, 8—10 surviving larvae complete development and emerge through the top of the capsule.

HEWATT'S (1934, 1937) food web studies carried out in the intertidal zone at the Hopkins Marine Station indicate that *Thais* tends to replace *Acanthina* in areas exposed to greater wave action. Hewatt found *T. emarginata* to feed on *Mytilus californianus, Balanus glandula*, and *Tetraclita* *squamosa rubescens.* According to RICKETTS & CALVIN (1962), snail eggs are also an important food item. In the present studies *Thais* was observed feeding on *B. glandula* at high water in the *Endocladia-Balanus* association. One individual made a hole in the valve of a small *M. californianus* (ca. 10 mm, greatest shell length). It is possible that *Thais* also feeds on *L. scutulata* and *L. cistula,* for many empty shells of these species contained holes made by a whelk.

Tegula funebralis (Adams, 1854)

Tegula funebralis is another transient species in the *Endocladia-Balanus* association. It is commonly found in the upper half of the rocky intertidal zone in more protected localities, where it is wetted at least once daily. The distribution of *Tegula* over the intertidal surfaces at low water is often highly contagious; most specimens are found clustered in crevices or other shaded areas, or under algae and in tide pools. Few individuals are seen on the exposed rock surface at low water. When the snails are wetted by the rising tide they begin to move out over the substrate, and thus become more evenly distributed.

Three, nonpreserved specimens of *T. funebralis* had a mean nitrogen content of 1.2 ± 0.08%.

The abundance of this species in the quadrat samples is representative only of the situation prevailing at low water periods on nearly flat surfaces. Most of the *Tegula* taken were concealed beneath the thalli of *Endocladia* and *Gigartina.* The mean occurrence of *Tegula* at the low level was 14.5 individuals/quadrat. However, one of these samples contained a single specimen, and the other 28 specimens. In the center of the *Endocladia-Balanus* association *Tegula* averaged 2.6 individuals/quadrat. However, it was absent from seven out of 12 quadrats taken here, and in the remainder the numbers ranged from one individual per quadrat, on two occasions, to 21 individuals in Quadrat VI (January 13, 1960). *Tegula* was absent from the upper margin of the association. The mean dry weight biomass of the species in the center of the association was 657.5 mg/quadrat, or 16.4 g/m^2. *Tegula* was found in the *Endocladia-Balanus* association in every month of the year, and was abundantly present in the general study area at all seasons.

On September 5, 1961, the numbers and total wet weight were determined for some *Tegula* which had moved onto the area of Quadrat VI during high water. Since the quadrat had previously been scraped clean, the surface presented to the upward-moving snails was unobstructed. At 9:30 A.M., 15 individuals were found in the quadrat, with a total wet weight of 15.57 g. When the same area was observed again after 30 minutes, an equal number of different individuals had moved into the quadrat. The upward movement of individuals outside the study plot appeared to be of the same order of magnitude. During the low water period, later in the day, no *Tegula* were observed in this quadrat.

Tegula funebralis is a browser and scraper, feeding on the encrusting algae of intertidal rock surfaces. Previous field observations made by HEWATT (1934) on the increased feeding activity of *Tegula* at night were confirmed on several occasions in this study. Three specimens of *Tegula* examined had their stomachs packed with spherical, unicellular algae (probably *Pseudoulvella applanata*) and some *Navicula* sp. Numerous rock fragments were also present in the gut. GALLI & GIESE (1959) investigated the nature of carbohydrate digestion in *T. funebralis*, and demonstrated the presence of an endogenous enzyme system capable of breaking down various ingested algae. As noted previously, *Tegula* is attacked and eaten by *Acanthina* under laboratory conditions.

Growth measurements were carried out over a period of nine months on a population of snails maintained in the laboratory. At the outset, 27 *Tegula*, ranging in size from 4.0 to 5.6 mm in greatest basal diameter of the shell, were confined in an aquarium provided with running sea water and aeration. The aquarium walls extended some distance above the surface of the water, permitting the snails to move freely between the submerged and exposed conditions. A light regime, simulating the natural day-night periods, was supplied by a 60 watt light bulb connected to an automatic timer. The aquarium was shielded with a running water bath to prevent warming. Stones with a rich film of encrusting algae were periodically supplied as a source of food. A rich algal film also developed on the sides of the aquarium after a few months.

The average wet weight per snail was determined each month for the period June 8, 1959 through March 11, 1960, excluding February, 1960, for (a) the total population, (b) the three largest individuals, and (c) the three smallest individuals (table XV). Prior to weighing, the specimens were blotted lightly with a paper towel to remove excess water. The greatest basal diameter of the shell of the largest and smallest individuals was also measured. Since there was some mortality in the population, the largest and smallest individuals selected for weighing and measuring each month do not necessarily represent the same individuals over the nine-month period.

In fig. 61 the curves indicating average gain in wet weight in the three size groups all show a seasonal decline in rate of growth for the period October through January. This tendency was noted also in *L. scutulata* from November through January of the same year (fig. 60).

The weight-gain increment for the entire population was 16.7 mg (wet weight)/snail/month. The greatest increase in basal diameter of the shell was from 5.6 to 9.8 mm, and the least from 4.0 to 5.6 mm. The rather high variation in growth rates among individuals maintained in the laboratory points up the desirability of examining large numbers of individuals under natural conditions. Further, since the respiratory rate in *Tegula funebralis* is dependent on such factors as exposure, salinity, temperature, and nutritional state (MCLEAN, 1962), it is pertinent to define as closely as possible the set of environmental conditions to which a particular population is subjected.

TABLE XV. Monthly measurements of wet weight (in mg) and size range (in mm) of surviving *T. funebralis* maintained in a laboratory aquarium over the period June, 1959 through March, 1960.

Date	Number of snails	Average individual wt. for whole population	Individual wt. of 3 largest snails	Average wt. of 3 largest snails	Individual wt. of 3 smallest snails	Average wt. of 3 smallest snails	Size range (greatest basal diameter) for whole population
June 8, 1959	27	27.0	41.7	38.4	17.8	18.5	4.0—5.6
			40.4		18.4		
			33.0		19.4		
July 8, 1959	27	35.6	57.9	53.1	15.1	19.3	4.5—5.8
			54.9		21.0		
			46.4		21.9		
Aug. 7, 1959	26	53.8	84.6	83.4	26.0	28.7	4.5—6.5
			83.2		29.4		
			82.5		30.6		
Sept. 7, 1959	26	75.8	125.0	118.8	33.2	38.6	5.2—7.0
			122.8		36.2		
			108.6		46.4		
Oct. 7, 1959	26	108.1	182.8	173.6	46.9	50.5	5.2—8.5
			174.8		52.2		
			163.2		52.4		
Nov. 10, 1959	24	127.5	231.0	214.3	47.5	55.1	5.2—8.9
			210.9		53.6		
			200.9		64.1		
Dec. 8, 1959	22	136.4	248.6	240.1	47.6	57.9	5.5—8.9
			235.9		54.9		
			235.9		71.2		
Jan 8, 1960	21	145.2	286.5	264.7	47.5	61.0	5.5—9.1
			257.1		57.7		
			250.6		77.7		
			342.0	296.7	43.6	82.2	5.6—9.8
Mar. 11, 1960	15	177.3	280.0		95.0		
			268.0		108.0		

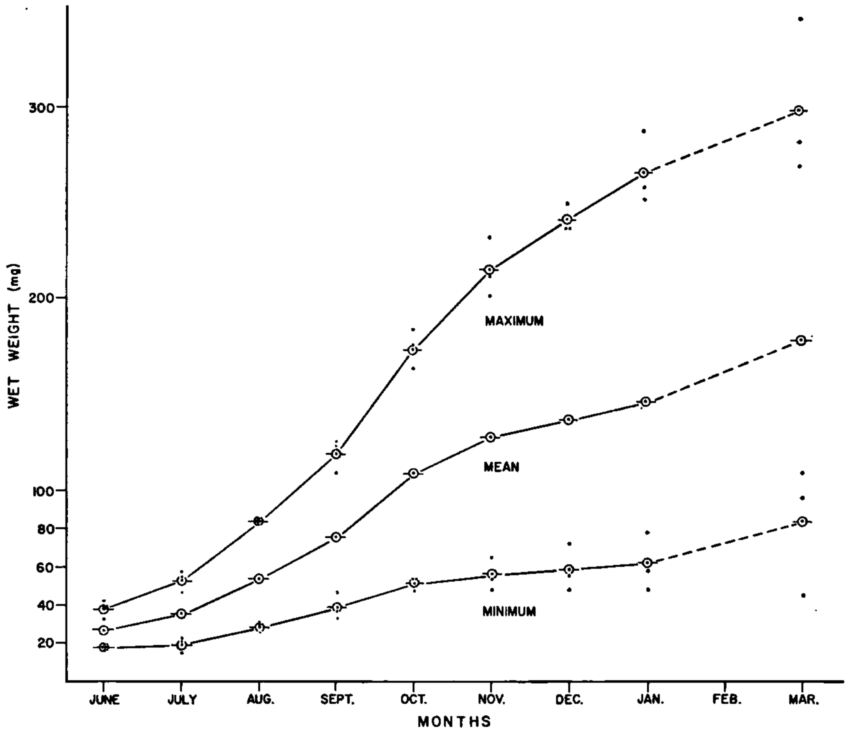


FIGURE 61. Increase in weight of *T. funebralis*, 1959—60. The curves indicate the average weight gain per individual for the entire population (mean), for the three smallest specimens (minimum), and for the three largest specimens (maximum). Individual weight measurements are indicated by dots for the largest and smallest size groups.

Mollusca-Amphineura

Cyanoplax dentiens (Gould, 1846)

Minute specimens of *Cyanoplax dentiens* (fig. 62) were the only amphineurans present in the *Endocladia-Balanus* assemblage. Apparently this species is more abundant to the north (e.g., Puget Sound), while Monterey lies near its southern-most limit of distribution (RICKETTS & CALVIN, 1962). Specimens taken in the present study usually ranged in length from 3 to 6 mm, and were distinguished by the granular texture of the valves, their six posteriorly directed beaks, and the presence of eight slits on the ventral surface of the anterior valve.

Cyanoplax, a secretive form, is found only in well-concealed places. Specimens were often attached to the interiors of the empty cups of *B. glandula* or to the exterior walls where these were completely obscured by the overgrowth of *E. muricata.*

The nitrogen content of one preserved specimen was 4.2% of the body weight.

No specimens were present in the high quadrats or in five of the center quadrat samples. There was a mean frequency of 2.2 individuals/quadrat at the center level and 4.5 individuals/quadrat in the low-level samples. A maximum of 12 specimens was present in Quadrat III (July 10, 1959).

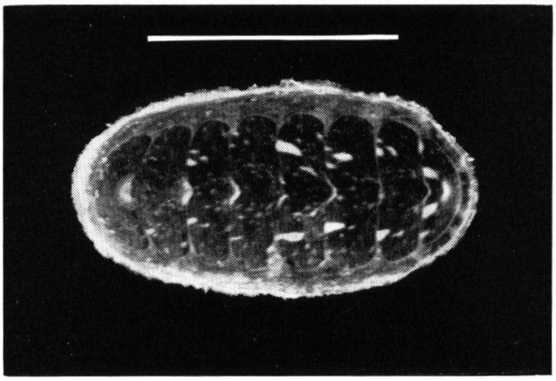


FIGURE 62. *Cyanoplax dentiens* (February 5, 1962). The scale represents 4 mm.

Cyanoplax was not detected in the month of May over the three-year period of study. Its mean dry weight biomass in the low and center levels was 13.8 and 5.4 mg/quadrat, respectively, equivalent to 345 and 140 mg/m^2.

Food habits were not studied, but presumably the animals use the radula to scrape the algal film from rocks and barnacle shells.

Arthropoda-Crustacea, Cirripedia
Balanus glandula Darwin, 1854

Balanus glandula is able to survive on relatively hard and stable surfaces in a variety of diverse habitats. It is found at the middle and upper intertidal levels on protected and exposed coasts, in relatively stagnant bays, and on protected piles (RICKETTS & CALVIN, 1962). While living at a rather high position in the intertidal belt, the time these barnacles are wetted by sea water is more than some workers have supposed. For example, of this species RICKETTS & CALVIN (1962) stated, "At extreme high tide, sometimes for only a few hours in a week, each animal throws open its operculum and rhythmically sweeps the water. . . .". However, the duration of submergence, in the center of the *Endocladia-Balanus* association where the most dense populations of *B. glandula* were encountered, amounted to 27% of the total time over a period of six months, or about 45 hrs/week.

An estimate of the organic matter in samples of *B. glandula* was determined from the nitrogen content (a) in barnacles of different sizes, (b) in barnacles collected in the different seasons of the year, and (c) in a comparison of fresh and preserved barnacle samples.

A sample of 15 specimens, ranging in individual dry weights from 24.3 to 1,211.4 mg, was examined to determine the relation between nitrogen content and body weight (including the calcareous test). A regression analysis shows a linear relationship between nitrogen content and weight, regardless of body size (fig. 63). A calculated *T*-statistic of 20.5 was obtained, as opposed to the tabulated value, $T_{0.05}$ (13) $= 2.16$ ($P < 0.05$). From the prediction equation, $\hat{Y} = 0.24+0.0045X$, where ($\hat{Y}$) is mg nitrogen and (X) is dry weight in mg, one may determine, for example, that barnacles weighing 100 and 1,000 mg will contain 0.69 and 4.74 mg nitrogen, respectively.

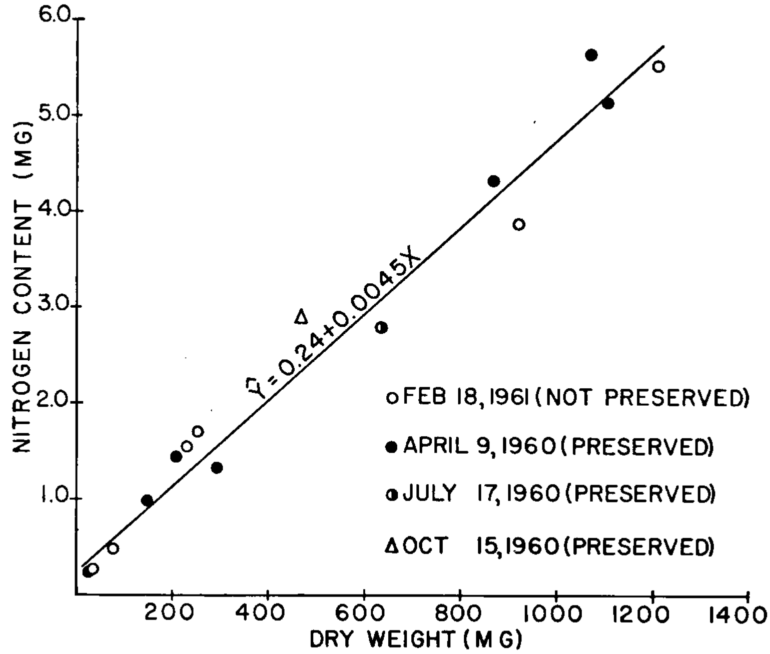


FIGURE 63. Linear relationship between dry weight (whole animal, including calcareous test) and nitrogen content in *B. glandula*. The prediction equation lies along the regression line for these data. The dates when the different individuals were taken from the field are indicated by the various symbols employed. The February specimens represent freshly-collected material; all other specimens were preserved in alcohol.

The percent nitrogen content in three preserved individuals from each of the months, April, July, October, and January are given in table XVI. The nitrogen levels in the four seasons were very similar. The most aberrant value was that of a 24.5 mg individual in January with a nitrogen content of 1.2%. The analysis of variance shows the hypothesis of equal means to be valid ($P < 0.05$). *A* calculated *F* ratio of 0.66 was obtained, as opposed to the tabulated value, $F_{0.05}$ (3,8) $= 4.07$.

Table XVII shows a comparison between the percent nitrogen content in fresh and preserved individuals. Size-classes are designated by the midpoint value of the greatest basal diameter. A visual estimate of the basal diameter was made in the field by matching the base of each specimen with a closely placed size-class scale. Where the bases were obscured or noticeably reduced in size, a common condition in dense populations, the size was determined from an estimate of the basal diameter in combination with the height. The five size-classes used for *B. glandula* in the present study are listed below with their accompanying limits:

Class	Limits (mm)
< 1	0— 0.9
2	1.0— 2.9
4	3.0— 5.9
8	6.0—11.9
16	12.0—Up

TABLE XVI. Percent nitrogen content of *B. glandula* in four different months of the year, April 1960—January 1961.

April		July		Oct.		Jan.	
Wt. (mg)	% N	Wt.	% N	Wt.	% N	Wt.	% N
867.4	0.5	633.1	0.4	993.1	0.4	985.0	0.5
207.3	0.7	60.4	0.8	463.0	0.6	320.2	0.8
23.5	0.6	20.1	0.7	19.8	0.8	24.5	1.2
$\bar{X}$ =	0.6		0.6		0.6		0.8

TABLE XVII. A comparison of the percent nitrogen contents in fresh and preserved individuals of *B. glandula*.

Size-classes (basal diameter, mm)	4	4	8	8	16	16
% N in preserved specimens (April 9, 1960)	0.65	0.84	0.66	0.70	0.52	0.46
% N in fresh specimens (Feb. 18, 1961)	0.69	0.67	0.66	0.68	0.42	0.46

No apparent trend was evident in the nitrogen contents of fresh and preserved specimens. The percent nitrogen content was equal in two comparisons, higher in preserved than in fresh for three comparisons, and higher in fresh than in preserved for one comparison. A *T* test indicates that there is no significant difference between these two groups ($P < 0.05$). The calculated *T*-statistic is 0.57, and the tabulated value, $T_{0.05}$ (10) = 2.23.

In summary, no significant differences were found in the percent nitrogen content of small and large specimens, in specimens taken at different seasons of the year, or between preserved and freshly-collected material.

As discussed under sampling methods, the barnacle census in quadrats was carried out subsequent to cropping of the larger algae. The total number of barnacles tabulated in some quadrat samples was minimal, because in dense clusters small individuals were hidden from view by over-towering adults.

Balanus glandula was abundant at all levels in the *Endocladia-Balanus* assemblage. In some regions a population was uniformly distributed over an area of about 6 m^2, whereas a highly patchy occurrence was characteristic of other surfaces. The mean frequency of individuals present at the low, middle, and high levels was 279.5, 473.0, and 367.0/quadrat, respectively. A minimum of 35 *B. glandula* was present in Quadrat IX (June 15, 1960) and a maximum of 1,619 in Quadrat X (September 23, 1961). More than 1,000 individuals were present in each of Quadrats XI (October 21, 1961) and XII (December 20, 1961). The mean frequency of *B. glandula* in the center of the association was 11,820 individuals/m^2. This figure is in reasonable agreement with HEWATT's (1937) observation of 15,305 individuals/m^2 (actually 14,004 individuals/yard^2) for a typical sample in the same habitat. A maximum of 40,480 individuals/m^2 was calculated for Quadrat X and a minimum of 880 individuals/m^2 for Quadrat IX.

The dry weight of *B. glandula* was computed from the actual average weights of five specimens in each of the five size-classes (table XVIII). These barnacles were measured in the association, according to regular procedure, and then removed and dried to a constant weight. To arrive at the total weight of *B. glandula* per quadrat the number of individuals in each size-class was tallied and then multiplied by the average size-class weight, as shown in table XVIII, and the weights for all size-classes totalled.

From this estimate, the mean dry weight of *B. glandula* in the center quadrat samples was 84,000 mg/quadrat, or 2.1 kg/m^2. A minimum weight of 8,300 mg was observed in Quadrat IX and a maximum weight of 187,000 mg in Quadrat IV (September 4, 1959). The mean dry weight in the two high quadrat samples was 78,000 mg. A weight estimate was not made for the two low-level samples.

Size-frequency distributions for the barnacles sampled in quadrats make it possible to view the changes in population structure through the three-year period of study. Figure 64 shows these distributions for the 12 center quadrat samples, in chronological sequence. The 8 mm size-class was noticeably dominant in the March, April, and May quadrat samples. Summer and early fall are marked by the recruitment of younger individuals, which appeared a bit earlier in 1960 than in 1959. The growth of this group, and the decline of older individuals, can be followed roughly in the distributions for later months.

Other observations indicate that settling of larvae may occur during a large part of the year. Between March 31 and April 21, 1959, two *B. glandula* that had settled in the center of the association attained a basal diameter of 1.24 and 1.09 mm, a size at which they could be seen easily in the field. This suggests that the smallest individuals observed on the rock surfaces in July 1959 had probably settled out of the plankton three or four weeks previously. Further, the three quadrats collected in September, October, and December, 1961 were again examined in March, 1962. At the latter date these sample areas contained, respectively, 1,798, 67, and 8 newly-settled *B. glandula.* All of the specimens measured belonged to the < 1, 2, and 4 mm size-classes. This preponderance of small individuals demonstrates a heavy larval settlement in the fall, and perhaps a small amount in the winter.

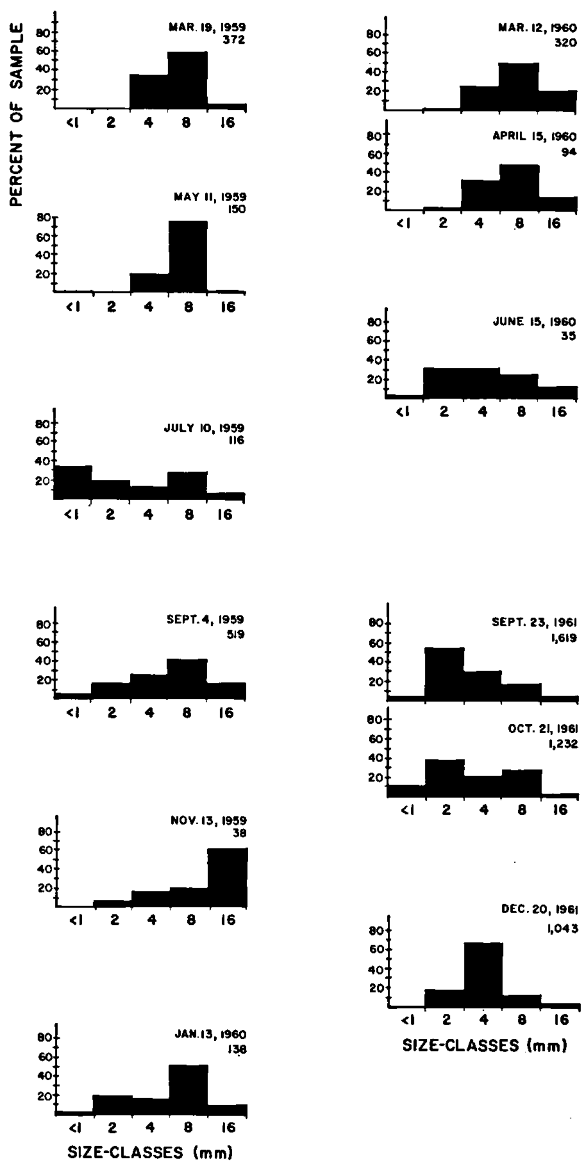


FIGURE 64. Size-class frequency distributions of *B. glandula* for the 12 center quadrat samples. The date of collection and number of individuals in each sample are indicated.

HEWATT (1935), in his succession studies in a mussel bed at the Hopkins Marine Station, observed a settlement of 95 *B. glandula* between the end

TABLE XVIII. An estimate of the average dry weights of five size-classes in *B. glandula,* as determined from freshly-collected specimens taken from the center of the *Endocladia-Balanus* association, December 29, 1961.

Size-classes (basal diameter, mm)	< 1	2	4	8	16
	0.6	4.5	35.3	451.4	1,525.5
Individual wt. (mg)	0.4	2.7	37.6	228.6	1,588.5
	0.3	5.1	61.5	329.7	1,068.1
	0.5	4.4	27.4	356.6	1,111.6
	0.5	2.5	50.9	358.4	1,044.6
	$\overline{X}$ = 0.5	3.8	42.5	344.9	1,267.7

of November and the first of March, and 2,031 from the first of March into the latter half of April. Settling in the mid and late fall was also evident in his studies. One may conclude from these observations, and those presented above, that at Pacific Grove the reproductive season in *B. glandula* is prolonged and not very clear cut, with minimal activity in the winter months, and possibly with poorly separated peaks in spring and fall. BARNES & BARNES (1956) investigated the reproductive period in *B. glandula* at La Jolla, California and at Ladysmith, Puget Sound. These workers found the more southern forms to release larvae from January through May, and those in the north from March through May, and again in August and September.

The gut contents of three *B. glandula,* killed while actually feeding, contained mostly unidentified organic debris, some fragments of blue-green algae, and a few broken-up diatom frustules.

Some indication of the rate of secondary net production in *B. glandula* was gained from calculations based on determinations of the number and size of individuals to reappear in the quadrat sites after the initial census. At the termination of all field work, a final survey was made on March 12—14, 1962, of the new populations which had re-established themselves on the denuded quadrat sample sites. The rate of net production as estimated by this procedure, is minimal, for losses through attrition, predation, and other reasons are not taken into account. However, the size-classes present, and the number of barnacles in each, are a result of larval settlement and growth, minus natural losses. The estimates are shown in table XIX. The time available for larval settlement and growth depend on the date at which the particular quadrat was originally cleared, and ranged from three to 36 months. It is at once obvious that regrowth differs greatly in the different quadrat sites. For example, in Quadrats III and XII, respectively, a weight gain of 0.6 and 1 g/m^2/month was estimated, in contrast to 270 g/m^2/month in Quadrat X. Some of these divergent values are explained by the time of year the quadrat sites were available for larval settlement. For example, Quadrat X, which demonstrated the greatest weight gain per unit time, was available for the heavy larval settlement which occurred in the early fall of 1961. In contrast, Quadrats XI and XII, where weight gains were small, were available for recruitment only from October 21, 1961 and December 20,

TABLE XIX. Resettlement and growth of the barnacle *B. glandula* on denuded quadrat sites in the center of the *Endocladia-Balanus* association.

Quadrat No.	Date quadrat site was originally cleared	Date of second examination of quadrat site	Time for resettlement and growth (months)	Number of individuals of each size-class counted in second examination					Calculated total dry weight biomass for all size-classes		Calculated average rate of gain in dry weight biomass (net production rate)	
				< 1	2	4	8	16	mg/400 cm^2	g/m^2	g/m^2/month	mg/m^2/day
I	Mar. 19, 1959	Mar. 12, 1962	36	7	126	556	113	3	67,000	1,700	47	1,600
II	May 11, 1959	Mar. 12, 1962	34	0	5	17	6	0	2,800	70	2	70
III	July 10, 1959	Mar. 12, 1962	32	0	11	10	1	0	810	20	0.6	20
IV	Sept. 4, 1959	Mar. 12, 1962	30	0	24	61	19	1	10,500	262	9	300
V	Nov. 13, 1959	Mar. 12, 1962	28	2	19	92	10	0	7,400	180	6	200
VI	Jan. 13, 1960	Mar. 13, 1962	26	1	40	101	2	0	5,100	130	5	200
VII	Mar. 12, 1960	Mar. 13, 1962	24	0	11	45	37	5	21,000	520	22	730
VIII	April 15, 1960	Mar. 13, 1962	23	2	15	64	14	0	7,600	190	8	300
IX	June 15, 1960	Mar. 13, 1962	21	1	11	23	1	0	1,360	34	2	50
X	Sept. 23, 1961	Mar. 14, 1962	6	2	269	1,527	0	0	66,000	1,600	270	9,000
XI	Oct. 21, 1961	Mar. 13, 1962	5	10	51	6	0	0	450	11	2	80
XII	Dec. 20, 1961	Mar. 13, 1962	3	2	4	2	0	0	101	3	1	30

1961 through March 14, 1962, during the season of minimal reproduction. It should also be pointed out that Quadrat X was located at a low elevation, viz., 3.9 ft above MLLW. Other variations noted (e.g. the poor repopulation of center Quadrats III and IX) are not so readily explained.

CONNELL (1959) pointed out that the distribution and abundance of *B. balanoides* in Scotland is controlled by (a) the extent of settlement, which is affected by conditions in the plankton and on the shore, (b) early mortality subsequent to settlement, which is affected largely by physical factors, and (c) such biological interactions as crowding and predation, occurring later in life. Connell also indicated that crowding and predation are most strongly felt at lower intertidal levels.

Genus *Chthamalus*

Chthamalus dalli and *C. microtretus* are small barnacles living together in the *Endocladia-Balanus* association in the study area. CORNWALL (1937) showed that the two forms are morphologically distinct, and described *C. microtretus* as a separate species (fig. 65). Externally, the aperture in *C. microtretus* is small and tilted to one side, and the parapet is highly crenulated where it fuses with the basal plate. Both species are found either attached to the granite substrate, often in small depressions or concavities in the rock surface, or on the plates of *B. glandula.* During most of the period of study the two species were not distinguished. The mean abundance of the genus in the center of the association was 111.7 individuals/quadrat, and mean calculated dry weight biomass of 1,100 mg/quadrat, or 28 g/m^2.

Chthamalus dalli Pilsbry, 1916

Four, freshly-collected specimens of *C. dalli* had a mean nitrogen content of 1.2 $\pm$ 0.38% of the body weight. The largest individual analyzed, weighing 92.4 mg, was taken from the upper border of the *Endocladia-Balanus* association, and contained 0.7% nitrogen.

Although the two species of *Chthamalus* were not counted separately until Quadrat X, the preserved quantitative and qualitative samples showed the presence of *C. dalli* throughout the three-year period of study. It was found in the *Endocladia-Balanus* association at the low, center, and high levels. In the last three center samples, where the two species were distinguished, *C. dalli* ranged in abundance from 18 individuals in Quadrat XI (October 21, 1961) to 240 individuals in Quadrat XII (November 18, 1961). The mean occurrence of the species in Quadrats X, XI, and XII was 140 individuals/quadrat. There were 46 and 33 individuals in Quadrats H_1 and H_2, respectively.

A size-class system, similar to that used for *B. glandula,* was established for making weight estimates. The size-classes are listed below with their corresponding limits:

Class	Limits (mm)
<1	0— 0.9
2	1.0— 2.9
4	3.0— 5.9
8	6.0—11.9

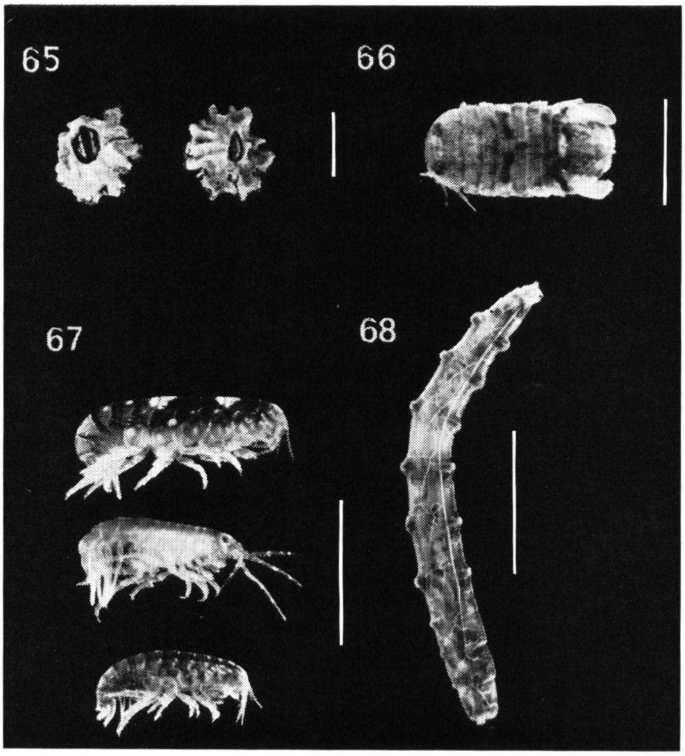


FIGURE 65. *Chthamalus dalli,* left and *C. microtretus,* right (January 26, 1962). The scale represents 5 mm.

FIGURE 66. *Dynamenella glabra* (February 14, 1962). The scale represents 3 mm.

FIGURE 67. Amphipods of the *Endocladia-Balanus* association (February 14, 1962). *Hyale* sp., at the top of the photograph, exhibits a characteristic mottling. *Pontogeneia* sp. is shown in the center and *Allorchestes ptilocerus* at the bottom. The scale represents 4 mm.

FIGURE 68. *Limonia marmorata* (February 14, 1962). The scale represents 4 mm.

Since this species is considerably smaller than *B. glandula,* the 16 mm size-class was not used. An estimate of the total dry weight of *C. dalli* in a quadrat sample was made by multiplying the number of individuals in each size-class by the average dry weight of individuals of the size-class, and then totalling the calculated weights of all the size-classes present. The average size-class weight was obtained from actual size-weight determinations, which are shown in table XX.

TABLE XX. An estimate of the average dry weights of three size-classes in *C. dalli*, as determined from freshly-collected specimens taken from the center of the *Endocladia-Balanus* association, December 29, 1961.

Size-classes (basal diameter, mm)	< 1	2	4
	0.6	4.5	42.2
Individual wt. (mg)	0.2	7.5	29.9
	0.2	7.1	57.0
	0.7	7.4	46.1
	0.2	5.5	41.0
	$\overline{X} = 0.4$	6.4	43.2

These calculations show maximum and minimum weights in the center samples of 4,600 and 230 mg.

The three quadrat sites collected in September, October, and December, 1961, were again examined in March, 1962, and showed, respectively, 249, 13, and 10 individuals of *C. dalli*. These barnacles had settled on the cleared quadrat sites sometime between the initial and final census. The large number present in the September sample, with an abrupt decline in October and December, suggest that heaviest larval settlement occurred during the late summer or early fall. Quadrat I, collected in March, 1959, contained 492 *Chthamalus* spp. belonging to the <1 mm size-class. This smallest size-class contained 70% of the total number of *Chthamalus* spp. present in the sample. About half of the sample was composed of *C. dalli*.

Stomach analyses were made on two specimens collected February 11, 1962 at high water while feeding. The greatest fraction of ingested material consisted of comparatively large fragments of broken-up algae and unidentified organic detritus. Both specimens examined had ingested many diatoms; some of those identified were *Asterionella* sp., *Navicula* sp., *Coscinodiscus* sp., *Chaetoceros* sp., and *Thalassiothrix* sp. Some *Peridinium* sp. were present in both, and one specimen contained a single radiolarian.

The rate of secondary net production in *C. dalli* was crudely estimated from the calculated dry weight biomasses of this species which accrued in Quadrats I—XII between the time of the initial collections and the final census on March 12—14, 1962 (table XXI). Estimates were arrived at using the same methods described earlier for *B. glandula*. *Chthamalus dalli* demonstrated a maximum net production of nearly 190 mg/m^2/day in Quadrat X, and a minimum net production in Quadrat XI of about 5 mg/m^2/day. A production of at least 20 mg/m^2/day was common. Roughly, the net production of *C. dalli* in the denuded quadrats was only about 5% of that of *B. glandula*. However, the production of *C. dalli* in different quadrats shows much less variability in this species than in *B. glandula*. The two highest production rates in both *C. dalli* and *B. glandula* occurred in the same quadrats, viz. I and X; the production figures for the two species were both noticeably low in Quadrat III.

Chthamalus microtretus Cornwall, 1937

The mean nitrogen content of six, freshly-collected specimens was 1.0 ± 0.16% of the body weight. Analyses were carried out on animals ranging in dry weight from 6.5 to 37.8 mg. The three largest specimens were collected near the upper border of the association, and actually exceeded the size commonly found in the center of the *Endocladia-Balanus* belt.

Chthamalus microtretus, where distinguished from *C. dalli* (in Quadrats X, XI, XII, H_1, and H_2), was present in all but one sample, and in every instance was less abundant than *C. dalli.* Among these five samples a maximum of 28 individuals was present in Quadrat H_1 (November 18, 1961) and none occurred in Quadrat XI (October 21, 1961). The average abundance of this species in center Quadrats X, XI, and XII was 3.0 individuals/quadrat. Its average abundance in the two, high-level samples was 17.0 individuals/quadrat. A re-examination of preserved samples from other quadrats, where a census was made of the genus only, showed the presence of *C. microtretus* in most cases. Qualitative samples confirmed the presence of this barnacle in every month during the period of study.

A final re-examination, March 12—14, 1963, of the 12 previously denuded center quadrat sites showed the establishment of both *C. dalli* and *C. microtretus* in all but two samples. *Chthamalus microtretus* was absent in Quadrats XI and XII. In the final census a grand total of 999 individuals of *C. dalli* and 348 of *C. microtretus* was present in the 12 sample plots. This amounts to an average abundance per quadrat of 83.2 individuals of *C. dalli* and 29.0 individuals of *C. microtretus.*

The procedure devised for dry weight biomass estimates in the other barnacles was also employed for *C. microtretus.* Where *C. microtretus* was distinguished from *C. dalli* in the center and high-level samples, it demonstrated mean dry weight biomasses of 32 and 583 mg/quadrat, respectively, or 0.8 and 14.6 g/m^2. A maximum biomass of 1,060 mg was observed in Quadrat H_1 (November 18, 1961).

After six months, September, 1961 to March, 1962, 26 *C. microtretus* in the <1 mm size-class were observed in Quadrat X. Also, 70% of the *Chthamalus* spp. present in Quadrat I (March 19, 1959) belonged to the <1 mm size-class. Approximately one half of the *Chthamalus* spp. in this quadrat were *C. microtretus.* These two observations show that some larvae are released in the September to March period. None of the samples examined in the summer contained appreciable numbers in the <1 mm size-class.

The stomach contents were examined in two animals collected at high water. The ingested food in this species was essentially the same as that found in *C. dalli,* viz., broken-up algal tissues, unidentified organic detritus, and diatoms.

TABLE XXI. Resettlement and growth of the barnacle *C. dalli* on denuded quadrat sites in the center of the *Endocladia-Balanus* association.

Quadrat No.	Date quadrat site was originally cleared	Date of second examination of quadrat site	Time for resettlement and growth (months)	Number of individuals of each size-class counted in second examination			Calculated total dry weight biomass for all size-classes		Calculated average rate of gain in dry weight biomass (net production rate)	
				< 1	2	4	mg/400 cm^2	mg/m^2	mg/m^2/month	mg/m^2/day
I	Mar. 19, 1959	Mar. 12, 1962	36	6	165	99	5,300	130,000	3,600	120
II	May 11, 1959	Mar. 12, 1962	34	0	11	11	540	14,000	410	14
III	July 10, 1959	Mar. 12, 1962	32	9	32	2	290	7,300	230	8
IV	Sept. 4, 1959	Mar. 12, 1962	30	2	51	14	940	24,000	800	27
V	Nov. 13, 1959	Mar. 12, 1962	28	10	65	6	680	17,000	610	20
VI	Jan. 13, 1960	Mar. 13, 1962	26	6	66	42	2,240	56,000	2,200	73
VII	Mar. 12, 1960	Mar. 13, 1962	24	2	16	27	1,270	31,800	1,320	44
VIII	April 15, 1960	Mar. 13, 1962	23	17	23	7	460	12,000	520	17
IX	June 15, 1960	Mar. 13, 1962	21	7	20	11	610	15,000	720	24
X	Sept. 23, 1961	Mar. 14, 1962	6	54	193	2	1,340	33,500	5,590	186
XI	Oct. 21, 1961	Mar. 13, 1962	5	9	4	0	29	720	140	5
XII	Dec. 20, 1961	Mar. 13, 1962	3	6	4	0	28	700	230	8

The rate of secondary net production in *C. microtretus* was crudely estimated from the calculated dry weight of barnacle regrowth in previously denuded quadrat sites (table XXII). The procedures followed are those outlined for *C. dalli*. The highest weight gain observed was 2,200 mg/m²/month in Quadrat X, the next to the lowest in elevation of the center quadrats; this was also the most productive plot for regrowth of *C. dalli* and *B. glandula*.

Arthropoda-Crustacea, Isopoda
Dynamenella glabra (Richardson, 1899)

Dynamenella glabra, a member of the suborder Flabellifera, was the only species of isopod commonly found in the *Endocladia-Balanus* assemblage (fig. 66), though *Excirolana chiltoni* was present in *Endocladia* tufts in areas subject to abrasive action from loose sand and shell debris. The fluted posterior portion of the telson is a unique feature of *D. glabra*. Grossly, the body color is a dull lead color, but reveals on closer inspection a delicate pattern of multi-colored pigmentation.

Dynamenella moves actively up and down the branchlets of *Endocladia* when submerged at high water. When disturbed these isopods can cling to the branchlets tenaciously, otherwise they move quite freely through the tuft. At times some individuals become free of the tuft and swim for short distances. A few *Dynamenella* were taken with a plankton net from the water passing over the *Endocladia-Balanus* association.

A combined sample of 20, freshly-collected individuals with a total dry weight of 12.9 mg had a nitrogen content of 5.1%. The animals making up the sample ranged in body length from 1.4 to 3.0 mm.

All of the low and center quadrats contained individuals of *Dynamenella*, but the species was absent in the two quadrat samples collected at the upper border of the association. The average number of isopods at the low and center levels was 44.0 and 125.2 individuals/quadrat, respectively. A maximum of 290 individuals was present in Quadrat X (September 23, 1961) and a minimum of one in Quadrat IV (September 4, 1959). The mean dry weight biomasses for the low and center samples were 5.8 and 28.0 mg/quadrat, respectively, or 140 and 700 mg/m². Qualitative collections confirmed the presence of the species in every month of the year.

Large yolky eggs are produced in this species, and young are retained in the brood pouch between thorax and oöstegites, as in other isopods. The average number of developing young retained in six females was 16. One of these animals contained 28 eggs, and another 10, well-formed juveniles. Some brooding females were present in every month of the year for the three-year period, 1959—61.

Frequently *Dynamenella* was observed feeding along the surface of the branchlets on *Endocladia*. The gut contents in three specimens consisted of green and blue-green algae and the sessile diatom *Navicula* sp. Apparently

TABLE XXII. Resettlement and growth of the barnacle *C. microtretus* on denuded quadrat sites in the center of the *Endocladia-Balanus* association.

Quadrat No.	Date quadrat site was originally cleared	Date of second examination of quadrat site	Time for resettlement and growth (months)	Number of individuals of each size-class counted in second examination			Calculated total dry weight biomass for all size-classes		Calculated average rate of gain in dry weight biomass (net production rate)	
				< 1	2	4	$mg/400\ cm^2$	mg/m^2	$mg/m^2/mo.$	$mg/m^2/day$
I	Mar. 19, 1959	Mar. 12, 1962	36	3	37	2	320	8,000	220	7
II	May 11, 1959	Mar. 12, 1962	34	1	6	16	730	18,000	530	18
III	July 10, 1959	Mar. 12, 1962	32	0	1	0	6	200	6	0.2
IV	Sept. 4, 1959	Mar. 12, 1962	30	28	25	15	820	20,000	670	22
V	Nov. 13, 1959	Mar. 12, 1962	28	20	20	0	136	3,400	120	4
VI	Jan. 13, 1960	Mar. 13, 1962	26	9	31	7	500	12,000	460	15
VII	Mar. 12, 1960	Mar. 13, 1962	24	4	5	2	120	3,000	120	4
VIII	April 15, 1960	Mar. 13, 1962	23	1	4	0	26	650	28	0.9
IX	June 15, 1960	Mar. 13, 1962	21	3	3	1	64	1,600	76	2.5
X	Sept. 23, 1961	Mar. 14, 1962	6	26	78	0	510	13,000	2,200	73
XI	Oct. 21, 1961	Mar. 13, 1962	5	0	0	0	0	0	0	0
XII	Dec. 20, 1961	Mar. 13, 1962	3	0	0	0	0	0	0	0

this isopod feeds on the rich, epiphytic growth encrusting the branchlets of *Endocladia.*

Arthropoda-Crustacea, Amphipoda

Three species of talitrid amphipods were present in the *Endocladia-Balanus* association (fig. 67). The three species can be distinguished in the field by a few easily-recognized characters, presented below in a dichotomous key.

1a. Body color uniformly green; eyes red .... *Pontogeneia* sp.
1b. Body color otherwise; eyes red or brown 2
2a. Body color uniformly ruddy; eyes red and relatively small (diameter of eye $^1/_3$ length of head); 2nd antennae highly plumose .... *Allorchestes ptilocerus.*
2b. Body color variable, with chocolate-brown, grass-green, and cream mottling; eyes brownish, markedly ovate and relatively large (diameter of eye ½ length of head); 2nd antennae with few, short hairs .. *Hyale* sp.

Pontogeneia sp. occurred in only two of the 12 center quadrat samples, and is not dealt with below.

Allorchestes ptilocerus Derzhavin, 1937

Bousfield (personal communication) noted two unique features in the external anatomy of *A. ptilocerus,* viz., the second antennae are moderately plumose and the dactyls of peraeopods 1—5 are pectinate. Also, he pointed out that heretofore the species was not known to occur outside the Sea of Japan and east Asiatic coast. In the *Endocladia-Balanus* association *A. ptilocerus* was found only in the tufts of *Endocladia.*

A combined sample of five, freshly-collected specimens contained 9.2% nitrogen.

The mean abundance of *A. ptilocerus* in the low and center samples was 79.5 and 5.3 individuals/quadrat, respectively. The species was not found at the upper margin of the association. The distribution of the population suggests that the amphipod may be even more numerous at a still lower intertidal level. *Allorchestes ptilocerus* was absent from six of the mid-level samples and demonstrated a maximum abundance of 21 individuals in Quadrat I (March 19, 1959). A mean dry weight biomass of 2.5 mg/quadrat, or 62 mg/m^2, was observed in the center of the association. Some specimens of *A. ptilocerus* were present in quantitative or qualitative samples in all months of the year except April and May.

The gut contents in two specimens of *A. ptilocerus* revealed fragments of *Endocladia* as well as some green algal cells apparently from the epiphytic algal film encrusting the branchlets of *Endocladia.*

Hyale sp.

The following features of *Hyale* sp. have led Bousfield (personal communication) to conclude that it is a new species. (a) Antennae short, stout and of few flagellar segments, (b) uropods very short and stout, (c) in the male the palm of segment six of gnathopod two is much longer than the posterior border, and (d) relatively small size attained at maturity.

At low water *Hyale* sp. was present most commonly in the tufts of *Endocladia*. When the amphipods were wetted by the rising tide they became very active, often moving away from the alga and into the apertures of live or dead *B. glandula*. Some individuals were observed moving on different barnacles for extended periods during the high tide.

A combined sample of five, freshly-collected specimens contained 9.5% nitrogen.

Hyale sp. was present at all levels in the *Endocladia-Balanus* association, and seasonally was absent only in April. The mean numbers present in the low, center, and high samples were 36.5, 14.4, and 10.0 individuals/quadrat, respectively. In the center of the association, *Hyale* sp. was nearly three times as abundant as *Allorchestes*. Here it was absent from only three quadrat samples, and numbers ranged as high as 46 individuals in Quadrat VII (March 12, 1960). A mean dry weight biomass of 6.2 mg/quadrat, or 160 mg/m^2, was observed in the center of the assemblage.

Three specimens, examined on three different occasions, showed large quantities of *Endocladia* in the gut. Pigmented spines were observed on many of the algal fragments, indicating that they were removed from the surface of the thallus. The gut of a fourth specimen contained only green algal cells.

Arthropoda-Crustacea, Decapoda

Pachygrapsus crassipes Randall, 1839

Juveniles of this crab were present in the *Endocladia-Balanus* association, taking refuge in the tufts of *Endocladia*. Occasionally adults were found in the association, but for brief periods only. As HIATT (1948) observed, the greatest proportion of adults live in crevices and tide pools, and not on the open rock surfaces where *Endocladia* and *B. glandula* flourish.

A combined sample of three, preserved juveniles, weighing 35.2 mg, contained 6.0% nitrogen.

The young crabs were found in one low quadrat sample and in six of the center quadrat samples, with a mean occurrence of 1.5 individuals/quadrat at the mid-level. A mean dry weight biomass of 13.3 mg/quadrat, or 332 mg/m^2, was observed at this level. On a seasonal basis, *Pachygrapsus* was absent from all samples for five consecutive months from August through December, and was also absent in February. No other species typical of the *Endocladia-Balanus* association was absent for such a prolonged period of time. As noted previously, female *Pachygrapsus* in this region carry eggs between March and August, and thus provide a supply of offspring which are present mainly during this period.

HIATT (1948) was successful in rearing two young crabs in the laboratory, from the megalops to the sixth crab stage, spanning a period of slightly over three months. During this time the crabs thrived on a diet of the polychaetous annelid *Mercierella enigmatica*. Hiatt also listed *Endocladia* among the important foods of the adult. The carapace width of the two young crabs maintained in the laboratory increased in one individual from 3.7 to 10.1 mm in 99 days, and in the other from 3.6 to 8.4 mm in a period of 103 days. The majority of juvenile *Pachygrapsus* found in the *Endocladia-Balanus* association had a carapace width of 4—5 mm, indicating a recent settlement from the plankton.

Arthropoda-Insecta

Diaulota densissima Casey, 1894

Diaulota densissima, a staphylinid beetle, is a small and highly motile species characteristic of the *Endocladia-Balanus* association. It is a common species in the upper intertidal zone of central California, and has been observed by the author as far south as Coronado, California. On March 26, 1962, many individuals were observed moving about actively among barnacles on the Coronado Beach jetty. When the *Endocladia-Balanus* level is not being wetted, the beetle moves about probing into the apertures of *B. glandula* and the fissures and spaces between closely situated individuals. The numbers moving over the surface seem to be greater on sunny days with little wind than at other times. At high water some *Diaulota* were found to take refuge in the air spaces formed between the basal plate of *B. glandula* and the underlying substrate.

Since the individual dry weight of the adult is so small, a combined sample of 199 specimens was prepared for nitrogen analysis. The sample consisted of preserved specimens pooled from five different collections, with a total dry weight of 15.6 mg. The nitrogen content of this sample was 12.1% of the dry weight.

Diaulota was present at the mid and high levels only, with a mean frequency of 42.7 and 20.0 individuals/quadrat, respectively. It occurred in every center quadrat, the numbers ranging from seven in Quadrat VI (January 13, 1960) to 93 in Quadrat VII (March 12, 1960). The species was abundantly represented at all seasons. At the upper margin of the association there were 39 individuals present in Quadrat H_2 (December 17, 1961) and a single specimen in Quadrat H_1 (November 18, 1961). A mean dry weight biomass of 3.6 mg/quadrat, or 90 mg/m^2, was observed in the mid-level samples.

Diaulota lays large yolky eggs which were found wedged in the spaces between closely-growing *B. glandula*. In the intermittently submerged habitat of the *Endocladia-Balanus* association the eggs develop into larvae which hatch out and maintain themselves on the exposed rock surface. After an undetermined period they develop into adult beetles. Eggs were found in February, March, April, May, October, and December; of these, one in March and nine in October had developed to well-formed larvae, ready to hatch. Two adults were observed copulating at low water on March 4,1962.

The above observations suggest that *Diaulota* reproduces at least during the autumn, winter, and spring months.

The gut contents of four specimens were examined. One specimen contained numerous *Navicula* sp. and other unidentified organic material. The alimentary canals of three beetles were tightly packed with green and blue-green algal cells, probably *Pseudoulvella* and *Coccochloris*, respectively, and one of these animals contained a fragment of a multicellular alga, perhaps *Gigartina* sp. In addition to gut examinations, some feeding experiments were carried out on the exposed rock surface at low water. Fresh tissues of *B. glandula* and *A. digitalis* were smeared over the substrate near a spot where many *Diaulota* were actively moving about. Within five minutes three larvae were feeding on *B. glandula* and three adults on *A. digitalis*. These feeding observations show that *Diaulota* is more or less omnivorous.

Tipulid larvae

Crane fly larvae of at least two species were present in the *Endocladia-Balanus* association. Only one of these, *Limonia marmorata* (Osten Sacken), was determined (fig. 68); the others remain unidentified. The larvae were most often present in the dense holdfasts of *Endocladia*, but occasionally appeared in the larger spaces formed between crowded individuals of *B. glandula*, or in the empty cups of this barnacle. Tipulid larvae were most active when submerged by the high tide. Adult flies were numerous in the *Endocladia-Balanus* association at low water, flying and walking over it during the day and at night.

A mean nitrogen content of 12.4% was obtained for a combined sample of four, freshly-collected larvae.

Tipulid larvae were present throughout the *Endocladia-Balanus* association, but had their greatest abundance at the center level. Their mean occurrence at the low, center, and high levels was 2.0, 14.9, and 3.0 individuals/quadrat, respectively. The larvae were absent from only Quadrat L_2 (February 3, 1959), and had a maximum occurrence of 40 individuals in Quadrat X (September 23, 1961). A mean dry weight biomass of 12.6 mg/quadrat, or 315 mg/m^2, was recorded for the mid-level samples. Both larvae and adults were present in all seasons, which suggests year-round reproduction for the group.

In the *Endocladia-Balanus* association the fly larvae are herbivorous; their food intake consisting almost exclusively of *Endocladia*. Specimens collected at high water on several different occasions had their guts filled with large fragments of this alga. The gut of one larva contained, in addition to the algal fragments, a single valve of *Lasaea*, which may well have been ingested incidentally. The adult flies were observed to feed indiscriminately on the dead tissues of such animals as *B. glandula* and *Acmaea* spp. From these observations the larvae have been classified as herbivores and the adults as carnivorous scavengers.

Arthropoda-Acarina, Tromibidiformes

Among tromibidiform mites, the family Halacaridae represents a successful marine group (see NEWELL, in LIGHT et al., 1957). Two genera in this family, *Rhombognathus* sp. and *Agauopsis* sp. were present in the *Endocladia-Balanus* assemblage. Newell examined the species taken and concluded that both are probably new. *Rhombognathus* sp., the smallest of the two, is barely visible to the unaided eye. For this reason its absolute abundance was not adequately assessed by the sampling methods used in this study, and only its presence or absence was tabulated (Appendix I). It was most numerous in the center and at the upper border of the association. A third tromibidiform mite present in the association, *Pronematus* sp., is a member of a typically terrestrial group.

Agauopsis sp.

Adults of this species are large enough (usually between 0.5—1.0 mm long) to be observed readily with a pocket lens. However, a census of the individuals present in a quadrat sample is difficult because these mites lurk within the holdfast spaces of *Endocladia* and in groups of two or three in the crevices between the shells of closely-growing *B. glandula*. The absolute numbers recorded per quadrat are thus minimal.

Preserved individuals totalling 419, from five different collections, were combined into one sample weighing 4.9 mg for a nitrogen determination. A nitrogen content of 12.4% was obtained, a value close to that noted for the insects analyzed in this study.

Agauopsis sp. was present in every quadrat sample, and occurred in greatest abundance at the center level. Its mean frequency at the low, center, and high levels, was 3.5, 40.2, and 6.0 individuals/quadrat, respectively. In the center of the association, a minimum of one individual was present in Quadrat IV (September 4, 1959) and a maximum of 160 in Quadrat X (September 23, 1961). At the same level a mean dry weight biomass of 0.5 mg/quadrat, or about 10 mg/m^2, was observed. Because of the small size and secretive habits of this mite, these figures are undoubtedly minimal. Qualitative sampling confirmed the presence of the species in every month of the year.

Members of the subfamily Halicarinae, to which *Agauopsis* belongs, are said to be predaceous (NEWELL, 1947). *Agauopsis* sp. was maintained in the laboratory, and offered a variety of foods thought likely to occur in its natural diet: harpacticoid copepods, smaller mite species, worms, fine pieces of barnacle flesh, and mat-forming algae. All of these organisms were refused as food.

Arthropoda-Acarina, other mites

In addition to the three tromibidiform species, five other mites in two different suborders were present. The suborder Mesostigmata was represented by one undetermined species of the family Parasitidae, and by another species which was not determined even to family. The suborder Sarcoptiformes was represented by *Suidasia* sp., *Hyadesia* sp., and *Ameronothrus* sp. Only the largest and most common of these species are given separate consideration here.

Suborder Mesostigmata, one species of undetermined family

This ruddy-colored form was never observed alive in the *Endocladia-Balanus* association, but was found as loose individuals in the preserved samples. Mites living in close association with *B. glandula* usually remain attached to these barnacles after preservation. It is possible this species lives in the tufts of *Endocladia*, where it would be more easily detached by preservation and handling.

A mean frequency of 18.3 and 1.5 individuals/quadrat was observed in the center and high-level samples, respectively. The mite was absent from Quadrat I (March 19, 1959), and had a maximum abundance of 52 individuals in Quadrat XI (October 21, 1961). In the mid-level samples the mean dry weight biomass of the species was 0.2 mg/quadrat, or 5 mg/m^2. Some specimens were present in every month of the year over the three-year period of study.

Suidasia sp.

The spaces formed between the appressed outer walls of closely-growing *B. glandula* afforded a common refuge for *Suidasia* sp. This species was also found where spaces were present between the basis of *B. glandula* and the substrate, and in pits in the outer walls of some of the older barnacles. The mites were never observed to leave these hidden positions.

Suidasia sp. was present in all the center and high quadrat samples. In three collections special care was taken to enumerate all of the individuals present in the material removed from the quadrat site. A total of 209 and 1,115 mites was present in Quadrats X (September 23, 1961) and XI (October 21, 1961), respectively. Quadrat H_1 (November 18, 1961) contained 242 individuals. Since the denuded rock surfaces of the study plots could not be adequately examined, these counts must be considered as minimal. The dry weight biomasses of this species in Quadrats X, XI, and H_1 were 0.8, 3.7, and 0.3 mg, respectively. *Suidasia* sp. was present in samples taken in every month of the year over the three-year period of study.

A well-developed film of the various mat-forming algae was usually found where the mites were present. On two occasions living *Suidasia* sp. were examined in this algal mat with a binocular dissecting microscope, but were not observed to feed on the plant material.

SPACE AND FOOD RELATIONS IN THE ASSOCIATION

To understand some of the functional interrelationships in a natural assemblage of organisms it is necessary to consider the constituent species together, both in terms of the spatial arrangement of their respective habitat niches, and in terms of the food relations existing between the different forms. In this section, spatial arrangement and food relations of the species occurring in the *Endocladia-Balanus* association are considered primarily from a qualitative standpoint.

Spatial arrangement of species

The spatial arrangement of organisms has been investigated in some of the major environments of the sea. For example, the spatial relations of species in shallow-bottom subtidal communities has received a great deal of attention (PETERSEN, 1918; GISLÉN, 1929 & 1930; SPÄRCK, 1933; THORSON, 1934, 1957; and others), and more recently considerable progress has been made in learning the spatial distribution of plankton species (BEKLEMISHEV, 1957; HARDY, 1958). The intertidal zone is readily accessible to this type of investigation, and accordingly the literature on this area is voluminous. Some of the most important contributions, apropos of the present study, are those giving information on habitat niches in the high intertidal belt of the English coast (COLMAN, 1940; MORTON, 1954; MORTON et al., 1957).

It is a difficult matter to portray in two or even three dimensions the spatial arrangement of the various species making up the *Endocladia-Balanus* association, for the structural properties of the assemblage are not static. Diel, seasonal, and tide-related changes in the presence and arrangement of species are constantly taking place. Some of these changes were noted earlier, under "Qualitative composition of the association, Transient species." Further, the plankton and detritus made available to the association at high water form integral components of the assemblage once or twice daily. The present discussion is restricted largely to the benthos; detailed consideration of the pelagic component is deferred to the next section, "Quantitative community composition".

The benthic component of the association includes some truly sessile forms, some animals which move relatively short distances, and some which are highly active. The spatial arrangement of some of the larger and more conspicuous of these species is shown pictorially in fig. 69-a, while the more intimate habitat niches of smaller forms are indicated in the magnified views of *B. glandula* (fig. 69-b), and a thallus of *E. muricata* (fig. 69-c).

Endocladia muricata, Gigartina agardhii, Filicrisia franciscana, B. glandula, Chthamalus dalli, and *C. microtretus* are the more numerous sessile species. The algae and barnacles are commonly distributed over the rock surface in small clumps. For example, a closely-spaced cluster of *B. glandula* may form the substrate for a tuft of *E. muricata*, and a sprig of *F. franciscana* can often be found attached to the holdfast of the alga. Aggregates of the sedentary species demonstrated an apparently random distribution in the center of the *Endocladia-Balanus* association.

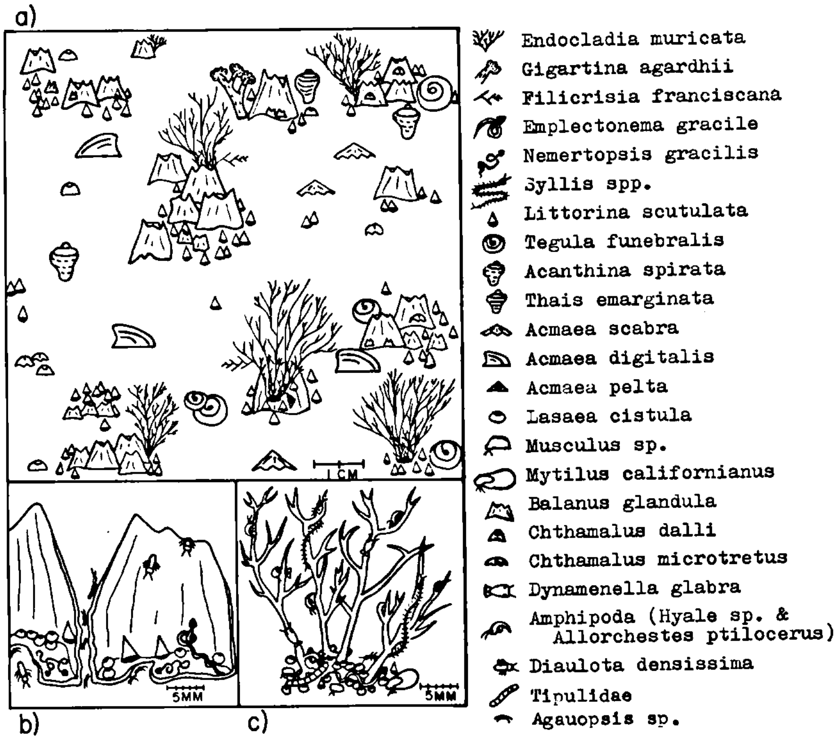


FIGURE 69. Spatial arrangement of some of the more common benthic species in the *Endocladia-Balanus* association. The quantities of organisms represented in fig. 69-a are proportional to those tallied in Quadrat VI. Fig. 69-b shows a magnified view of portions of the interiors of two empty shells of *B. glandula*. Fig. 69-c. shows an enlarged portion of the thallus of *E. muricata*.

Acmaea digitalis, A. scabra, A. pelta, Littorina scutulata, and *L. planaxis,* although active when wetted at high tide, move about very little during most of the day. At low water *A. digitalis* and *A. scabra* are attached firmly to the bare rock surface, whereas *A. pelta* is present beneath tufts of *Endocladia* or in the empty cups of *B. glandula. Littorina scutulata* and *L. planaxis* show a tendency to clump together at low water, either around the basal portion of *Endocladia* or where a cluster of several barnacles affords some degree of protection. *Tegula* and the two whelks, *Thais emarginata* and *Acanthina spirata,* are the most mobile of the larger gastropod species. Sporadically, these snails remain behind when the tide falls, and may take refuge under tufts of *Endocladia.*

Small nestling animals are not readily observed. Vacant *B. glandula* tests were often occupied by many minute animal species, among them *Emplectonema gracile, Nemertopsis gracilis, Syllis spenceri, Lasaea cistula,* and

Littorina scutulata. Diaulota densissima was often found in small spaces between the basal plate of *B. glandula* and the underlying substrate. Sometimes the mites, *Agauopsis* sp., *Suidasia* sp., *Rhombognathus* sp., and *Pronematus* sp. were also found in this niche. However, great numbers of mites were always found living in the spaces between closely-growing *B. glandula.* The outer walls of many older barnacles were pitted, and mites were also numerous in these cavities.

Many different animal species live in the holdfast branchlets of *Endocladia* (fig. 69-c). The bivalve mollusks, *L. cistula, M. californianus,* and *Musculus* sp. were especially abundant here, usually anchored in place by byssal threads. Of the various mites, *Agauopsis* sp. was the species most frequently found in the holdfasts. At least five species of polychaetous annelids were present in this particular habitat niche, viz., *Syllis spenceri, S. vittata, S. armillaris, Nereis grubei,* and *Perinereis monterea.* Finally, tipulid larvae also were present in the basal portion of the alga. More motile species were found in the holdfasts and along the terminal branchlets, e.g., the amphipods *Hyale* sp. and *Allorchestes ptilocerus,* the isopod *Dynamenella,* and unidentified harpacticoid copepods. Littorines and nemerteans also find refuge in the holdfast branchlets of *Endocladia,* and in fact the majority of organisms living in thick barnacle clusters are found as well with *Endocladia. Acmaea digitalis* and *A. scabra* are the only mobile animals very frequently present on the open rock surface at low water.

Many species in the *Chthamalus-Pygmaea* zone in England have microhabitats similar to those of forms present in the *Endocladia-Balanus* association. MORTON (1954) and MORTON et al. (1957) discussed the fauna typically taking refuge in dense clusters of *Chthamalus stellatus. Lasaea rubra, Littorina neritoides, L. rudis,* and *Campecopea hirsuta* (Isopoda) were a few of the species found by these workers in the empty cups and spaces provided by *Chthamalus. Lasaea rubra* was more abundant in fissures and cracks rather than on exposed rock surfaces. In these studies attention was given primarily to the so-called crevice faunas. COLMAN (1940) investigated the fauna contained in the lichen, *Pygmaea pumila,* and found the following animal species intimately associated with it: Mollusca- *Lasaea rubra, Mytilus edulis, Littorina saxatalis, L. obtusata,* and *L. littorea*; Arthropoda- *Chthamalus stellatus, Balanus balanoides, Hyale nilssoni, Campecopea hirsuta, Rhombognathus* (two species), and probably several species of dipteran larvae, one of which was *Geranomyia unicolor.* Nemertean and polychaete worms, common among the branchlets of *Endocladia,* were conspicuously absent from the lichen.

Food relations

Food-web diagrams are a useful means of qualitatively portraying community food interrelations. Two investigators have published food webs for selected localities in the littoral region of California. MACGINITIE (1935) presented a scheme for Elkhorn Slough; and HEWATT (1937) presented a scheme for the rocky shore habitat, in both protected and exposed situations, at the Hopkins Marine Station. These workers investigated relatively extensive regions with rich biotas, and perforce expressed the food relations in broad and simplified terms. For example, Hewatt included in his food webs only about one third of the 90 relatively common species considered in his survey, and such groups as sponges, nudibranchs, tunicates, and fishes were not further separated into species. Because the *Endocladia-Balanus* association is more delimited in space and contains fewer species it has been possible to outline qualitatively the food relations in more precise terms for well over three-quarters of the common macroscopic species present (fig. 70). Principal food items available to members of this assemblage are: (a) plant fragments, (b) other organic detritus, (c) phytoplankton, (d) zooplankton, (e) encrusting and mat-forming algae, (f) large benthic algae, and (g) benthic animals. All of these organic foods are consumed in quantity by different animals in the association.

Plant fragments, particulate organic detritus, phytoplankton, and zooplankton are the main foods which become available at high water (fig. 70, center). A number of filter-feeding animals depend on one or more of these substances, viz. *Chthamalus microtretus, C. dalli, Balanus glandula, Lasaea cistula, Musculus* sp., *Mytilus californianus*, and probably *Filicrisia franciscana*. While the diagram indicates that some zooplankton is consumed by all of the above-named species, few zooplankters actually were found in the gut analyses.

Different species of encrusting and mat-forming algae, although grouped together for convenience, do not necessarily contribute equally to the diet of herbivorous browsers and scrapers. Not only are the animals here more selective than most filter feeders, but the plants involved are not all present in the same habitat niche. Thus the plants that are available to the herbivores which feed on the rock substrate are not identical with the plants available to herbivores feeding among the branches of *Endocladia. Coccochloris stagnina* and *Pseudoulvella applanata* grow on the exposed rock surface and in the fissures and cavities provided by *B. glandula*; *Entophysalis conferta, Oscillatoria* sp., and *Lyngbya* sp. grow as epiphytes on the blades of *Endocladia*; *Navicula* sp. is commonly present in both situations. Radula-scraping herbivores, like *Littorina scutulata, L. planaxis, Tegula funebralis, Acmaea digitalis, A. scabra, A. pelta*, and *Cyanoplax dentiens*, feed predominantly on *Coccochloris* and *Pseudoulvella*, whereas *Syllis spenceri, S. vittata, Dynamenella glabra, Hyale* sp., and *Allorchestes ptilocerus*, living in the tufts of *Endocladia*, are more apt to select a greater proportion of the epiphytic species. The gut contents of *Diaulota densissima* reveal that this form sometimes feeds on the microscopic algae. *Suidasia* sp., a secretive and sluggish mite, may also feed on *Coccochloris* and *Pseudoulvella*; at least the mite was always found in close association with these algae.

Seven species of animals were observed to feed on the large benthic algae. Tipulid larvae apparently consume the greatest quantity of *E. muricata. Nereis grubei* feeds on *E. muricata* and *G. agardhii*, while only pieces of

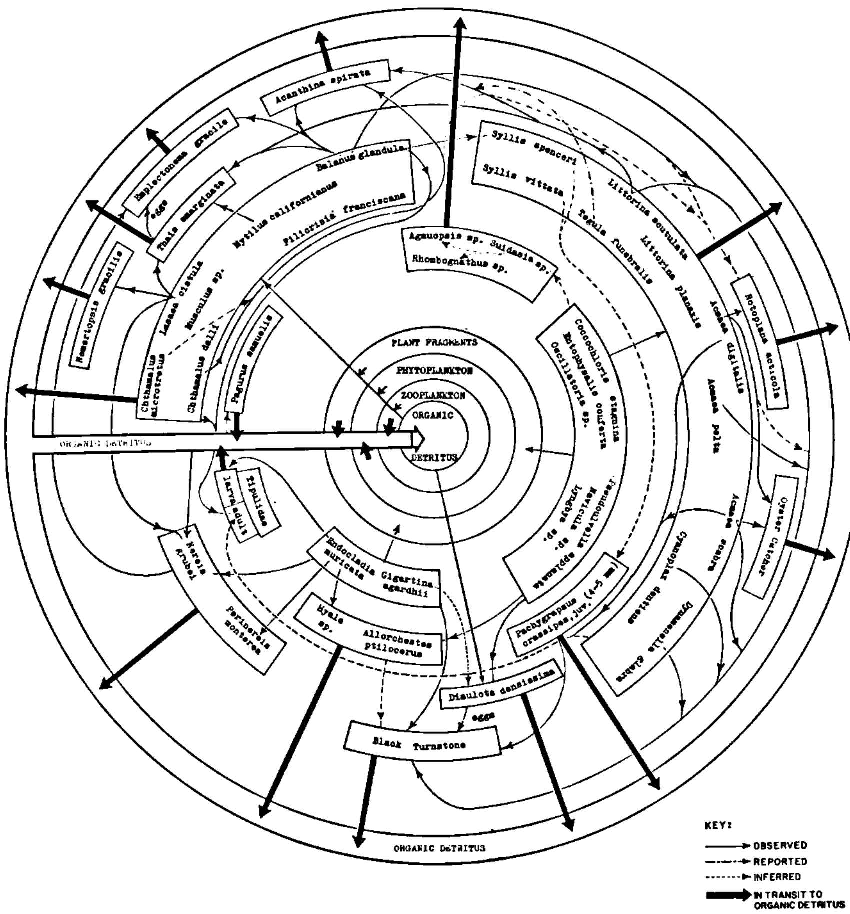


FIGURE 70. Web diagram of food relations existing among 43 common species in the *Endocladia-Balanus* association. The scheme is easily read by starting from the center and working out toward the periphery. The central portion of the diagram shows the most abundant substances brought into the association at high water. A marginal band denoting organic detritus girdles the food web, showing that ultimately all forms pass through this state of degradation. Much of the organic detritus so generated is suspended in the sea water washing the intertidal area; this detritus is demonstrated by the large arrow pointing inward to the center of the web. An arrow beginning or ending on the outside surface of a rectangle indicates that all organisms within that rectangle are involved. Arrows breaking through rectangles indicate the particular species involved. For example, of the two nereid worms, *Nereis grubei* feeds on *Endocladia* and *Gigartina* (as well as *Lasaea cistula* and organic detritus), but *Perinereis monterea* feeds only on *Endocladia*. Groups of organisms not studied (e.g. fungi, bacteria, protozoa) are not included.

E. muricata were found in the gut of *Perinereis monterea*. *Endocladia* was found in the guts of *Hyale* sp. and *Allorchestes ptilocerus*, but the alga is probably a more important food item in *Hyale* sp. since many large fragments were frequently ingested. Both algae were found in the stomach of the Black Turnstone. A single fragment of *Gigartina* sp. was identified among the gut contents of *Diaulota densissima.*

Pagurus samuelis was seen to feed on organic detritus in the holdfasts of *Endocladia*, and similar material was observed in the gut of *D. densissima.* Since juveniles of *Pachygrapsus crassipes* were raised by HIATT (1948) on small polychaetes, the species is represented in the food web as possibly feeding on syllids. However, adults of *P. crassipes* while primarily herbivorous, take a great variety of foods, and it is possible that juveniles do so as well.

Numerous field observations, supplemented by two stomach analyses, indicate that the diet of the Black Turnstone is highly diversified. Stomach contents were obtained from birds killed while feeding in the *Endocladia-Balanus* association. On several occasions these birds fed on *Endocladia, G. agardhii,* and *B. glandula.* Some other organisms found in the stomachs were *Littorina scutulata, Acmaea scabra, A. pelta, Cyanoplax dentiens, Dynamenella glabra,* amphipods (probably *Hyale* sp. and *A. ptilocerus*), a juvenile crab (probably *P. crassipes*), and eggs of *D. densissima.*

Nemertopsis gracilis, Emplectonema gracile, Thais emarginata, and *Acanthina spirata* probably derive the bulk of their food from the relatively inactive filter feeders. *Notoplana acticola* and the Oyster Catcher fed on *Acmaea digitalis* and *A. scabra. Hyadesia* sp. (Acarina) is not shown in the web diagram, but it is relatively large and highly active at low water like *Halotydeus hydrodromus,* a mite found in the upper intertidal zone in England. This latter form was reported by Halbert to feed on smaller mites (cited in GLYNNE-WILLIAMS & HOBART, 1952). Several individuals of *Hyadesia* sp. were followed for considerable distances as they raced over the rock surface, but never was one actually observed feeding.

In summary, among the species considered, seven are filter feeders, ten are herbivorous browsers or scrapers, six derive at least part of their food from large benthic algae, five have varied diets, and six depend on other living animals for food. In view of both space and feeding relations it is now evident that HEWATT's (1937) original notion, "Practically all forms found in the zone [*Endocladia-Balanus* association] are dependent upon the barnacles for food or for protection against desiccation.", is no longer tenable.

Quantitative community composition

Thus far, the biotic composition of the *Endocladia-Balanus* association has been discussed primarily in qualitative terms, though quantitative data derived from analysis of quadrat samples have been presented in Appendices I, II, and III, and noted in the discussions of individual species.

In the present section the biotic composition of the assemblage is considered in quantitative terms. Major attention is devoted to the more common animal species forming the resident benthos in the center of the association. Transient benthic marine species, such as *Tegula funebralis, Thais emarginata,* and *Acanthina spirata,* are treated in a separate section. Likewise the pelagic biotic components of the assemblage, consisting of plankton and suspended organic detritus available at periods of high water, are treated in a separate section. A few sporadic terrestrial invaders such as shore birds were not analyzed quantitatively, and thus are excluded from the discussion.

Resident benthos

Numbers of individuals

The absolute numbers of the 28 commonest species of animals in the center of the *Endocladia-Balanus* association are shown in table XXIII, while some statistical parameters relating to these absolute numbers are given in table XXIV.

Notoplana acticola demonstrated the lowest mean number per quadrat, with 0.5 individuals, and *Lasaea cistula* the highest, with 6,200 individuals. Mollusks and arthropods were the only groups represented by species whose mean numbers exceeded 100 individuals/quadrat. Five of the nine species with a mean number of less than 10 individuals/quadrat were soft-bodied forms, viz. *N. acticola, Emplectonema gracile,* and three species of polychaetous annelids. The range in numbers exhibited by most species was large, and over half of the species listed were absent from at least one quadrat sample. *Musculus* sp. showed the greatest range in numbers, reflecting well its erratic distribution in the tufts of *Endocladia.* Some of the species (e.g., *Syllis spenceri,* fig. 71-b) show more or less normal frequency distributions in the samples. However, the majority of species show more or less skewed distributions. In *Musculus* sp., for example, the frequency distribution of the numbers of individuals taken in the 12 quadrat samples (fig. 71-a) are positively skewed, with over 80% of the sample population in the least abundant numerical class (0—400 individuals/quadrat). Since most of the species counts are for Poisson or other non-normal distributions, only the range, median, and mean are included in table XXIV.

The relative abundance of the numerically most common animal species in the low, center, and high quadrats, is shown in table XXV. In the center and high quadrats these species included more than 98% of the individuals taken in the samples; they formed slightly less than 95% in Quadrats L_1

TABLE XXIII. Absolute numbers of individuals of 28 animal species present in the center of the *Endocladia-Balanus* association. Quadrat samples are arranged in order of the months in the year, regardless of the year in which they were collected. Species are arranged in order of decreasing numbers according to the mean number present in these samples.

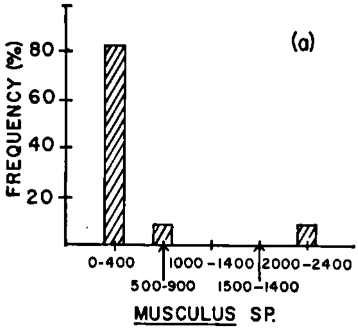
Quadrat number & month taken	Absolute numbers of individuals/400 cm² quadrat											
	Jan.	Mar.	Mar.	April	May	June	July	Sept.	Sept.	Oct.	Nov.	Dec.
Species	VI	VII	I	VIII	II	IX	III	IV	X	XI	V	XII
Lasaea cistula	7,600	5,500	6,400	6,600	11,100	6,800	3,700	4,700	7,600	5,600	7,400	1,100
Littorina scutulata	337	113	188	326	541	95	1,053	1,149	482	772	444	1,126
Balanus glandula	138	320	372	94	150	35	116	519	1,619	1,232	38	1,043
Musculus sp.	7	6	876	6	36	53	319	0	2,382	34	7	15
Littorina planaxis	0	545	10	8	33	1	12	106	94	808	7	0
Mytilus californianus	55	220	521	38	495	44	0	4	46	32	55	78
Dynamenella glabra	262	10	129	41	122	95	194	1	290	12	229	117
Chthamalus spp.	45	77	706	5	14	13	8	32	163	18	11	248
Syllis armillaris	123	1	21	66	140	54	127	25	22	24	78	2
Diaulota densissima	7	93	21	20	44	31	32	45	89	62	31	37
Agauopsis sp.	76	5	71	63	14	13	13	1	160	49	7	11
Syllis spenceri	43	82	58	24	41	35	39	1	17	39	53	37
Acmaea scabra	11	28	59	18	27	10	45	16	10	16	7	43
Acmaea digitalis	11	39	18	32	43	2	36	11	8	31	6	5
Mesostigmatid mites	15	29	0	51	24	3	3	2	1	52	37	3
Nemertopsis gracilis	18	8	48	3	55	2	42	1	8	2	3	8
Tipulidae (larvae)	13	15	3	31	1	20	1	14	40	7	25	9
Hyale sp.	18	46	1	0	0	1	2	31	15	15	0	44
Oligochaete	1	0	7	19	31	1	5	68	5	0	3	0
Syllis vittata	14	1	29	13	1	19	2	2	7	0	22	0
Acmaea pelta	3	6	21	15	22	1	21	2	0	3	3	11
Allorchestes ptilocerus	1	0	21	0	0	15	0	0	7	0	18	2
Emplectonema gracile	0	0	2	5	12	1	10	1	3	2	6	13
Cyanoplax dentiens	0	0	5	3	0	2	12	0	1	1	3	0
Perinereis monterea	4	0	6	2	3	1	3	0	1	0	3	0
Pachygrapsus crassipes (juv.)	8	0	2	3	2	2	1	0	0	0	0	0
Nereis grubei	2	0	3	0	0	2	2	1	5	0	2	0
Notoplana acticola	0	0	1	0	0	1	0	0	1	0	3	0

Table XXIV. Statistical parameters relating to the absolute numbers of individuals per unit area, for the 28 species most abundant in the resident benthos of the *Endocladia-Balanus* association.

Species	Number of individuals/400 cm^2 quadrat			Number of individuals/M^2		
	Range	Median	Mean	Range	Median	Mean
Lasaea cistula	1,100—11,100	6,500	6,200	28,000—278,000	160,000	160,000
Littorina scutulata	95—1,149	463	552.2	2,400—28,720	11,600	13,800
Balanus glandula	35—1,619	235	473.0	880—40,480	5,880	11,820
Musculus sp.	0—2,382	24	311.8	0—59,550	600	7,795
Littorina planaxis	0—808	11	135.3	0—20,200	280	3,382
Mytilus californianus	0—521	50	132.3	0—13,000	1,200	3,308
Dynamenella glabra	1—290	120	125.2	20—7,250	3,000	3,130
Chthamalus spp.	5—706	25	111.7	100—17,600	620	2,792
Syllis armillaris	1—140	40	56.9	20—3,500	1,000	1,420
Diaulota densissima	7—93	34	42.7	200—2,300	850	1,070
Agauopsis sp.	1—160	32	40.2	20—4,000	800	1,000
Syllis spenceri	1—82	39	39.1	20—2,000	980	978
Acmaea scabra	7—59	17	24.2	200—1,500	420	605
Acmaea digitalis	2—43	14	20.2	50—1,100	350	505
Mesostigmatid mites	0—52	9	18.3	0—1,300	200	458
Nemertopsis gracilis	1—55	8	16.5	20—1,400	200	412
Tipulidae (larvae)	1—40	14	14.9	20—1,000	350	372
Hyale sp.	0—46	8	14.4	0—1,200	200	360
Oligochaete	0—68	4	11.7	0—1,700	100	292
Syllis vittata	0—29	4	9.2	0—720	100	230
Acmaea pelta	0—22	4	9.0	0—550	100	220
Allorchestes ptilocerus	0—21	0.5	5.3	0—520	10	130
Emplectonema gracile	0—13	2	4.6	0—320	50	115
Cyanoplax dentiens	0—12	1	2.2	0—300	20	55
Perinereis monterea	0—6	2	1.9	0—200	50	48
Pachygrapsus crassipes (juv.)	0—8	0.5	1.5	0—200	10	38
Nereis grubei	0—5	2	1.4	0—100	50	35
Notoplana acticola	0—3	0	0.5	0—80	0	10

TABLE XXV. Relative abundance of individuals of 28 animal species in the low, center, and high portions of the *Endocladia-Balanus* association. Quadrat samples I through XII are arranged in order of the months of the year, regardless of the year in which they were collected. Species are arranged in order of decreasing numbers, according to the mean number present in the 12 center quadrats. The percentage listed at the bottom of each column represents the sum of percentages for all the species listed except those with an abundance of < 0.1%.

Quadrat number & month taken / Species	Relative numbers of individuals/400 cm² quadrat															
	Jan. L_1	Feb. L_2	Jan. VI	Mar. VII	Mar. I	April VIII	May II	June IX	July III	Sept. IV	Sept. X	Oct. XI	Nov. V	Dec. XII	Nov. H_1	Dec. H_2
Lasaea cistula	5.0	8.9	85.1	76.7	66.4	87.4	85.6	92.3	63.1	69.9	58.0	63.5	86.6	27.6	11.6	40.3
Littorina scutulata	0.6	0.5	3.7	1.6	2.0	4.3	4.2	1.3	17.9	17.1	3.7	8.7	5.2	28.4	18.5	27.2
Balanus glandula	11.0	14.1	1.5	4.4	3.9	1.2	1.2	0.5	2.0	7.7	12.3	13.9	0.4	26.3	42.0	24.8
Musculus sp.	15.4	25.2	<0.1	<0.1	9.1	<0.1	0.3	0.7	5.4	0.0	18.2	0.4	<0.1	0.4	0.0	<0.1
Littorina planaxis	0.0	0.0	0.0	7.5	0.1	0.1	0.3	<0.1	0.2	1.6	0.7	9.1	<0.1	0.0	8.1	2.3
Mytilus californianus	2.3	18.4	0.6	3.0	5.4	0.5	3.8	0.6	0.0	<0.1	0.4	0.4	0.6	2.0	0.0	0.0
Dynamenella glabra	1.4	2.6	2.9	0.1	1.3	0.5	0.9	1.3	3.3	<0.1	2.2	0.1	2.7	2.9	0.0	0.0
Chthamalus spp.	51.4	10.7	0.5	1.1	7.3	<0.1	0.1	0.2	0.1	0.5	1.2	0.2	0.1	6.2	13.0	2.0
Syllis armillaris	0.9	0.3	1.4	<0.1	0.2	0.9	1.1	0.7	2.2	0.4	0.2	0.3	0.9	<0.1	0.0	0.0
Diaulota densissima	0.0	0.0	<0.1	1.3	0.2	0.3	0.3	0.4	0.5	0.7	0.7	0.7	0.4	0.9	0.2	2.0
Agauopsis sp.	0.2	0.1	0.8	<0.1	0.7	0.8	0.1	0.2	0.2	<0.1	1.2	0.6	<0.1	0.3	1.6	0.2
Syllis spenceri	0.2	0.7	0.5	1.1	0.6	0.3	0.3	0.5	0.7	<0.1	0.1	0.4	0.6	0.9	0.0	0.0
Acmaea scabra	0.6	1.5	0.1	0.4	0.6	0.2	0.2	0.1	0.8	0.2	<0.1	0.2	<0.1	1.1	1.2	0.3
Acmaea digitalis	<0.1	<0.1	0.1	0.5	0.2	0.4	0.3	<0.1	0.6	0.2	<0.1	0.3	<0.1	0.1	0.9	0.1
Mesostigmatid mites	0.0	0.0	0.2	0.4	0.0	0.7	0.2	<0.1	<0.1	<0.1	<0.1	0.6	0.4	<0.1	0.0	0.2
Nemertopsis gracilis	<0.1	0.0	0.2	0.1	0.5	<0.1	0.4	<0.1	0.7	<0.1	<0.1	<0.1	<0.1	0.2	0.0	0.0
Tipulidae (larvae)	0.2	0.0	0.1	0.2	<0.1	0.4	<0.1	0.3	<0.1	0.2	0.3	<0.1	0.3	0.2	0.2	0.3
Hyale sp.	1.0	2.3	0.2	0.6	<0.1	0.0	0.0	<0.1	<0.1	0.5	0.1	0.2	0.0	1.1	1.4	0.0
Oligochaete	0.0	0.0	<0.1	0.0	<0.1	0.3	0.2	<0.1	<0.1	1.0	<0.1	0.0	<0.1	0.0	0.2	0.0
Syllis vittata	0.1	1.3	0.2	<0.1	0.3	0.2	<0.1	0.3	<0.1	<0.1	<0.1	0.0	0.3	0.0	0.0	0.0
Acmaea pelta	0.7	1.2	<0.1	<0.1	0.2	0.2	0.2	<0.1	0.4	<0.1	0.0	<0.1	<0.1	0.3	0.0	0.0
Allorchestes ptilocerus	3.1	4.0	<0.1	0.0	0.2	0.0	0.0	0.2	0.0	0.0	<0.1	0.0	0.2	<0.1	0.0	0.0
Emplectonema gracile	0.1	0.1	0.0	0.0	<0.1	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1	<0.1	0.3	0.0	0.0
Cyanoplax dentiens	0.3	<0.1	0.0	0.0	<0.1	<0.1	0.0	<0.1	0.2	0.0	<0.1	<0.1	<0.1	0.0	0.0	0.0
Perinereis monterea	0.0	0.0	<0.1	0.0	<0.1	<0.1	<0.1	<0.1	<0.1	0.0	<0.1	0.0	<0.1	0.0	0.0	0.0
Pachygrapsus crassipes (juv.)	<0.1	0.0	<0.1	0.0	<0.1	<0.1	<0.1	<0.1	<0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nereis grubei	0.3	0.2	<0.1	0.0	<0.1	0.0	0.0	<0.1	<0.1	<0.1	<0.1	0.0	<0.1	0.0	0.0	0.0
Notoplana acticola	0.0	<0.1	0.0	0.0	<0.1	0.0	0.0	<0.1	0.0	0.0	<0.1	0.0	<0.1	0.0	0.0	0.0
Σ	94.8	93.4	98.1	99.0	99.2	98.7	99.7	99.6	98.5	100.0	99.3	99.6	98.7	99.2	98.9	99.7



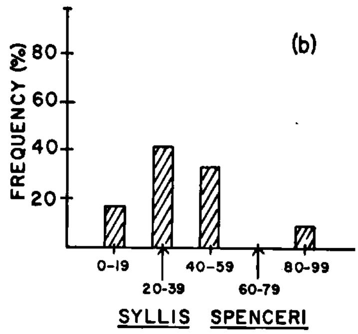


FIGURE 71. Frequency distributions of the numbers of individuals of *Musculus* sp. (a), and *Syllis spenceri* (b) observed in the 12 center quadrat samples. Ordinates indicate the percent of the quadrats with the various numerical classes denoted on the abscissas.

and L_2. *Musculus* sp., *Chthamalus* spp., and *B. glandula* showed the highest relative abundance among the animals present in the low quadrats, while *B. glandula, L. cistula,* and *L. scutulata* dominated in the high quadrats. *Lasaea cistula, L. scutulata,* and *B. glandula* demonstrated the highest population densities in the center quadrats, the three species combined making up over 80% of the total number of individuals in all the samples except Quadrats I and X. On the other hand, fifteen of the 28 species considered did not contribute more than 1% of the individuals present in any of the center quadrat samples.

It is apparent from simple inspection of tables XXIII and XXV that the biotic composition of the assemblage remains relatively stable throughout the year. This stability was also reflected in the qualitative collections, and is shown more clearly in the following quantitative analysis of species composition in the quadrat samples from low, center, and high regions in the *Endocladia-Balanus* belt.

The procedure followed in this analysis is demonstrated in the following simplified example, illustrated in fig. 72. Assume an association containing only four species, A, B, C, and D. This association is sampled three times (Samples I, II, and III). Sample I contains a total of 50 individuals of the four species, and Samples II and III contain totals of 25 and 100 specimens, respectively. Counts of the numbers of individuals of each species in each sample are indicated in the table (fig. 72-a) along with calculations of the percent of individuals in each sample contributed by each of the four species.

The composition of each sample is then compared with that of every other sample, to determine the minimum number and percent of each of the various species which occurs in both samples. The data thus obtained are then presented pictorially in a trellis diagram (fig. 72-b). For example, the numerical composition of Samples I and II, with respect to species A, is 25 and 20 individuals, respectively. Now, the minimum number of individuals of species A in the two samples is the lower number, or 20 indi-

(a)

SPECIES	SAMPLES I NO.	I %	II NO	II %	III NO.	III %
A	25	50	20	80	60	60
B	15	30	3	12	20	20
C	5	10	1	4	20	20
D	5	10	1	4	0	0
TOTAL	50	100	25	100	100	100

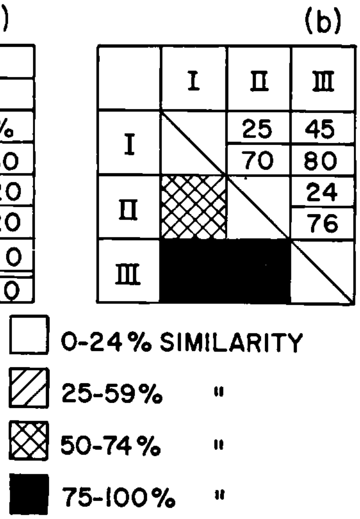
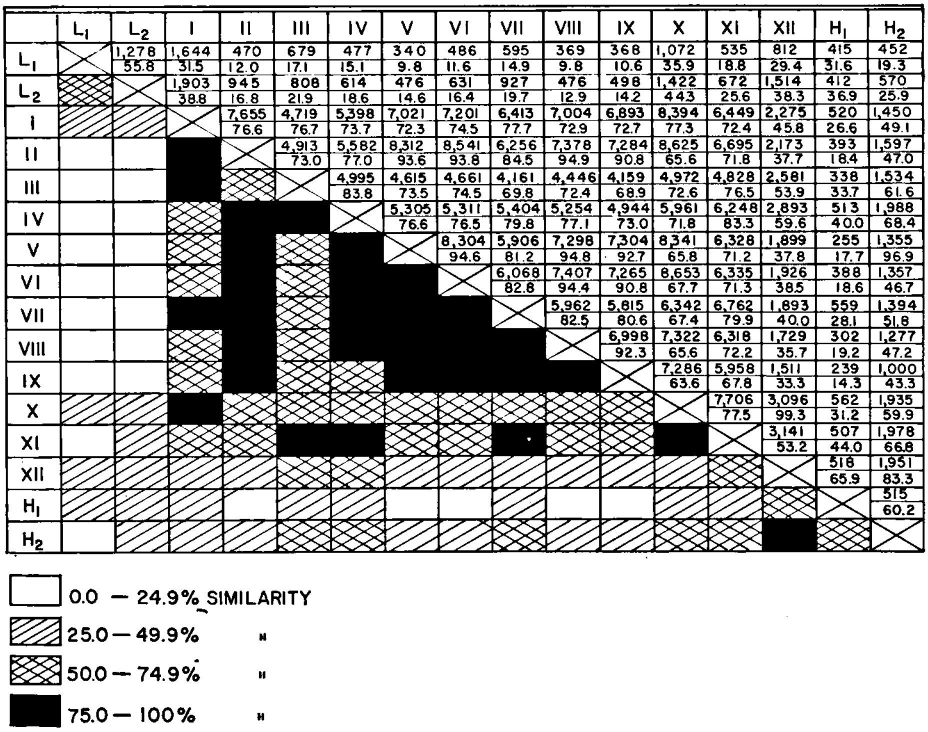


FIGURE 72. A simplified example illustrating how the quantitative species composition of samples is compared in a trellis diagram, for a hypothetical association containing only four species. (a) Tabulation of the numbers and percent of each species present in each of three samples. (b) Trellis diagram showing numerically (above the diagonal) and pictorially (below the diagonal) the degree of similarity in species composition of all possible pairwise combinations of the samples. The upper and lower figures in each square above the diagonal represent, respectively, the total number and the total percent of individuals "shared" by the two samples under comparison.

viduals. In the same manner, the minimum number of individuals of species B obtained in comparing Samples I and II is 3 individuals. The total number of individuals of the four species "shared" by Samples I and II is 20 + 3 + 1 + 1, or 25 individuals. The data may be treated similarly with regard to the percentage composition of each species. The minimum percentages of species A, B, C, and D found in both Samples I and II are, 50%, 12%, 4%, and 4%, respectively, yielding a total for the four species of 70%. Using this type of analysis, the absolute and relative numbers of all possible pair combinations of 47 species were calculated for the quadrats at all three levels in the *Endocladia-Balanus* belt. The results are shown graphically in fig. 73.

The greatest faunal similarity is evident between Quadrats I through XI. Low quadrats when compared among themselves also show a fairly close agreement in their faunal composition, as do high quadrats. Quadrat XII, which deviates most from the mid-level samples, demonstrates a close affinity with Quadrats H_1 and H_2. From table XXV it can be seen that the faunal composition of these three quadrats contains a high percentage of *L. cistula*, *L. scutulata*, and *B. glandula*. This rather high degree of affinity is peculiar in view of the low elevation of Quadrat XII (3.6 ft above MLLW), as compared with the high-level samples (5.7 and 5.8 ft above



	L1	L2	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	H1	H2
L1		1,278 55.8	1,644 31.5	470 12.0	679 17.1	477 15.1	340 9.8	486 11.6	595 14.9	369 9.8	368 10.6	1,072 35.9	535 18.8	812 29.4	415 31.6	452 19.3
L2			1,903 38.8	945 16.8	808 21.9	614 18.6	476 14.6	631 16.4	927 19.7	476 12.9	498 14.2	1,422 44.3	672 25.6	1,514 38.3	412 36.9	570 25.9
I				7,655 76.6	4,719 76.7	5,398 73.7	7,021 72.3	7,201 74.5	6,413 77.7	7,004 72.9	6,893 72.7	8,394 77.3	6,449 72.4	2,275 45.8	520 26.6	1,450 49.1
II					4,913 73.0	5,582 77.0	8,312 93.6	8,541 93.8	6,256 84.5	7,378 94.9	7,284 90.8	8,625 65.6	6,695 71.8	2,173 37.7	393 18.4	1,597 47.0
III						4,995 83.8	4,615 73.5	4,661 74.5	4,161 69.8	4,446 72.4	4,159 68.9	4,972 72.6	4,828 76.5	2,581 53.9	338 33.7	1,534 61.6
IV							5,305 76.6	5,311 76.5	5,404 79.8	5,254 77.1	4,944 73.0	5,961 71.8	6,248 83.3	2,893 59.6	513 40.0	1,988 68.4
V								8,304 94.6	5,906 81.2	7,298 94.8	7,304 92.7	8,341 65.8	6,328 71.2	1,899 37.8	255 17.7	1,355 96.9
VI									6,068 82.8	7,407 94.4	7,265 90.8	8,653 67.7	6,335 71.3	1,926 38.5	388 18.6	1,357 46.7
VII										5,962 82.5	5,815 80.6	6,342 67.4	6,762 79.9	1,893 40.0	559 28.1	1,394 51.8
VIII											6,998 92.3	7,322 65.6	6,318 72.2	1,729 35.7	302 19.2	1,277 47.2
IX												7,286 63.6	5,958 67.8	1,511 33.3	239 14.3	1,000 43.3
X													7,706 77.5	3,096 99.3	562 31.2	1,935 59.9
XI														3,141 53.2	507 44.0	1,978 66.8
XII															518 65.9	1,951 83.3
H1																515 60.2
H2																

FIGURE 73. Trellis diagram showing the degree of faunal similarity between and within the low, center, and high quadrat samples, based on 47 species which were tabulated numerically and observed at least once in the center quadrats. The upper figure shown in each of the squares above the diagonal gives the total number of individuals of all species which were "shared" by the two quadrats under comparison. The lower figure shows the total percent of individuals of all species which were "shared" by the two quadrats concerned. Below the diagonal the percent of individuals "shared" between the various samples is illustrated pictorially. For further explanation see text.

MLLW). The numerical composition of Quadrat H_2 is somewhat discordant, too, in that fair affinity with several mid-level samples is indicated. In general, however, results demonstrate that the middle portion of the *Endocladia-Balanus* association is a relatively distinctive region. Reference to table XXV shows that the high relative abundance of *Lasaea cistula* in the center quadrats is in large measure responsible for this similarity.

A relatively high degree of stability and constancy in qualitative and quantitative biotic composition, from place to place and through the seasons, is a characteristic feature of the *Endocladia-Balanus* association. This is of particular interest, for MACGINITIE (1939) has supported the view that variation is a characteristic feature of marine communities in general. MacGinitie points to the divergence in the numerical composition of three samples, taken from a *Mytilus* community (so-named because of the presence of this one species) over three consecutive years, and from two habitats. However, one of these habitats was continuously submerged, and the other subject to the tidal fluctuations in the intertidal zone; thus living conditions in the two localities were certainly different. The degree of constancy found in the biota of the *Endocladia-Balanus* belt within the study area is, in part, a reflection of the similarity of conditions wherever the association occurs. In part, too, it is a reflection of the more or less continuous reproductive activity or colonizing propensities apparent in many of the more characteristic species. *Nereis grubei, Lasaea cistula, Musculus* sp., *Littorina planaxis, Dynamenella glabra*, and *Limonia marmorata* breed in all seasons of the year, while *Acmaea digitalis, A. scabra, A. pelta, Littorina scutulata, Mytilus californianus, Balanus glandula*, and *Diaulota densissima* are reproductively inactive for only relatively short periods. Finally, in MOKYEVSKY's (1960b) recent summary of the geographical zonation of marine littoral types, it was remarked that north-boreal faunas (which may or may not include the *Endocladia-Balanus* assemblage) undergo slight seasonal changes.

Dry weight biomass

Tables XXVI and XXVII show, respectively, the absolute and relative dry weight biomasses of 31 benthic species common in the association. *Endocladia muricata, Gigartina agardhii*, and *Filicrisia franciscana* are tabulated in the two lists since weight measurements were made of these species.

Three animal species (*B. glandula, L. scutulata*, and *L. cistula*) and two plant species, (*Endocladia muricata* and *Gigartina agardhii*), contributed most of the biomass of the association. Originally, the *Endocladia-Balanus* association was named after the two most conspicuous organisms present. Weight determinations show that *E. muricata* and *B. glandula* do indeed make up the bulk of the mass of the assemblage.

The three animal species most important on the basis of weight (*Balanus glandula, Littorina scutulata, Lasaea cistula*) were also the most important numerically, but in a different order (*L. cistula, L. scutulata, B. glandula*; cf. Appendix I). Some species, which were present in high numbers, demonstrated a relatively low weight, e.g., *Musculus* sp., *D. glabra, S. armillaris, D. densissima*, and *Agauopsis* sp. On the other hand, *A. digitalis*, while not numerous, ranked sixth in position with respect to weight. Two-thirds of the species listed contributed very little to the total biomass.

Nitrogen content

The percent nitrogen determined for each of the species analyzed is listed in table XXVIII. These values were used in transforming weight measurements to the nitrogen values shown in tables XXIX and XXX. In species

TABLE XXVI. Absolute dry weight biomasses per quadrat for 31 plant and animal species characteristic of the center of the *Endocladia-Balanus* association. Quadrat samples are arranged in order of the months in the year regardless of the year collected, and species are listed in order of decreasing average biomass.

Species / Quadrat number & month taken	Jan. VI	Mar. VII	Mar. I	April VIII	May II	June IX	July III	Sept. IV	Sept. X	Oct. XI	Nov. V	Dec. XII
	Dry weight biomass in mg/400 cm² quadrat											
Balanus glandula	42,000	151,000	105,000	35,000	46,000	8,300	19,400	187,000	113,000	154,000	32,000	114,000
Endocladia muricata	12,790	11,550	14,670	7,320	18,180	13,070	15,630	6,420	10,260	2,900	8,070	5,030
Littorina scutulata	3,597.1	882.6	1,036.3	7,747.1	2,610.6	3,595.0	4,146.8	10,299.8	2,397.5	2,222.5	4,228.9	488.0
Gigartina agardhii	1,050	390	0	8,490	340	9,700	15.7	1,760	830	40.0	2,840	0
Lasaea cistula	2,215.6	1,562.8	3,025.1	1,923.0	2,777.2	3,601.9	1,814.8	1,607.1	1,718.1	2,160.1	2,393.3	362.7
Acmaea digitalis	363.4	1,151.8	821.8	748.8	1,249.5	389.7	783.1	339.1	72.4	1,693.7	187.5	843.8
Chthamalus spp.	420	2,700	1,920	142	380	210	45	400	4,600	230	83	2,200
Littorina planaxis	0	431.0	235.1	626.0	1,261.7	33.6	50.3	1,055.1	73.6	1,197.8	52.9	0
Acmaea scabra	213.0	1,073.5	644.6	91.6	302.9	74.1	294.8	131.3	631.8	112.3	91.9	972.9
Mytilus californianus	13.7	62.8	1,947.0	50.4	297.3	30.3	0	0.9	564.6	9.1	39.6	8.5
Musculus sp.	1.5	1.8	218.2	2.8	15.0	14.7	23.2	0	585.7	8.5	2.0	6.0
Syllis spenceri	53.8	185.4	90.7	31.8	71.0	20.7	43.5	2.7	38.1	69.6	43.7	96.1
Acmaea pelta	35.3	32.7	44.4	35.1	64.8	0.5	38.6	8.5	0	28.0	12.5	87.9
Dynamenella glabra	27.7	3.3	20.8	5.7	17.2	18.0	34.3	0.1	94.8	3.8	59.1	51.5
Nemertopsis gracilis	20.5	23.2	54.1	6.8	86.1	1.0	64.0	0.8	17.5	4.3	5.5	5.3
Emplectonema gracile	0	0	4.7	21.5	37.6	5.6	38.2	1.0	20.0	19.5	58.3	61.2
Pachygrapsus crassipes (juv.)	50.4	0	12.0	35.2	10.5	32.1	19.0	0	0	0	0	0
Tipulidae (larvae)	23.3	25.7	0.9	38.7	0.3	11.3	0.2	7.7	8.1	5.9	27.4	1.4
Perinereis monterea	22.1	0	18.3	2.3	57.0	2.1	32.1	0	0.4	0	11.0	0
Filicrisia franciscana	34.8	9.2	3.3	2.4	8.2	4.4	1.1	0.1	0.3	0.9	3.8	14.7
Hyale sp.	2.5	19.0	0.3	0	0	0.4	1.9	10.9	5.0	6.6	0	28.4
Cyanoplax dentiens	0	0	4.9	25.0	0	3.1	9.2	0	0.1	<0.1	21.9	0
Syllis vittata	9.6	0.4	16.8	9.8	0.8	5.7	1.9	0.1	0.9	0	11.0	0
Syllis armillaris	8.0	0.1	5.2	3.2	4.9	3.2	8.1	3.4	3.3	4.7	7.4	0.1
Diaulota densissima	0.4	9.3	1.5	1.3	3.5	2.6	2.1	4.1	7.6	4.8	2.9	3.2
Notoplana acticola	0	0	7.8	0	0	2.1	0	0	0.9	0	22.0	0
Allorchestes ptilocerus	0.6	0	8.5	0	0	11.6	0	0	1.0	0	7.2	1.1
Nereis grubei	4.0	0	5.8	0	0	0.4	1.4	<0.1	0.2	0	2.8	0
Agauopsis sp.	0.9	<0.1	0.9	0.8	0.3	0.1	<0.1	<0.1	1.7	0.6	0.2	0.1
Oligochaete	<0.1	0	0.1	0.2	0.9	<0.1	0.1	3.5	0.1	0	0.1	0
Mesostigmatid mites	0.2	0.3	0	0.6	0.4	<0.1	0.1	<0.1	<0.1	0.5	0.5	0.1

TABLE XXVII. Relative dry weight biomasses for 31 plant and animal species characteristic of the center of the *Endocladia-Balanus* association. Quadrat samples are arranged in order of the months in the year regardless of the year collected, and species are listed in order of decreasing average relative biomass.

Quadrat number & month taken	Percent of total dry weight biomass in each quadrat											
	Jan.	Mar.	Mar.	April	May	June	July	Sept.	Sept.	Oct.	Nov.	Dec.
Species	VI	VII	I	VIII	II	IX	III	IV	X	XI	V	XII
Balanus glandula	66.7	88.4	80.8	56.5	62.2	21.2	45.6	89.5	83.7	93.4	64.0	92.0
Endocladia muricata	20.3	6.8	11.3	11.8	24.6	33.4	36.8	3.1	7.6	1.8	16.1	4.0
Littorina scutulata	5.7	0.5	0.8	12.5	3.5	9.2	9.7	4.9	1.8	1.3	8.4	0.4
Gigartina agardhii	1.7	0.2	0	13.7	0.5	24.8	<0.1	0.8	0.6	<0.1	5.7	0
Lasaea cistula	3.5	0.9	2.3	3.1	3.8	9.2	4.3	0.8	1.3	1.3	4.8	0.3
Acmaea digitalis	0.6	0.7	0.6	1.2	1.7	1.0	1.8	0.2	<0.1	1.0	3.8	0.7
Chthamalus spp.	0.7	1.6	1.5	0.2	0.5	0.5	0.1	0.2	3.4	0.1	0.2	1.8
Littorina planaxis	0	0.3	0.2	1.0	1.7	0.1	1.2	0.5	<0.1	0.7	0.1	0
Acmaea scabra	0.3	0.6	0.5	0.1	0.4	0.2	0.7	0.1	0.5	0.1	0.2	0.8
Mytilus californianus	<0.1	<0.1	1.5	0.1	0.4	0.1	0	<0.1	0.4	<0.1	0.1	<0.1
Musculus sp.	<0.1	<0.1	0.2	<0.1	<0.1	<0.1	<0.1	0	0.4	<0.1	<0.1	<0.1
Syllis spenceri	0.1	0.1	<0.1	<0.1	0.1	<0.1	0.1	<0.1	<0.1	<0.1	0.1	0.1
Acmaea pelta	0.1	<0.1	<0.1	0.1	0.1	<0.1	0.1	<0.1	0	<0.1	<0.1	0.1
Dynamenella glabra	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	0.1	<0.1	0.1	<0.1	0.1	<0.1
Nemertopsis gracilis	<0.1	<0.1	<0.1	<0.1	0.1	<0.1	0.2	<0.1	<0.1	<0.1	<0.1	<0.1
Emplectonema gracile	0	0	<0.1	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1	0.1	<0.1
Pachygrapsus crassipes (juv.)	0.1	0	<0.1	0.1	<0.1	0.1	<0.1	0	0	0	0	0
Tipulidae (larvae)	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Perinereis monterea	<0.1	0	<0.1	<0.1	0.1	<0.1	0.1	0	<0.1	0	<0.1	0
Filicrisia franciscana	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Hyale sp.	<0.1	<0.1	<0.1	0	0	<0.1	<0.1	<0.1	<0.1	<0.1	0	<0.1
Cyanoplax dentiens	0	0	<0.1	<0.1	0	<0.1	<0.1	0	<0.1	<0.1	<0.1	0
Syllis vittata	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	0	<0.1	0
Syllis armillaris	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Diaulota densissima	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Notoplana acticola	0	0	<0.1	0	0	<0.1	0	0	<0.1	0	<0.1	0
Allorchestes ptilocerus	<0.1	0	<0.1	0	0	<0.1	0	0	<0.1	0	<0.1	<0.1
Nereis grubei	<0.1	0	<0.1	0	0	<0.1	<0.1	<0.1	<0.1	0	<0.1	0
Agauopsis sp.	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Oligochaete	<0.1	0	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	0	<0.1	0
Mesostigmatid mites	<0.1	<0.1	0	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1

where the nitrogen content was found to vary significantly with season, the months in which different conversion factors were used are indicated.

An examination of table XXIX shows that the species with the highest numbers and weights also contain most of the nitrogen present in the association, even though some of these species contained comparatively low percentages of nitrogen. However, some of the soft bodied forms such as *Syllis spenceri*, *N. gracilis*, *E. gracile*, *P. monterea*, and others occupy relatively higher positions on the list. Animals not particularly abundant, but with well developed skeletal structures, e.g., *L. planaxis* and *F. franciscana*, take up correspondingly lower positions.

Comparative quantitative relations

Since little seasonal change was noted it is valid to compare the values obtained for number of individuals, dry weight biomass, and quantity of nitrogen for the species dealt with earlier, based on the average composition of Quadrats I—XII. These values are shown in table XXXI, along with protein contents which were calculated by multiplying the mean quantity of nitrogen per m² in each species by 6.25 (FRUTON & SIMMONDS, 1958, p. 27). It can be seen that the two species, *B. glandula* and *E. muricata* contributed more than 90% of the biomass and 80% of the nitrogen and protein in the association. More than 99% of the protein is accounted for by the 14 species heading the list. Weight measurements demonstrated the greatest range of variation, where *B. glandula* averaged 2,100 g/m² and mesostigmatid mites only 5 mg/m². Numerically, the *Endocladia-Balanus* belt is an exceedingly rich assemblage. Excluding macroscopic algae, *Filicrisia franciscana*, and the more transient and incidental species, the total mean number amounted to 210,000 individual organisms/m². Individuals of *Lasaea cistula* made up over 70% of this figure. The total amount of protein represented approximately six percent of the total dry weight biomass.

Discussion

A review of the literature shows that quantitative community studies in the upper intertidal zone are few. Those which seem pertinent to the present investigation are discussed below.

HEWATT (1937) made a census of the animal species in a dense population of *B. glandula* (Square No. 24) in his transect study on the shore at the Hopkins Marine Station. Hewatt's quadrat covered an area of one square yard, and his counts have here been adjusted to one m² for comparative purposes. A total of 13 species was enumerated. The three most abundant forms, with their corresponding numbers per m², were: *Balanus glandula*, 16,770; *Littorina scutulata*, 453; *Acmaea scabra*, 432. Hewatt recorded the following species which were found also in the *Endocladia-Balanus* association (cf. Appendix I): *Cribrina* (= *Anthopleura*) *elegantis-*

TABLE XXVIII. Nitrogen values used in converting dry weight biomass to weight of nitrogen.

Species	Nitrogen content as percent of dry weight of entire body, including shell, if present	Remarks
Notoplana acticola	13.9	—
Perinereis monterea	13.4	This value also used for *N. grubei* and the oligochaete.
Syllis spenceri	13.4	January through Sept.
	10.4	Oct. through Dec.
Tipulidae (larvae)	12.4	—
Agauopsis sp.	12.4	This value also used for mesostigmatid mites.
Diaulota densissima	12.1	—
Syllis vittata	11.8	This value also used for *S. armillaris.*
Nemertopsis gracilis	11.4	—
Hyale sp.	9.5	—
Allorchestes ptilocerus	9.2	—
Emplectonema gracile	8.3	—
Pachygrapsus crassipes (juvenile)	6.0	—
Dynamenella glabra	5.1	—
Cyanoplax dentiens	4.2	—
Acmaea pelta	3.2	—
Musculus sp.	3.2	—
Endocladia muricata	3.6	July through Sept.
	3.1	Oct. through Mar.
	2.6	April through June
Gigartina agardhii	3.4	Jan. through Mar.
	2.4	April through Dec.
Acmaea scabra	2.5	—
Mytilus californianus	2.2	—
Acmaea digitalis	2.5	Jan. through Mar.
	2.0	April through Dec.
Lasaea cistula	1.8	July through Mar.
	1.6	April through June
Littorina scutulata	1.2	—
Chthamalus spp.	1.1	Average value of *C. dalli* and *C. microtretus.*
Littorina planaxis	1.0	—
Filicrisia franciscana	0.7	—
Balanus glandula	0.6	—

sima, 53; *Tegula funebralis*, 44; *Pagurus samuelis*, 22; *Leptasterias aequalis*, 11; *Acanthina lapilloides* (= *spirata*), 7; *Acmaea limatula*, 5; *Spirorbis* sp., common; *Cirolana harfordi*, rare. Although not observed in the present study, the gammarid amphipod, *Amphithoe* (= *Ampithoe*) sp. and the hermit crab, *Pagurus granosimanus* were represented by few (rare) and 28 individuals, respectively, in Hewatt's survey.

The abundance of most animal species listed by Hewatt is commensurate with that observed in the *Endocladia-Balanus* association. However, while Hewatt recorded spirorbid polychaetes as common, in the present study

TABLE XXIX. Absolute quantities of nitrogen (mg/quadrat) contained in 31 plant and animal species characteristic of the center of the *Endocladia-Balanus* association. Quadrat samples are arranged in order of the months in the year regardless of the year collected, and species are listed in order of decreasing mean weight of nitrogen per quadrat.

Quadrat number & month taken	Mg of nitrogen per quadrat											
	Jan.	Mar.	Mar.	April	May	June	July	Sept.	Sept.	Oct.	Nov.	Dec.
Species	VI	VII	I	VIII	II	IX	III	IV	X	XI	V	XII
Balanus glandula	250	906	630	210	280	50	116	1,120	678	924	190	684
Endocladia muricata	396.5	358.0	454.8	190.3	472.7	339.8	562.7	231	369.4	90	250	156
Gigartina agardhii	35.7	13	0.0	204	8.2	233	0.4	42.2	20	1.0	68.2	0.0
Littorina scutulata	43.1	10.6	12.4	92.9	31.3	43.1	49.7	123.4	28.8	26.6	50.7	5.9
Lasaea cistula	39.9	28.1	54.4	30.8	44.4	57.6	32.7	28.9	30.9	38.9	43.1	6.5
Acmaea digitalis	9.1	28.8	20.5	15.0	25.0	7.8	15.7	6.8	1.4	33.9	3.8	16.9
Chthamalus spp.	4.6	30	21.1	1.6	4.2	2.3	0.5	4.4	51	2.5	0.9	24
Acmaea scabra	5.3	26.8	16.1	2.3	7.6	1.9	7.4	3.3	15.8	2.8	2.3	24.3
Syllis spenceri	7.2	24.8	12.2	4.3	9.5	2.8	5.8	0.4	5.1	7.2	4.5	10.0
Mytilus californianus	0.3	1.4	42.8	1.1	6.5	0.7	0.0	<0.1	12.4	0.2	0.9	0.2
Littorina planaxis	0.0	4.3	2.4	6.3	12.6	0.3	0.5	10.6	0.7	12.0	0.5	0.0
Nemertopsis gracilis	2.3	2.6	6.2	0.8	9.8	0.1	7.3	0.1	2.0	0.5	0.6	0.6
Musculus sp.	<0.1	<0.1	7.0	0.1	0.5	0.5	0.7	0.0	18.7	0.3	<0.1	0.2
Emplectonema gracile	0.0	0.0	0.4	1.8	3.1	0.5	3.2	0.1	1.7	1.6	4.8	5.1
Perinereis monterea	2.9	0.0	2.4	0.3	7.6	0.3	4.3	0.0	<0.1	0.0	1.5	0.0
Tipulidae (larvae)	2.9	3.2	0.1	4.8	<0.1	1.4	<0.1	1.0	1.0	0.7	3.4	0.2
Dynamenella glabra	1.4	0.2	1.1	0.3	0.9	0.9	1.7	<0.1	4.8	0.2	3.0	2.6
Acmaea pelta	1.1	1.0	1.4	1.1	2.1	<0.1	1.2	0.3	0.0	0.9	0.4	2.8
Pachygrapsus crassipes (juv.)	3.0	0.0	0.7	2.1	0.6	1.9	1.1	0.0	0.0	0.0	0.0	0.0
Hyale sp.	0.2	1.8	<0.1	0.0	0.0	<0.1	0.2	1.0	0.5	0.6	0.0	2.7
Syllis vittata	1.1	<0.1	2.0	1.2	0.1	0.7	0.2	<0.1	0.1	0.0	1.3	0.0
Syllis armillaris	0.9	<0.1	0.6	0.4	0.6	0.4	0.9	0.4	0.4	0.6	0.9	<0.1
Diaulota densissima	<0.1	1.1	0.2	0.2	0.4	0.3	0.3	0.5	0.9	0.6	0.4	0.4
Notoplana acticola	0.0	0.0	1.1	0.0	0.0	0.3	0.0	0.0	0.1	0.0	3.1	0.0
Allorchestes ptilocerus	<0.1	0.0	0.8	0.0	0.0	1.1	0.0	0.0	0.1	0.0	0.7	0.1
Cyanoplax dentiens	0.0	0.0	0.2	1.0	0.0	0.1	0.4	0.0	<0.1	<0.1	0.9	0.0
Nereis grubei	0.5	0.0	0.8	0.0	0.0	<0.1	0.2	<0.1	<0.1	0.0	0.4	0.0
Oligochaete	<0.1	0.0	<0.1	<0.1	0.1	<0.1	<0.1	0.5	<0.1	0.0	<0.1	0.0
Filicrisia franciscana	0.2	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	0.1
Agauopsis sp.	0.1	<0.1	0.1	0.1	<0.1	<0.1	<0.1	<0.1	0.2	0.1	<0.1	<0.1
Mesostigmatid mites	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1

TABLE XXX. Relative quantities of nitrogen contained in 31 plant and animal species characteristic of the center of the *Endocladia-Balanus* association. Quadrat samples are arranged in order of the months in the year regardless of the year collected, and species are listed in order of decreasing mean percent nitrogen per quadrat.

Species / Quadrat number & month taken	Percent of total nitrogen in each quadrat: Jan. VI	Mar. VII	Mar. I	April VIII	May II	June IX	July III	Sept. IV	Sept. X	Oct. XI	Nov. V	Dec. XII
Balanus glandula	30.9	62.9	48.8	27.2	30.2	6.7	14.3	71.1	54.5	80.6	29.9	72.5
Endocladia muricata	49.0	24.8	35.6	24.6	51.0	45.5	69.2	14.7	29.7	7.9	39.3	16.6
Gigartina agardhii	4.4	0.9	0.0	26.4	0.9	31.2	<0.1	2.7	1.6	0.1	10.7	0.0
Littorina scutulata	5.3	0.7	1.0	12.0	3.4	5.8	6.1	7.8	2.3	2.3	8.0	0.6
Lasaea cistula	4.9	1.9	4.2	4.0	4.8	7.7	4.0	1.8	2.5	3.4	6.8	0.7
Acmaea digitalis	1.1	2.0	1.6	1.9	2.7	1.0	1.9	0.4	0.1	3.0	0.6	1.8
Chthamalus spp.	0.6	2.1	1.6	0.2	0.5	0.3	0.1	0.3	4.1	0.2	0.1	2.5
Acmaea scabra	0.7	1.9	1.2	0.3	0.8	0.3	0.9	0.2	1.3	0.2	0.4	2.6
Syllis spenceri	0.9	1.7	0.9	0.6	1.0	0.4	0.7	<0.1	0.4	0.6	0.7	1.1
Mytilus californianus	<0.1	0.1	3.3	0.1	0.7	0.1	0.0	<0.1	1.0	<0.1	0.1	<0.1
Littorina planaxis	0.0	0.3	0.2	0.8	1.4	<0.1	0.1	0.7	0.1	1.0	0.1	0.0
Nemertopsis gracilis	0.3	0.2	0.5	0.1	1.1	<0.1	0.9	<0.1	0.2	<0.1	0.1	0.1
Musculus sp.	<0.1	<0.1	0.5	<0.1	0.1	0.1	0.1	0.0	1.5	<0.1	<0.1	<0.1
Emplectonema gracile	0.0	0.0	<0.1	0.2	0.3	0.1	0.4	<0.1	0.1	0.1	0.8	0.5
Perinereis monterea	0.4	0.0	0.2	<0.1	0.8	<0.1	0.5	0.0	<0.1	0.0	0.2	0.0
Tipulidae (larvae)	0.4	0.2	<0.1	0.6	<0.1	0.2	<0.1	0.1	0.1	0.1	0.5	<0.1
Dynamenella glabra	0.2	<0.1	0.1	<0.1	0.1	0.1	0.2	<0.1	0.4	<0.1	0.5	0.3
Acmaea pelta	0.1	0.1	0.1	0.1	0.2	<0.1	0.1	<0.1	0.0	0.1	0.1	0.3
Pachygrapsus crassipes (juv.)	0.4	0.0	<0.1	0.3	0.1	0.3	0.1	0.0	0.0	0.0	0.0	0.0
Hyale sp.	<0.1	0.1	<0.1	0.0	0.0	<0.1	<0.1	0.1	<0.1	0.1	0.0	0.3
Syllis vittata	0.1	<0.1	0.2	0.2	<0.1	0.1	<0.1	<0.1	<0.1	0.0	0.2	0.0
Syllis armillaris	0.1	<0.1	<0.1	0.1	0.1	0.1	0.1	<0.1	<0.1	0.1	0.1	<0.1
Diaulota densissima	<0.1	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	0.1	0.1	0.1	<0.1
Notoplana acticola	0.0	0.0	0.1	0.0	0.0	<0.1	0.0	0.0	<0.1	0.0	0.5	0.0
Allorchestes ptilocerus	<0.1	0.0	0.1	0.0	0.0	0.1	0.0	0.0	<0.1	0.0	0.1	<0.1
Cyanoplax dentiens	0.0	0.0	<0.1	0.1	0.0	<0.1	<0.1	0.0	<0.1	<0.1	0.1	0.0
Nereis grubei	0.1	0.0	0.1	0.0	0.0	<0.1	<0.1	<0.1	<0.1	0.0	0.1	0.0
Oligochaete	<0.1	0.0	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	0.0	<0.1	0.0
Filicrisia franciscana	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Agauopsis sp.	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Mesostigmatid mites	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1

TABLE XXXI. Comparison of values obtained for number of individuals, dry weight biomass and quantity of nitrogen and protein in 31 forms characteristic of the center of the *Endocladia-Balanus* association, based on average composition of Quadrats I-XII. Values are arranged in order of decreasing amounts of nitrogen and protein.

Species	Per Quadrat (400 cm²) Number	Weight (mg)	Nitrogen (mg)	Per m² Number	Weight (mg)	Nitrogen (mg)	Protein (mg)
Balanus glandula	473.0	84,000	500	11,820	2,100,000	12,000	75,000
Endocladia muricata	—	10,490	322.6	—	262,300	8,065	50,410
Gigartina agardhii	—	2,120	52.1	—	53,000	1,300	8,120
Littorina scutulata	552.2	3,604.4	43.2	13,800	90,110	1,080	6,750
Lasaea cistula	6,200	2,096.8	36.4	160,000	52,420	910	5,690
Acmaea digitalis	20.2	720.4	15.4	505	18,010	385	2,410
Chthamalus spp.	111.7	1,100	12.0	2,792	28,000	300	1,880
Acmaea scabra	24.2	386.2	9.7	605	9,655	240	1,500
Syllis spenceri	39.1	62.3	7.8	978	1,560	200	1,200
Mytilus californianus	132.3	252.0	5.5	3,308	6,300	140	880
Littorina planaxis	135.3	418.1	4.2	3,382	10,450	100	620
Nemertopsis gracilis	16.5	24.1	2.7	412	602	68	420
Musculus sp.	311.8	73.3	2.3	7,795	1,830	58	360
Emplectonema gracile	4.6	22.3	1.9	115	558	48	300
Perinereis monterea	1.9	12.1	1.6	48	302	40	250
Tipulidae (larvae)	14.9	12.6	1.6	372	315	40	250
Dynamenella glabra	125.2	28.0	1.4	3,130	700	35	220
Acmaea pelta	9.0	32.4	1.0	220	810	25	160
Pachygrapsus crassipes (juv.)	1.5	13.3	0.8	38	332	20	100
Hyale sp.	14.4	6.2	0.6	360	160	20	100
Syllis vittata	9.2	4.8	0.6	230	120	20	100
Syllis armillaris	56.9	4.3	0.5	1,420	110	10	60
Diaulota densissima	42.7	3.6	0.4	1,070	90	10	60
Notoplana acticola	0.5	2.7	0.4	10	68	10	60
Allorchestes ptilocerus	5.3	2.5	0.2	130	62	5	30
Cyanoplax dentiens	2.2	5.4	0.2	55	140	5	30
Nereis grubei	1.4	1.2	0.2	35	30	5	30
Oligochaete	11.7	0.4	(0.05)	292	10	1	6
Filicrisia franciscana	—	6.9	(0.05)	—	170	1	6
Agauopsis sp.	40.2	0.5	(0.05)	1,000	10	1	6
Mesostigmatid mites	18.3	0.2	(0.02)	458	5	<1	3
Σ	8,400	106,000	1,000	210,000	2,640,000	25,000	160,000

Dexiospira spirillum was never observed in the center portion of the association, and was represented by only 15 individuals in Quadrat L_1, at the lower margin of the assemblage. Another obvious discrepancy is apparent in the case of *L. cistula,* which was found to be very abundant in the present study, but was not reported at all in Hewatt's study, despite his qualifying statement that, "The work is mainly concerned with 90 of the most commonly occurring macroscopic species of the intertidal area" (1937, p. 163). Evidently Hewatt censused the organisms *in situ*, and ignored or missed the great variety of species living in intimate contact with *B. glandula.* The total number recorded in Hewatt's typical sample of the *B. glandula* habitat was 17,825 individuals of all species/m², or approximately 8% of the mean number (210,000 individuals/m²) observed in the present study.

In the *Littorina-B. glandula* and *Littorina-B. cariosus* Faciations in Puget Sound, the two barnacles, *B. glandula* and *B. cariosus,* and the periwinkle, *L. scutulata* were the most numerous animal species reported by SHELFORD et al. (1935). An average of 2,400 *B. glandula* and 200 *L. scutulata*/m² was observed in the *Littorina-B. glandula* Faciation, and 3,140 *B. cariosus* and 228 *L. scutulata*/m² in the adjacent but lower *Littorina-B. cariosus* Faciation. In the latter association the two remaining species listed were *Acmaea digitalis umbonata* with 70, and *Thais emarginata* with 38 individuals/m². Other animals, also present in the *Endocladia-Balanus* association, were observed but intermingled with forms typical of lower intertidal horizons. As many as 3,000 *Chthamalus dalli*/m² were present in association with *Anthopleura* (= *Cribrina*) *xanthogrammica* and *Pisaster ochraceus.* In conclusion, the observations made by these investigators indicate that the numbers of individuals of dominant species were considerably smaller than at Pacific Grove. However, Rice (a member of the Shelford team) found that *B. glandula* and *C. dalli* reached maximum densities of 202,800 and 236,600 individuals/m² in one muddy embayment.

Pertinent numerical and biomass measurements made by MOKYEVSKY (1960a) in the *Gloiopeltis-Chthamalus* association in the Sea of Japan were as follows. Although not counted, *Gloiopeltis capillaris* showed a range in weight of 180 to 507 g/m². *Chthamalus dalli* ranged in numbers from 100 to 21,100 individuals/m², and in weight from 0.5 to 344.85 g/m². Tabulated as single occurrences with *Gloiopeltis* were the following crustaceans: *Dynamenella glabra* (Isopoda) — 1,600 individuals/m², with a biomass of 1 g/m²; *Allorchestes malleolus* and *Hyale bassargini* (both Amphipoda) — 100 individuals/m², with a biomass of 0.25 g/m², and 200 individuals/m², with a biomass of 2 g/m², respectively. Dipteran larvae were frequently numerous. These were Syrphidae — 100 individuals/m², with a biomass of 0.25 g/m²; Tipulidae — 66 to 300 individuals/m², with a range in biomass of 0.17 to 0.75 g/m². Of the two mollusks *Acmaea testudinalis* was the least abundant, with numbers ranging from 400 to 600 individuals/m² and with a range in biomass of 7 to 56 g/m². *Littorina sitchana subtenebrosa* demonstrated the highest frequency of occurrence in the association, with 726 to 41,300 individuals/m², and contributed significantly to the total biomass of the samples, ranging from 5 to 184 g/m².

A comparison of mean biomass values of similar forms in the *Gloiopeltis-Chthamalus* (computed from tables 2, 9, 13, 21, and 38 in MOKYEVSKY's 1960a account) and *Endocladia-Balanus* associations reveals comparable orders of magnitude. *Gloiopeltis,* with 291.11 g/m², is very close to *Endocladia,* with 262.30 g/m². The greatest difference is noted between *C. dalli,* with a mean biomass of 127.87 g/m² in the *Gloiopeltis* belt, and *C. dalli* + *C. microtretus,* with 28.00 g/m² in the present study. It is possible that the greater biomass of *Chthamalus* in the *Gloiopeltis* belt is related to the absence of *Balanus.* Other animals are contrasted as follows in terms of mean biomass/m²: *Littorina sitchana subtenebrosa,* 65.09 and *Littorina scutulata,* 90.1; *Acmaea testudinalis,* 31.5 and *Acmaea digitalis,* 18.01; syrphid + tipulid larvae, 0.33 and tipulid larvae, 0.32.

The number of species included in MOKYEVSKY's samples were usually around a half-dozen, but even so the total maximum numerical and biomass measurements were considerably lower than the total mean observations in the present study, viz. *Gloiopeltis-Chthamalus* association — 41,600 individuals/m² and 737.25 g/m², which amount to only 19.8% and 27.9%, respectively, of the total mean number and biomass of the *Endocladia-Balanus* association.

MOKYEVSKY's (1960b) account of the "north-boreal littoral type" in different regions of the north-western Pacific gives high biomass values of *Littorina* and *Balanus balanoides* + *Chthamalus* in the upper portion of this habitat. Preliminary data show that in the Okhotsk Sea, *Littorina* and *Balanus* + *Chthamalus* have mean biomasses which range from 109 to 271 g/m² and from 1,112 to 1,915 g/m², respectively. Correspondingly high biomass figures were also tabulated for the Barents Sea with respect to these three genera.

The kinds and numbers of species reported by COLMAN (1939) and MORTON (1954) in the *Chthamalus-Pygmaea* zone in England were remarkably similar to those enumerated in the present analysis. Colman investigated the faunas contained in nine different plants, and found that the lichen *Pygmaea pumila* supported the densest populations. He estimated that 274,320 individuals of several species inhabited the tufts of *P. pumila* over an area of one m². He compared this figure with those of some typical soil populations, the highest of which was a meadow habitat, containing 66,747 individuals/m² (mostly Insecta and Acarina).

As a standard procedure Colman investigated the numbers of the animal species inhabiting 100 g fresh weight samples of plants. He found an average of about 2,000 g of *P. pumila*/m². In contrast, the average weight of *E. muricata* was 877 g/m² (dry weight 29.9% fresh weight). The higher weight of the lichen is understandable, for the tufts often grow in close proximity, sometimes forming continuous patches over the rock surface. In the *Endocladia-Balanus* association *E. muricata* was more sparsely distributed, usually interspersed with clusters of *B. glandula* (figs. 3—6). From

Colman's account, then, it seems that the lichen, over an equal area of habitat, provides more living space for the contained animal populations. Having considered this possible difference, however, a critical comparison of these two widely separated assemblages reveals some striking similarities.

The following major groups found in the tufts of *P. pumila* are listed in order of decreasing abundance, and their numbers per m^2 will be contrasted with those of the *Endocladia-Balanus* association in this sequence: Pelecypoda, Isopoda, Gastropoda, Acarina, Cirripedia, Insecta, Amphipoda, and Oligochaeta. Bivalves of the genus *Lasaea* were the most numerous forms in the two habitats, with 188,940 *L. rubra* recorded in England and 160,000 *L. cistula* in California. Both species showed an irregular occurrence in numbers. A distinct difference in the abundance of isopods is evident; *Campecopea hirsuta* in England demonstrated an abundance of 57,720 individuals/m^2, in contrast with *Dynamenella glabra* in California with 3,130 individuals/m^2. The *Endocladia-Balanus* association contained nearly two times as many littorinid snails as the *Chthamalus-Pygmaea* association. *Littorina littorea*, *L. obtusata*, and *L. saxatilis*, the three English species, totalled about 9,060 individuals/m^2, while *L. scutulata* and *L. planaxis* in California totalled about 17,200 individuals/m^2. Colman found that the distribution of mites was highly irregular, and that their center of distribution was probably located at a lower level. Of all the acarids found *Rhombognathus pascens* and *R. seahami* formed the major portion of the samples; the total number tallied of these two species was 8,720 individuals/m^2. In California the total number of *Agauopsis* sp. and of mesostigmatids taken together was 1,460 individuals/m^2. If *Suidasia* and some of the other smaller species had been censused (for example 209 individuals of *Suidasia*/400 cm^2 were counted in Quadrat X) the total number would certainly exceed 50,000 individuals/m^2. Dense populations of terrestrial mites were not reported in Colman's study. The barnacles in England were *Chthamalus stellatus* and *Balanus balanoides*, the same two genera present in the *Endocladia-Balanus* association. The total number of barnacles of all species observed by Colman was much less than in the present study: 5,740 individuals/m^2 in England as compared with 14,610 individuals of *B. glandula* and *Chthamalus* spp./m^2 in California. In England *Chthamalus stellatus* outnumbered *B. balanoides* by about 20 to one, but in Pacific Grove about four *B. glandula* were present for every one individual of the genus *Chthamalus* (*Chthamalus dalli* and *C. microtretus* combined). Actually, the numbers of barnacles recorded by Colman cannot be compared directly with those observed in this study, since Colman considered only individuals adhering to the lichen. Population studies carried out by MOORE (1935) show that *B. balanoides* does attain high levels of abundance at the *Chthamalus-Pygmaea* level. In an exposed location on Dub Reef at Port Erin two samples, one above and the other below mean high water neap tide, contained 8,800 and 84,800 *B. balanoides*/m^2. Moore also determined that the dry tissue weights of these samples were 0.85 and 19.2 g/m^2, respectively. On the assumption these tissues contain 75% protein, the protein contents of the two populations were 0.64 and 14.4 g/m² (protein = nitrogen × 6.25, cf. p. 145), in contrast with an average protein content of 75.0 g/m² in *B. glandula* populations at Pacific Grove.

Collembola, Thysanura and Diptera were the principal insect orders present in the *Chthamalus-Pygmaea* association, and of these dipteran larvae were the most numerous. Of the 3,220 insects present/m², 2,680 were larvae of *Geranomyia unicolor* and other unidentified Diptera. Fly larvae were scarcer in the *Endocladia-Balanus* association, with 372 tipulids/m² making up the bulk of this group. Collembola and Thysanura were not observed in the *Endocladia-Balanus* association, but 1,070 *Diaulota densissima* (Coleoptera, Staphylinidae) were present/m². Coleoptera were not found by Colman in the lichen; however MORTON (1954) recorded *Aepus robini* as a typical crevice dweller in England at the same intertidal level. Only one amphipod species was commonly observed in *Pygmaea*, *Hyale nilssoni*, with an abundance of 700 individuals/m². *Hyale* sp. was represented in Pacific Grove by 360 individuals/m², and if combined with *Allorchestes ptilocerus* a total of 490 individuals/m² was present. *Lumbricillus pumilio* was present in *Pygmaea* to about the same extent as the unidentified oligochaete found in the present study, viz., 220 versus 292 individuals/m², respectively.

Transient benthos

An influential and highly mobile component of the benthos consists of the gastropod mollusks *Tegula funebralis*, *Acanthina spirata*, and *Thais emarginata*. As pointed out earlier, numerical and biomass measurements derived from quadrat samples collected at low water provide only minimal estimates of the abundance of these forms.

Even though all three species were absent from at least half of the center quadrats at the time of sampling, *T. funebralis* demonstrated a mean abundance of 65 individuals/m², while samples of *T. emarginata* and *A. spirata* contained 38 and 35 individuals/m², respectively (table XXXII). These species are relatively scarce when compared with some of the animal species of the resident benthos, but a comparison of tables XXXI and XXXII shows that they contribute significantly to the total biomass, nitrogen, and protein of the *Endocladia-Balanus* assemblage.

Plankton and suspended detritus

The kinds and quantities of substances brought into the association at high tide were sampled from the water washing over this intertidal level. Samples were taken at weekly intervals, from April 24, 1959 to May 27, 1960 (Appendix V). Each sample consisted of approximately 30 liters which were dipped from the water in five, six-liter fractions. Plankton and suspended detritus were then collected by pouring the sample through a Hensen egg-larvae plankton net (# 20 bolting silk).

For a period of four months, April-August, 1959, water coming into the

TABLE XXXII. Comparison of values obtained for number of individuals, dry weight biomass and quantity of nitrogen and protein in three transient species which move through the center of the *Endocladia-Balanus* association, based on average composition of Quadrats I-XII. Values are arranged in order of decreasing amounts of nitrogen and protein. Nitrogen values (as percent of dry weight biomass) for the three species were: *Tegula* 1.2%, *Acanthina* 0.88%, and *Thais* 1.4%.

Species	Per Quadrat (400 cm²) Number	Wt. (mg)	Nitrogen (mg)	Per m² Number	Wt. (mg)	Nitrogen (mg)	Protein (mg)
Tegula funebralis	2.6	657.5	7.9	65	16,440	200	1,200
Acanthina spirata	1.4	510.9	4.5	35	12,770	110	690
Thais emarginata	1.5	38.8	0.5	38	970	10	60

association was sampled in two different localities, one directly exposed to combers breaking on the shore, the other in a sheltered region protected by outlying reefs. Samples were also taken during the day and at night. No appreciable difference was noted in the samples collected from the localities subject to heavy and moderate wave action or in the samples collected during the light, crepuscular, and dark hours of the day. Thus, the assessment of plankton and detritus is based mainly on samples collected each week in the semi-protected station near the 3.82 ft bench mark during (a) two high water phases of the tidal cycle, from September through December, 1959, and (b) a single high tide period, from January through May, 1960.

Material retained in the jar in the cod-end of the Hensen net was preserved in buffered 10% formalin, concentrated to 20 ml, poured into a 20 ml graduated cylinder (0.1 ml graduations), and allowed to settle for at least 10 hours before reading off the wet settled volume. Dry weights of the settled materials were made by collecting them on Schleicher and Schnell analytical filter paper (No. 589, White Ribbon), and drying at 105° C to a constant weight.

Figure 74-a shows the monthly averages of the settled volume and dry weight per 100 ml. A maximum volume of 2.4 ml was observed in June, 1959; the volume dropped abruptly to 0.6 ml in August, and a relatively low volume was then characteristic of the remainder of the year. Conversely, the dry weight was lowest during the summer months and highest in the autumn, winter, and spring. As shown below, this seems to agree reasonably well with the increase in percentage composition of relatively heavy plant fragments and inorganic debris during these seasons (fig. 74-b).

The great variety of substances present in the samples could be divided into the following categories: (a) relatively large plant fragments, (b) other organic detritus, (c) phytoplankton, (d) zooplankton, and (e) inorganic detritus. A visual estimate of the percent by volume of each of the above categories in all samples was made by scanning under magnification (100 ×) a concentrated, 1 ml fraction.

Plant fragments, consisting of the broken-up remains of algae and of the marine phanerogam *Phyllospadix torreyi*, always formed a conspicuous fraction of the suspended materials taken in the samples (figs. 74-b and 75-a). Although the relative concentration of these plant remains was less in the spring and summer months the absolute quantities presented in fig.

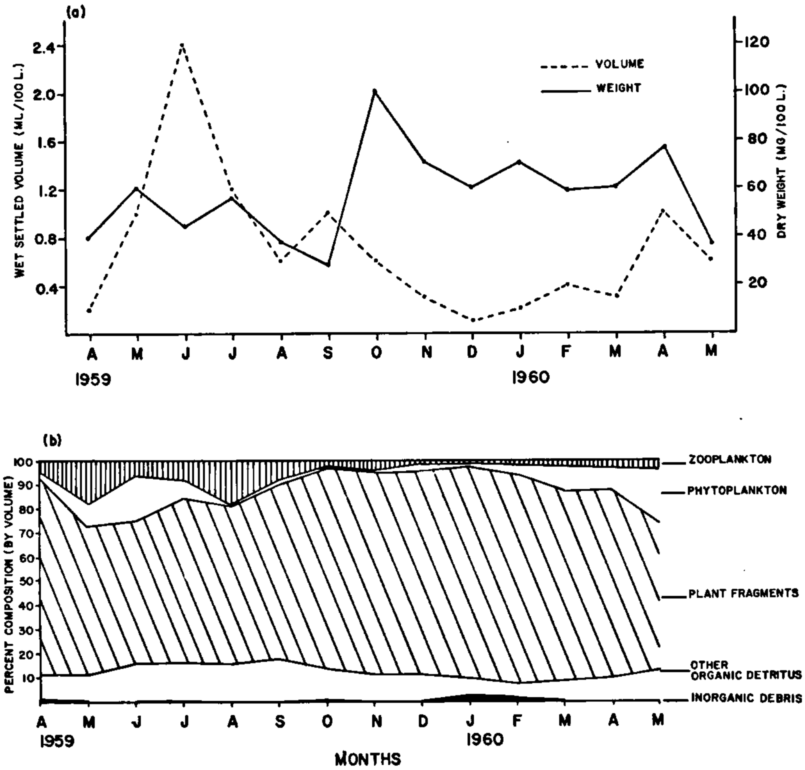


FIGURE 74. (a) Monthly averages of wet settled volume and dry weight of plankton and detritus per 100 liters of water. All averages for volume are based on four samples collected each week, from May through December, 1959, and on two samples collected each week, from January through May, 1960. In April, 1959, the average volume is based on only four samples for the whole month. Average weight measurements are based on four to five weekly samples except for April, 1959, which consisted of a single sample for the month. (b) Average percent composition by volume of plankton samples where monthly averages are based on the following numbers of samples: one in April, 1959, five in May, eight to ten from June through December, and four to five (weekly) in January through May, 1960.

75-a show that the winter months, especially December, January, and March, contained the smallest amount of this material. Other organic detritus was made up of feces, exuvia, and other unidentified material. Often relatively large numbers of fecal pellets were present. The relative and absolute amounts of this miscellaneous suspended organic detritus was highest in the summer months, reaching a maximum volume of 0.43 ml/100 ml in June, then steadily declining through the autumn and early winter until in January a minimum volume of 0.01 ml/100 ml was observed. Phytoplankton consisted principally of diatoms, e.g. *Biddulphia* sp., *Eucampia* sp., *Nitzschia* sp., *Asterionella* sp., *Chaetoceros* sp., and *Thalassiothrix* sp.; dinoflagellates and small blue-green algae were also present. Seasonally, these phytoplankters were most abundant in the spring and summer months. In June, 1959, the phytoplankton formed 37% of the total volume, and in May, 1960, 31%. By August, 1959, the phytoplankton had declined sharply, and a relatively low level was maintained until March, 1960.

The zooplankton taken in the samples included a variety of forms, e.g., nauplius and cypris larvae, ostracods, copepods, isopods, amphipods, shrimps, *Oikopleura*, jelly fishes (mostly hydromedusae), and eggs. The relative abundance of zooplankters was highest in the spring and summer months in 1959, declined in the fall, and remained at a rather low level until the termination of the survey in May, 1960. Nauplius larvae were present in nearly every sample, except those from the period December 4, 1959 through January 15, 1960. Occasionally, some of the permanent *Endocladia-Balanus* associates were found in the plankton samples. For example, the amphipod *Pontogeneia* sp. was collected on three different occasions during the night. *Dynamenella glabra*, harpacticoid copepods, and mites were also observed in the samples.

The volume of inorganic detritus, which included such things as rock fragments, shell and clay, was slight. Maximum absolute volumes of 0.01 and 0.02 ml/100 ml were observed in January and February, respectively, when wave action was strong.

For comparison with the shore waters, fig. 75-b shows monthly averages of the volume of phytoplankton collected about 1,000 yards offshore of the study area. Peak abundance occurred in both regions in June, 1959, and in May, 1960. Phytoplankton "blooms" usually occur during the spring and summer months, in coincidence with the upwelling period (cf. section on "Physical environment"), though in some years other pulses are also evident. Very little phytoplankton was observed from August through February.

In summary, these studies show that the suspended substances available at high water are, in decreasing amounts, plant fragments, phytoplankton, other organic detritus, zooplankton, and inorganic materials. Relatively large plant fragments were always abundantly present, as might be expected in view of the high standing crop and productivity of littoral benthic algae in the temperate zone (BLINKS, 1955). PETERSEN & JENSEN (1911), and MACGINITIE (1935) have argued that fragments derived from large plants form an essential food supply in certain communities. Furthermore, at a more advanced stage of degradation plant tissues contribute greatly to particulate organic detritus (FOX, 1957). Finally, phytoplankton and zooplankton, which proved most abundant in the spring and summer months in both intertidal and offshore waters, contribute significantly to the diets of filter feeders in the *Endocladia-Balanus* association.

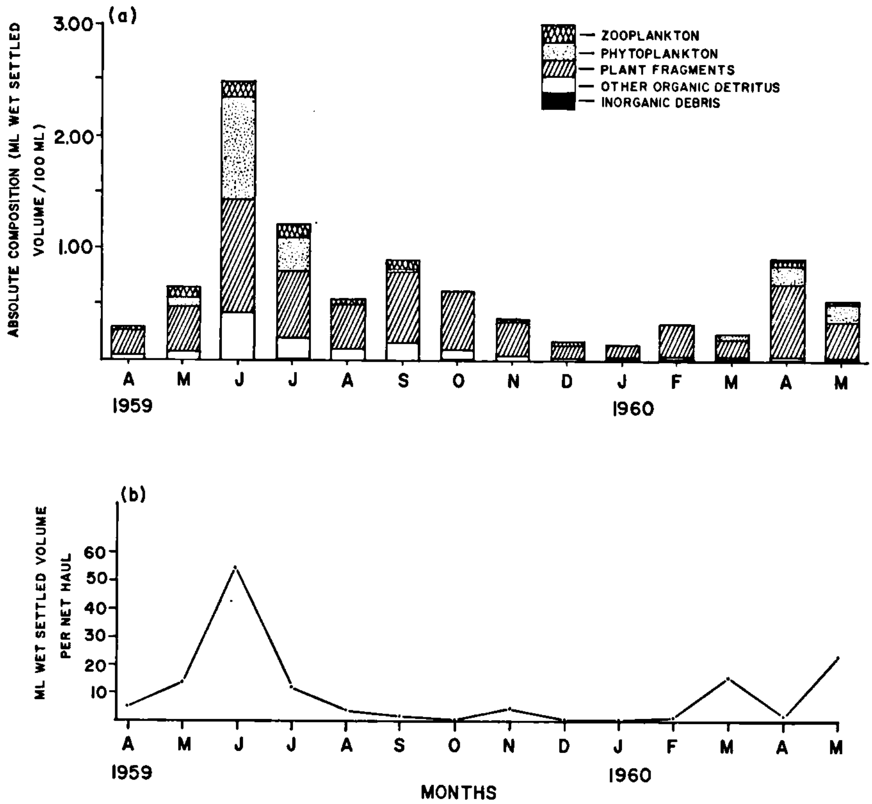


FIGURE 75. (a) Monthly averages of relative and absolute amounts of each material taken in the *Endocladia-Balanus* association at high water over the period, April, 1959-May, 1960. (b) Monthly averages of wet settled volume of phytoplankton captured per haul at bell buoy in southern Monterey Bay, approximately 1,000 yards offshore of the *Endocladia-Balanus* study area. Based on vertical hauls, 15 meters to surface, made weekly, using a truncated Apstein net 1/4 meter in greatest diameter, mouth ring 18 cm in diameter, and filtering surface of # 20 bolting silk. Data collected by Hopkins Marine Station personnel as part of the California Cooperative Oceanic Fisheries Investigations program.

FOOD RELATIONS AND COMMUNITY STRUCTURE

It has been noted that the majority of the animal species present in the *Endocladia-Balanus* association can be assigned to one of the following groups: (a) filter feeders, (b) scraping and grazing herbivores, (c) omnivores and scavengers, and (d) carnivores. With the data presented in tables XXXI and XXXII it is now possible to express community composition in terms of the dry weight biomasses and quantity of protein represented by each of the various categories of feeders forming the assemblage (fig. 76).

Studies of suspended substances showed that the water washing over the association contains large plant fragments, plankton, and other materials which possess an average dry weight biomass of 570 mg/m^3. Some of these suspended materials originate in the *Endocladia-Balanus* association, but the great bulk of the pelagic organic matter represents import from other associations. As already shown (see "Physical environment, Exposure and submersion") these suspended particles are available to organisms in the *Endocladia-Balanus* belt 28% of the total time, or usually for two periods each day totalling nearly seven hours, when the association is awash or submerged by the sea. Filter feeders, and omnivores and scavengers consume the major share of the plankton and detritus, and it is clear from the prominence of these groups that suspended food materials imported at high tide play a major nutritional role in the association.

In order of decreasing importance in terms of mg protein per m^2 the major filter feeding invertebrates are: *Balanus glandula*, *Lasaea cistula*, *Chthamalus* spp., *Mytilus californianus*, *Musculus* sp., and *Filicrisia franciscana*. The average total weight of these forms per m^2 was 2,200 g, representing about 84 g of protein/m^2. The comparatively low protein value reflects the presence in all of these species of heavy calcareous skeletal structures.

Of the benthic plants, *Endocladia muricata* and *Gigartina agardhii* make up most of the macroscopic element, totalling about 315 g dry weight, or 58 g protein/m^2. A rich growth of microscopic epiphytes on *E. muricata* is included in the biomass and protein values for this alga. Biomass and protein measurements were not made for the microscopic encrusting algae and protistans found on other surfaces in the association. A maximum order of magnitude of this component can be approximated, however, from CASTENHOLZ's (1961) weight determinations of diatom films in ungrazed intertidal study plots in Oregon. His values ranged from 32.1 to 66.6 mg/1,008 cm^2, or 318 to 661 mg/m^2. Since mixed diatom cultures contain from 2.10 to 5.40% nitrogen (VINOGRADOV, 1953) one would expect the protein content of the diatom films to be on the order of 40 to 200 mg/m^2.

The resident scraping and grazing herbivores form the second largest group of animal consumers. The dry weight and protein content per m^2 of those species adequately assessed with the quadrat sampler were 131 g and 12 g, respectively. The most abundant transient herbivore, *T. funebralis*, weighed 16.4 g and contained 1.2 g protein per m^2. Encrusting autotrophs made up the bulk of the diet in the following resident species (in order of decreasing weight): *Littorina scutulata, Acmaea digitalis, Littorina planaxis, Acmaea scabra, A. pelta, Dynamenella glabra, Cyanoplax dentiens, Syllis vittata,* and *Allorchestes ptilocerus.* This kind of food was consumed by *Tegula funebralis* as well. Tipulid larvae, *Perinereis monterea,* and *Hyale* sp., (in order of decreasing weight) fed mainly on the larger algae.

Proportionately, resident carnivores contributed very little to the biomass of the assemblage, making up less than 0.1% of the total mass present. The following carnivorous species (in order of decreasing weight), had a dry weight of 1,560 mg/m^2 and contained 880 mg protein/m^2: *Nemertopsis gracilis, Emplectonema gracile, Pachygrapsus crassipes,* and *Notoplana acticola.* The transient carnivores, *Acanthina spirata* and *Thais emarginata* (in order of decreasing weight), contributed a significantly greater fraction of the total biomass and protein content of the assemblage, with 13.7 g/m^2 and 750 mg/m^2, respectively. Omnivores and scavengers, like the resident carnivores, also contributed less than 0.1% of the total biomass; in order of decreasing weight they were represented by *Syllis spenceri, Diaulota densissima,* and *Nereis grubei.* The combined dry weight of these species was 1,680 mg/m^2 with 1,290 mg protein/m^2. Both resident carnivores and the omnivore-scavenger group contained more than 50% protein.

Four species, which were taken in the quadrat samples but not classified in the diagram (fig. 76), are *Syllis armillaris,* the unidentified oligochaete, *Agauopsis* sp., and the unidentified mesostigmatid mite. These forms together had a dry weight of 135 mg/m^2, and contained 75 mg of protein/m^2. Still smaller organisms, particularly micro-crustaceans, mites and assorted micro-organisms, and larger but highly mobile influents like the Black Turnstone, are not accounted for in fig. 76.

While the flow of materials through the association (the local ecomix) is fairly clear, it is not possible with present information to set up an energy budget for the association, such as has been done for Silver Springs, Florida by H. T. ODUM (1957), or a fresh water spring in Massachusetts by TEAL (1957). To establish such a budget it would be desirable to gain further information on quantities of food produced and consumed within the community, measures of import and export of organic matter to and from the association, and values for growth and metabolic efficiency in the more important species. Nevertheless, the ground work for such further studies has been laid, and it is hoped that the present contribution may serve to stimulate them.

SUMMARY

1. Studies of the composition, structure, and species interrelationships of the *Endocladia-Balanus* association were carried out in the rocky intertidal area at the Hopkins Marine Station, Pacific Grove, California.
2. The *Endocladia-Balanus* association is marked by the presence of two conspicuous species, the red alga *Endocladia muricata,* and the acorn

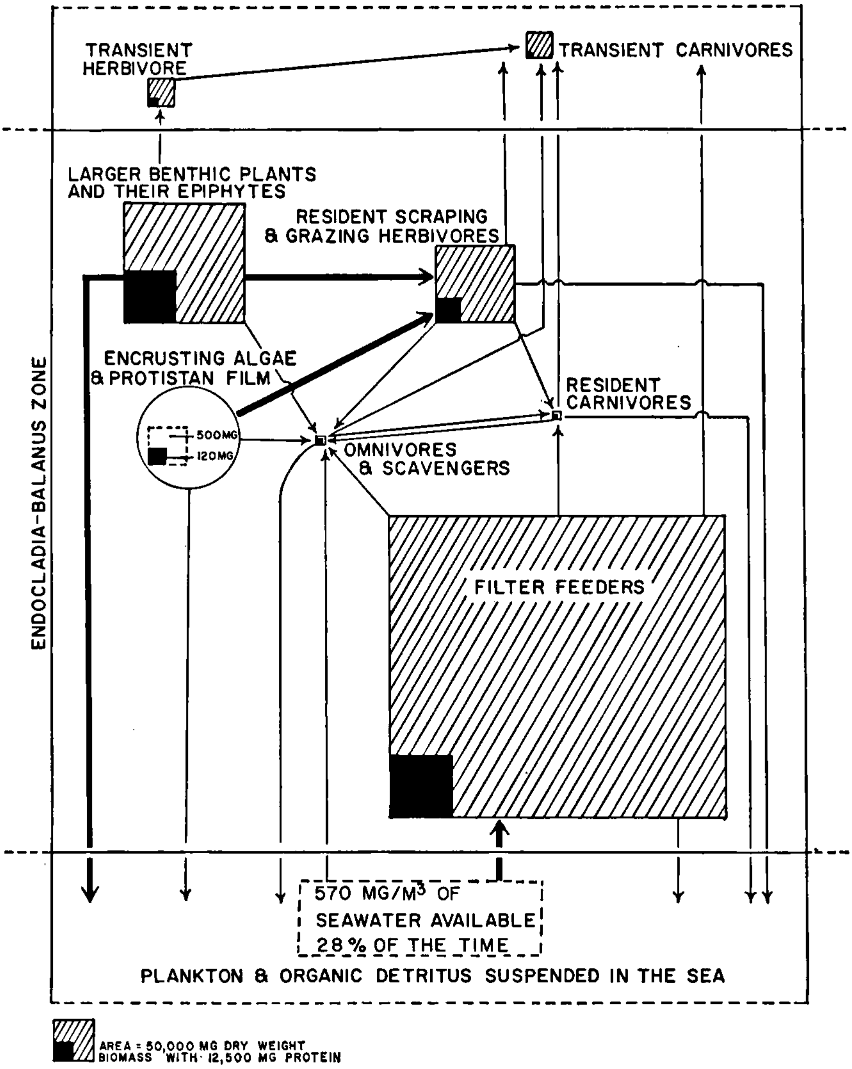


FIGURE 76. Block diagrams showing average dry weight biomass and protein content of the organisms of the *Endocladia-Balanus* association, grouped in categories according to food relations. The area of the shaded and solid block for each group is proportional to its dry weight biomass and protein content per m² (see key, lower left-hand corner). Arrows show the main pathways in flow of food. Unknown quantities of certain groups are delineated by broken lines, and for the encrusting algae and protistan film an estimate of the very small quantities present is shown in a magnified view.

barnacle *Balanus glandula.* These two species formed a band or belt, approximately two feet in width, on suitable high intertidal rocks, over a geographical range extending from northern Baja California to the Aleutian Islands.

3. In the study area the association was best developed on a firm granite base. While the center of the association averaged 4.6 ft in height above tidal datum as surveyed from a U.S.C.G.S. tidal bench mark, observations indicate that the zone experiences the conditions of tidal exposure and submersion predicted by tide tables for the 3.8 ft level. The existing tidal pattern results in semidaily submersion of the association for three-quarters of the days in the year, and a single daily submersion for the remainder. On a long-term basis the center of the association is submerged 27% of the total time. The longest continuous periods of exposure and submersion at this level are 20.25 and 6.5 hrs, respectively. Maximum periods of continuous exposure to air (assuming a dead-calm sea) extend to nearly 24 days at the upper margin of the association, and drop to only nine hours at the lower margin.
4. The marine climate bathing the association is mild. Thermal conditions demonstrate an annual pattern of three recognizable seasons: the Oceanic Period, August or September and October (warm), the Davidson Current Period, November-February (warm with a low thermal gradient), and the Upwelling Period, March-July or August (cold). The range in monthly mean ocean shore temperature over the three-year period of study (1959—1961) was 12.0 to 15.4° C, and the extreme range during this period was 10.5 to 16.5° C. The monthly mean salinities over the same period ranged from 33.32 to 33.89‰, with individual extreme values of 32.32 and 34.22‰. Records of extreme conditions in temperature and salinity occurring over a 42-year period are shown graphically.
5. The atmospheric climate to which the *Endocladia-Balanus* association is exposed at low water includes low temperatures and high precipitation in the winter, moderate temperatures and higher wind velocities in the spring, moderate temperatures and foggy mornings in the summer, high temperatures and reduced wind velocities in the autumn. With respect to atmospheric conditions the most critical periods of the year for the *Endocladia-Balanus* association are: (1) the late winter and early spring months when wetting of the zone occurs in the early morning hours, and is followed by day-long exposure to the drying action of the wind; and (2) in the late summer when the single daily period of submersion follows the hottest and calmest hours of the day. Although some rather extreme weather conditions occurred during the period of study, the biota of the association was not adversely affected.
6. The composition of the resident benthos of the association was determined from 16 quadrat samples, two taken from the lower and two from the upper margins of the belt, and 12 from the center of the zone, each quadrat covering an area of 400 cm^2. Quadrats were collected in every month of the year, excluding August, and 20 qualitative samples taken monthly, from May, 1959 to December, 1961. Field observations were made at frequent intervals throughout the year, during the day and night hours, and at high and low water.
7. Exclusive of microorganisms and most parasites, which were not studied,

a total of at least 93 species was enumerated, belonging to 15 major groups as follows: Myxophyceae (8 or more spp.), Chrysophyta (2 or more spp.), Chlorophyta (2 spp.), Rhodophyta (5 spp.), Phaeophyta (2 spp.), Angiospermae (1 sp.), Coelenterata (3 spp.), Platyhelminthes (1 sp.), Nemertea (2 spp.), Nematoda (1 or more spp.), Annelida (8 spp.), Bryozoa (1 sp.), Mollusca (20 spp.), Arthropoda (29 or more spp.), and Aves (8 spp.). None of these species was confined solely to the center of the assemblage. A study of the vertical distribution of 47 common resident species demonstrated that the number of species present at the upper margin of the belt was less than 40% of the number present in the center and at the lower margin, that soft-bodied worms were restricted to the central and lower levels, and that species of terrestrial origin increased from 5 to 28% in passing from the lower to the upper margins of the association.

8. Trellis diagram analysis indicates great similarity and stability in species composition among quadrats taken near the center of the association, with little seasonal variation. Superimposed on this consistent background of resident species is an important transient element whose species composition varies with height of the tide, time of day, and season of the year. Qualitatively, the biotic composition of the *Endocladia-Balanus* association resembles quite closely that of some high intertidal assemblages in the Puget Sound region and in the Sea of Japan, and is strikingly similar to that of the *Chthamalus-Pygmaea* zone on English shores.
9. Thirty-five of the 93 or more species present in the assemblage were of common occurrence, and where feasible the following aspects of their biology were studied: (a) habitat niche, (b) activity patterns, (c) organic matter content of the body, based on the dry weight and nitrogen content, (d) seasonal occurrence, (e) population structure, (f) reproductive activity, (g) food relationships, and (h) growth rate. Characteristic species were: Rhodophyta- *Endocladia muricata, Gigartina agardhii*; Platyhelminthes- *Notoplana acticola;* Nemertea- *Emplectonema gracile, Nemertopsis gracilis*; Annelida- *Syllis spenceri, S. vittata, S. armillaris, Nereis grubei, Perinereis monterea*; Bryozoa- *Filicrisia franciscana*; Mollusca- *Acmaea digitalis, A. scabra, A. pelta, Littorina scutulata, L. planaxis, Acanthina spirata, Thais emarginata, Tegula funebralis, Cyanoplax dentiens, Lasaea cistula, Mytilus californianus, Musculus* sp.; Arthropoda- *Balanus glandula, Chthamalus dalli, C. microtretus, Dynamenella glabra, Allorchestes ptilocerus, Hyale* sp., *Pachygrapsus crassipes, Diaulota densissima, Limonia marmorata, Agauopsis* sp., Mesostigmata (one undetermined species), and *Suidasia* sp.
10. A few large species dominate the outward appearance of the assemblage. The spatial relationships of these and a multitude of smaller species living among the holdfast branchlets and along the blades of *E. muricata*, and in the spaces formed by the tests of both living and dead *B. glandula* are portrayed. Many similar species find refuge in the tufts of the

lichen *Pygmaea pumila* and in the empty cups of the barnacle *Chthamalus stellatus* in a comparable habitat on the English coast.

11. The food relations of 43 common plant and animal species were studied and portrayed in a web diagram. The main foods available to animals are: plankton and other pelagic organic materials suspended in littoral waters, encrusting and mat-forming algae, large benthic algae, other animals, and organic detritus in the association. Of the 34 major animal species considered, seven are filter feeders, ten are herbivorous browsers and scrapers feeding on encrusting forms, six are herbivores feeding on the large benthic algae, five are omnivores and scavengers, and six are carnivores which prey mostly on filter feeders and scraping herbivores. Ultimately, all these organisms contribute to the organic detritus suspended in the water.
12. The quadrat samples were analyzed quantitatively, for numbers of individuals, dry weight biomass, and nitrogen content for each species present. Variation in the average absolute numbers per 400 cm^2 quadrat ranged from 0.5 individuals of the flatworm *Notoplana acticola* to 6,200 individuals of the bivalve *Lasaea cistula*. The remaining mean levels of abundance per quadrat were regularly distributed, with eight species between 0—10, eleven between 10—100, and seven between 100—1,000. The range in numbers within each species was usually great, and over half the species were absent from at least one quadrat.

    In the center quadrats, 28 animal species accounted for more than 98% of the total number of individuals of all species present (excluding microscopic forms). *Lasaea cistula, Littorina scutulata,* and *Balanus glandula* were most abundant, in order of decreasing numbers, and the remaining species were typically present to the extent of less than 1%. Trellis diagram analysis of the percent of individuals held in common between all possible pairwise combinations of species in the 16 quadrat samples shows greatest faunal affinity among the center samples. No seasonal variation was apparent in absolute or relative numbers of any species except in the case of juveniles of the crab *Pachygrapsus crassipes.*

    On the basis of dry weight, *B. glandula* and *E. muricata* formed the greatest portion of the total biomass of the samples. Also ranking high were *Gigartina agardhii, L. scutulata,* and *L. cistula.* Most of the remaining species contributed less than 0.1% to the total biomass. The percent nitrogen, determined for each species by Conway's modification of the Kjeldhal method, was commonly low in abundant forms with heavy shells, and higher in most of the rarer and smaller organisms. For the center of the *Endocladia-Balanus* zone the mean number of individuals present was 210,000/m^2, the mean dry weight biomass was 2,640 g/m^2, and the mean nitrogen content was 25 g/m^2. In quantitative as well as qualitative terms, the *Endocladia-Balanus* association shows considerable similarity with the *Gloiopeltis-Chthamalus* association in the Sea of Japan and with the *Chthamalus-Pygmaea* zone on English rocky shores.

13. The plankton and other material suspended in the water present during high tide periods was sampled and analyzed at weekly intervals for a 14-month period. These pelagic materials, in order of decreasing absolute volume, were: (a) large plant fragments, (b) phytoplankton, (c) other organic detritus, (d) zooplankton, (e) inorganic detritus. Large plant fragments, composed mainly of algae and *Phyllospadix*, were abundant throughout the year and made up more than 50% in absolute volume of the samples except in June and July. The absolute volume of phytoplankton and zooplankton was noticeably higher in the spring and summer months. On a yearly basis, approximately 570 mg dry weight of suspended materials are available per m^3 of sea water.
14. Analysis of the association in terms of the protein content of the standing crop of the major trophic groups shows the following: filter feeding animals, 84 g/m^2; larger red algae and their attached epiphytes, 58 g/m^2; resident herbivores, 12 g/m^2; transient herbivore, 1.2 g/m^2; resident carnivores, 0.9 g/m^2; transient carnivores, 0.8 g/m^2; omnivores and scavengers, 1.3 g/m^2. Although the scraping and grazing herbivores feed on algae produced in the zone, much of the food consumed in the association is derived by importation of suspended detritus and plankton at high water.

Literature cited

ANONYMOUS
1958 California cooperative oceanic fisheries investigations. Progress Report. 1 July 1956—1 January 1958. — Calif. Dept. Fish & Game, mar. Res. Com.: 14—17.
1961 Eminent ecologist (Charles S. Elton). — Bull. ecol. Soc. Amer., **42** : 124—128.

ALLEE, W. C.
1934 Concerning the organization of marine coastal communities. — Ecol. Monog., **4** : 541—554.

American Ornithologist's Union
1957 Check-list of North American birds: 1—691. (Lord Baltimore Press, Inc. Baltimore).

BAKER, E. W. & G. W. WHARTON
1952 An introduction to acarology: 1—465. (Macmillan Publishing Co., New York).

BALLANTINE, D. & J. E. MORTON
1956 Filtering, feeding, and digestion in the lamellibranch Lasaea rubra. — J. mar. biol. Assoc. U. K., **35** : 241—274.

BARNES, H. & M. BARNES
1956 The general biology of Balanus glandula Darwin. — Pacific Sci., **10** : 415—422.

BEKLEMISHEV, K. V.
1957 The spatial interrelationships of marine zoo- and phytoplankton. — Trans. Inst. Oceanol., **20** : 206—226 (A.I.B.S. translation; original in Russian, with different pagination, not seen).

BENNETT, C. A. & N. L. FRANKLIN
1954 Statistical analysis in chemistry and the chemical industry: 1—724. (John Wiley & Sons, Inc., New York).

BENT, A. C.
1929 Life histories of North American shore birds. Order Limicolae, 2. — Bull. U. S. nation. Mus., **146**: 1—412.

BERKELEY, E. & C. BERKELEY
1938 Notes on Polychaeta from the coast of western Canada, 2. Syllidae. — Ann. Mag. nat. Hist., (11) **1**: 33—49.

BLINKS, L. R.
1955 Photosynthesis and productivity of littoral marine algae. — Sears Found. J. mar. Res., **14**: 363—373.

BOLIN, R. L.
1949 The linear distribution of intertidal organisms and its effect on their evolutionary potential. — Proc. XIII Intern. Congr. Zool.: 459.

BOLIN, R. L. & D. P. ABBOTT
1963 Studies on the marine climate and phytoplankton of the central coastal area of California. — Rept. Calif. Coop. oceanic Fisheries Invest., **8** (in press).

BOOLOOTIAN, R. A., A. C. GIESE, A. FARMANFARMAIAN & J. TUCKER
1959 Reproductive cycles of five west coast crabs. — Physiol. Zool., **32**: 213—220.

CASTENHOLZ, R. W.
1961 The effect of grazing on marine littoral diatom populations. — Ecology, **42**: 783—794.

COE, W. R.
1948 Nutrition, environmental conditions, and growth of marine bivalve mollusks. — J. mar. Res., **7**: 586—601.

COE, W. R. & D. L. FOX
1944 Biology of the California sea-mussel (Mytilus californianus), 3. Environmental conditions and rate of growth. — Biol. Bull., **87**: 59—72.

COLMAN, J.
1933 The nature of the intertidal zonation of plants and animals. — J. mar. biol. Assoc. U. K., **18**: 435—476.
1940 On the faunas inhabiting intertidal seaweeds. — J. mar. biol. Assoc. U. K., **24**: 129—183.

CONNELL, J. H.
1959 Studies of some factors affecting the recruitment and mortality of natural populations of intertidal barnacles: 226—233. In D. L. RAY (ed.), Mar. boring fouling organisms. (Univ. Washington Press, Seattle).

CONWAY, E. J.
1947 Microdiffusion analysis and volumetric error: 1—357. (C. Lockwood, London).

CORNWALL, I. E.
1937 A new species of barnacle from the coast of California. — Ann. Mag. nat. Hist., (10) **20**: 232—235.

CUPP, E. E.
1943 Marine plankton diatoms of the west coast of North America. — Univ. Calif. Publ. Oceanog., **5**: 1—238.

DOTY, M. S.
1946 Critical tide factors that are correlated with the vertical distribution of marine algae and other organisms along the Pacific Coast. — Ecology, **27**: 315—328.
1957 Rocky intertidal surfaces: 535—585. In J. W. HEDGPETH (ed.), Treatise mar. ecology & paleoecology. — Geol. Soc. America, **1**: 1—1296.

DROUET, F. & W. A. DAILY
1956 Revision of the coccoid Myxophyceae. — Butler Univ. botan. Studies, **12**: 1—218.

ELTON, C.
1927 Animal ecology: 1—207. (Macmillan, New York).

FAUVEL, P.
1923 Polychètes errantes. — Faune de France, **5**: 1—488.
FEDERER, W. T.
1955 Experimental design: 1—544. (Macmillan, New York).
FISCHER, P. H.
1940 Sur l'habitat de Lasaea rubra. — Bull. Mus. nation. Hist. nat. Paris, **12** 433—435.
FORBES, E.
1844 Report on the Mollusca and Radiata of the Aegean Sea, and on their distribution, considered as bearing on geology. — Rept. Meeting British Assoc. Adv. Sci., **13**: 130—193.
FOX, D. L. (ed.)
1936 The habitat and food of the California sea mussel. — Bull. Scripps Inst. Oceanog., **4**: 1—64.
FOX, D. L.
1957 Particulate organic detritus: 383—389. In J. W. HEDGPETH (ed.), Treatise mar. ecology & paleoecology. — Geol. Soc. America, **1**: 1—1296.
FRITCHMAN II, H. K.
1960 Acmaea paradigitalis sp. nov. (Acmaeidae, Gastropoda). — Veliger, **2**: 53—57.
1961 A study of the reproductive cycle in the California Acmaeidae (Gastropoda), 1. — Veliger, **3**: 57—63.
1961 Ibid., 2. — Veliger, **3**: 95—101.
1961 Ibid., 3. — Veliger, **4**: 41—47.
1962 Ibid., 4. — Veliger, **4**: 134—140.
FRUTON, J. S. & S. SIMMONDS
1958 General biochemistry: 1—1077. (John Wiley & Sons, Inc., New York).
GALLI, D. R. & A. C. GIESE
1959 Carbohydrate digestion in a herbivorous snail, Tegula funebralis. — J. exptl. Zool., **140**: 415—440.
GALLIHER, E. W.
1932 Sediments of Monterey Bay, California. — Mining Calif., Calif. Dept. nat. Resources., Div. Mines, **28**: 42—79.
GIESE, A. C.
1962 Cell physiology: 1—592. (W. B. Saunders Co., Philadelphia).
GISLÉN, T.
1929 Epibioses of the Gullmar Fjord, 1. — Kristineberg zool. Sta., **3**: 1—123.
1930 2. — Ibid., **4**: 1—380.
1943 Physiographical and ecological investigations concerning the littoral of the northern Pacific. — Lunds Univ. Arsskr. (N. F.) 2, **39**: 1—63.
1944 Do., 2. — Lunds Univ. Arsskr., (N.F.) 2, **40**: 1—92.
GLYNNE-WILLIAMS, J. & J. HOBART
1952 Studies on the crevice fauna of a selected shore in Anglesey. — Proc. zool. Soc. London, **122**: 797—824.
GRANT, A. R.
1938 The genus Acmaea. — Ph. D. Thesis. Dept. Zool. Univ. Calif., Berkeley.
GRINNELL, J. & A. H. MILLER
1944 The distribution of the birds of California. — Contrib. Mus. Vert. Zool. (Univ. Calif. Press, Berkeley): 1—608.
HAAS, F.
1942 The habits of some west coast bivalves. — Nautilus, **55**: 109—113.
HARDY, A. C.
1958 Toward prediction in the sea: 159—186. In A. A. BUZZATI-TRAVERSO (ed.) Perspectives in Marine Biology. (Univ. Calif. Press, Berkeley).

HARTMAN, O.
1959 Catalogue of the polychaetous annelids of the world, 1. — Allan Hancock Found. Publ., **23** : 1—353.

HEDGPETH, J. W.
1957 Introduction : 1—16. In J. W. HEDGPETH (ed.), Treatise on marine ecology & paleoecology. — Geol. Soc. America., **1**.

HEWATT, W. G.
1934 Ecological studies on selected marine intertidal communities of Monterey Bay. — Ph.D. Thesis, Dept. Biol. Stanford Univ.: 1—150.
1935 Ecological succession in the Mytilus californianus habitat as observed in Monterey Bay, California. — Ecology, **16** : 244—251.
1937 Ecological studies on selected marine intertidal communities of Monterey Bay, California. — Amer. Midland Natural., **18** : 161—206.
1938 Notes on the breeding seasons of the rocky beach fauna of Monterey Bay, California. — Proc. Calif. Acad. Sci., **23** : 283—288.

HIATT, R. W.
1948 The biology of the lined shore crab, Pachygrapsus crassipes Randall. — Pacific Sci., **2** : 135—213.

Hopkins Marine Station
1959/61 CCOFI hydrographic data collected on approximately weekly cruises on Monterey Bay, California. — Calif. Dept. Fish & Game, mar. Res. Com. (mimeo.).

HYMAN, L. H.
1951 The invertebrates. Platyhelminthes & Rhynchocoela. The acoelomate Bilateria : 1—550. (McGraw-Hill, New York).

KEEN, A. M.
1938 New pelecypod species of the genera Lasaea and Crassinella. — Proc. malacol. Soc., **23** : 18—32.

KIRK, P. L.
1950 Kjeldahl method for total nitrogen. — Anal. Chem., **22** : 354—358.

KYLIN, H.
1928 Entwicklunggeschichtliche Florideenstudien. — Lunds Univ. Arsskr., **24** : 1—127.
1956 Die Gattungen der Rhodophyceen: 1—673. (C.W.K. Gleerups Förlag, Lund).

LIGHT, S. F., R. I. SMITH, F. A. PITELKA, D. P. ABBOTT & F. M. WEESNER
1957 Intertidal invertebrates of the central California coast : 1—446. (Univ. Calif. Press, Berkeley).

MACGINITIE, G. E.
1935 Ecological aspects of a California marine estuary. — Amer. Midland Natural., **16** : 629—765.
1939 Littoral marine communities. — Ibid., **21** : 28—55.

MANSON, D. C. M.
1963 A new species of Hyadesia. — Entomol. Soc. Washington, **65** : 163—167.

MCLEAN, J. H.
1962 Manometric measurements of respiratory activity in Tegula funebralis. — Veliger, **4** : 191—193.

MEULEN, H. TER
1930 Note sur le dosage de l'azote dans les composés organiques par la méthode d'hydrogénation. — Rec. Trav. chim. Pays-Bas, **49** : 396—400.

MÖBIUS, K.
1883 The oyster and oyster-culture. — Rept. U. S. Fish Comm., **1880** (8): 683—751.

MOKYEVSKY, O. B.
1960a Littoral fauna of the northwestern shore of the Sea of Japan. — Trudy Inst. Oceanol., **34** : 242—328 (1959).

1960b Geographical zonation of marine littoral types. — Limnol. Oceanog., **5**, 389—396.

MOORE, H. B.
1935 The biology of Balanus balanoides, 4. Relation to environmental factors. — J. mar. biol. Assoc. U. K., **20** : 279—307.

MORTON, J. E.
1954 The crevice faunas of the upper intertidal zone at Wembury. — J. mar. biol. Assoc. U. K., **33** : 187—224.
1960 Molluscs. An introduction to their form and functions: 1—232. (Harper & Brothers, New York).

MORTON, J. E., A. D. BONEY & E. D. S. CORNER
1957 The adaptations of Lasaea rubra (Montagu), a small intertidal lamellibranch. J. mar. biol. Assoc. U. K., **36** : 383—405.

NEWELL, I. M.
1947 A systematic and ecological study of the Halacaridae of eastern North America. — Bull. Bingham oceanog. Coll., **10** : 1—232.

NICOL, J. A. C.
1960 The biology of marine animals : 1—707. (Interscience Pub. Inc., New York).

NORTH, W. J.
1954 Size distribution, erosive activities, and gross metabolic efficiency of the marine intertidal snails, Littorina planaxis and L. scutulata. — Biol. Bull., **106** : 185—197.

NORTHCRAFT, R. D.
1946 Colonization of bare rock surfaces by marine algae. — Ph. D. Thesis, Dept. Biol. Stanford Univ. : 1—45 and appendix.

ODUM, E. P.
1957 The ecosystem approach in the teaching of ecology illustrated with sample class data. — Ecology, **38** : 531—535.
1959 Fundamentals of ecology : 1—546. (W. B. Saunders Co., Philadelphia & London).

ODUM, H. T.
1957 Trophic structure and productivity of Silver Springs, Florida. — Ecol. Monogr., **27** : 55—112.

PETERSEN, C. G. J.
1918 The sea bottom and its production of fish-food. A survey of the work done in connection with the valuation of the Danish waters from 1883—1917. — Rept. Danish biol. Sta., **25** : 1—62.

PETERSEN, C. G. J. & P. B. JENSEN
1911 Valuation of the sea, 1. Animal life of the sea-bottom, its food and quantity. — Ibid., **20** : 3—81.

REISH, D. J.
1954 The life history and ecology of the polychaetous annelid Nereis grubei (Kinberg). — Allan Hancock Found. Publ., **14** : 1—75.

RICKETTS, E. F. & J. CALVIN
1952 Between Pacific tides (3rd ed., rev., J. W. Hedgpeth): 1—502. (Stanford Univ. Press, Stanford).
1962 Ibid. (3rd ed., 2nd rev., J. W. Hedgpeth): 1—516.

RIGG, G. B. & R. C. MILLER
1949 Intertidal plant and animal zonation in the vicinity of Neah Bay, Washington. — Proc. Calif. Acad. Sci., **26** : 323—351.

RYTHER, J. H.
1956 The measurement of primary production. — Limnol. Oceanog., **1** : 72—84.

SANDERS, H. L.
1960 Benthic studies in Buzzards Bay, 3. The structure of the soft-bottom community. — Limnol. Oceanog., **5** : 138—153.

SAUR, J. F. T.
1962 The variability of monthly mean sea level at six stations in the eastern North Pacific Ocean. — J. geophys. Res., **67** : 2781—2790.
SEGAL, E.
1956 Microgeographic variations as thermal acclimation in an intertidal mollusc. — Biol. Bull., **111** : 129—152.
SETTE, O. E. & J. D. ISAACS (eds.)
1960 Symposium on "The changing Pacific Ocean in 1957 and 1958". — Rept. Calif. coop. oceanic Fisheries Invest., **7** : 13—217.
SHELFORD, V. E.
1930 Geographic extent and succession in Pacific North American intertidal (Balanus) communities. — Publ. Puget Sound biol. Sta., **7** : 217—223.
SHELFORD, V. E., A. O. WEESE, L. A. RICE, D. I. RASMUSSEN, N. M. WISMER & J. H. SWANSON
1935 Some marine biotic cummunities of the Pacific coast of North America. — Ecol. Monogr., **5** : 249—354.
SHOTWELL, J. A.
1950 The vertical zonation of Acmaea, the limpet. — Ecology, **31** : 647—649.
SKOGSBERG, T.
1936 Hydrography of Monterey Bay, California. Thermal conditions, 1929—1933. — Trans. American phil. Soc., (n.s.) **29** : 1—152.
SMITH, G. M.
1944 Marine algae of the Monterey Peninsula : 1—622. (Stanford Univ. Press, Stanford).
SMITH, A. G. & M. GORDON, Jr.
1948 The marine mollusks and brachiopods of Monterey Bay, California, and vicinity. — Proc. Calif. Acad. Sci., **26** : 147—245.
SPÄRCK, R.
1933 Contributions to the animal ecology of the Franz Joseph Fjord and adjacent waters, 1—2. — Medd. Grønland, **100** : 1—38.
STEPHENSON, T. A. & A. STEPHENSON
1949 The universal features of zonation between tidemarks on rocky coasts. — J. Ecology, **37** : 289—305.
STOHLER, R.
1930 Beitrag zur Kenntnis des Geschlechtszyklus von Mytilus californianus Conrad. — Zool. Anz., **90** : 263—268.
TEAL, J. M.
1957 Community metabolism in a temperate cold spring. — Ecol. Monogr., **27** : 283—302.
TEST, A. R. (GRANT)
1945 Ecology of California Acmaea. — Ecology, **26** : 395—405.
THORSON, G.
1934 Contributions to the animal ecology of the Scoresby Sound Fjord complex (East Greenland). — Medd. Grønland, **100** : 1—67.
1957 Bottom communities (sublittoral or shallow shelf): 461—534. In J. W. HEDGPETH (ed.), Treatise on marine ecology & paleoecology. — Geol. Soc. America, **1** : 1—1296.
TUKEY, J. W.
1949 Comparing individual means in the analysis of variance. — Biometrics, **5** : 99—114.
UMEZAKI, I.
1961 The marine blue-green algae of Japan. — Mem. Coll. Agr., **83** : 1—149.
United States Department of Commerce
1959 Tide tables. High and low water predictions, 1961. West coast of North and South America, including the Hawaiian Islands : 1—223. (Coast Geodetic Survey, Washington, D.C.).

USINGER, R. L. (ed.)
1956 Aquatic insects of California, with keys to North American genera and California species: 1—508. (Univ. Calif. Press, Berkeley).

VERRILL, A. E.
1873 Report upon the invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical characters of the region. — Rept. U. S. Fish Comm., **1871—72** : 295—778.

VINOGRADOV, A. P.
1953 The elementary chemical composition of marine organisms. — Mem. Sears Found. mar. Res., Yale Univ.: 1—647.

WHEDON, W. F.
1936 Spawning habits of the mussel Mytilus californianus Conrad, with notes on the possible relation to mussel poison. Mussel poison, 1. — Univ. Calif. Publ. Zool., **41** : 35—44.

WIESER, W.
1952 Investigations of the microfauna inhabiting seaweeds on rocky coasts. — J. mar. biol. Assoc. U. K., **31** : 145—174.
1960 Benthic studies in Buzzards Bay, 2. The meiofauna. — Limnol. Oceanog., **5** : 121—137.

YONGE, C. M.
1962 Ciliary currents in the mantle cavity of species of Acmaea. — Veliger, **4** : 119—123.

YOUNG, R. T.
1941 The distribution of the mussel (Mytilus californianus) in relation to the salinity of its environment. — Ecology, **22** : 379—386.
1945 Stimulation of spawning in the mussel (Mytilus californianus). Ecology, **26** : 58—69.

Appendix I

Numbers or presence of all species collected from sixteen quadrat samples

Each number indicates total number of individuals of all ages present in the quadrat sample. The presence of some species that were not counted is indicated in the tabulation by a plus mark (+). Dashes (—) indicate the absence of a species.

The numbers of *Lasaea cistula* in each of the quadrats from I through XII were extrapolated from the dry weights of known portions of the samples. A direct count and dry weight determination was made of a fraction (between 300 to 500 individuals) of the *Lasaea* specimens in each of the quadrat samples. An estimation of the total number of *Lasaea* present was then calculated from the dry weight of the entire sample.

All counts of the Cirripedia were made on freshly-killed animals still adhering to the rock surface. The numbers per quadrat given in this tabulation are minimal values, because some of the quadrat samples were taken where populations were so closely crowded that high accuracy of counts was unattainable.

The numbers of *Suidasia* sp. were determined in quadrat samples X, XI and H_1 only. This species was the smallest of the mites actually counted, and was especially difficult to enumerate because of its intimate situation between the closely appressed shell plates of *Balanus glandula*.

APPENDIX I

Species / Quadrats	L_1	L_2	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	H_1	H_2
CHLOROPHYTA																
Cladophora sp.	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—
RHODOPHYTA																
Endocladia muricata	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Gigartina agardhii	+	+	—	+	+	+	+	+	+	+	+	+	+	—	+	—
Gelidium coulteri	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—
Porphyra schizophylla	—	—	+	+	+	—	—	—	—	—	+	+	—	—	—	—
Rhodoglossum affine	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—
PHAEOPHYTA																
Pelvetiopsis limitata	—	—	—	—	+	—	—	—	—	—	—	—	+	+	—	—
ANGIOSPERMAE																
Phyllospadix torreyi (seedling)	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
COELENTERATA																
Abietinaria sp.	—	+	+	+	+	+	—	+	+	+	+	—	+	+	—	—
Sertularia sp.	—	+	—	—	+	—	—	—	—	—	+	—	—	—	—	—
Anthopleura elegantissima	—	—	—	—	1	—	—	—	—	1	—	—	—	—	—	—
PLATYHELMINTHES																
Notoplana acticola	—	1	1	—	—	—	3	—	—	—	1	1	—	—	—	—
NEMERTEA																
Emplectonema gracile	3	3	2	12	10	1	6	—	—	5	1	3	2	13	—	—
Nemertopsis gracilis	1	—	48	55	42	1	3	18	8	3	2	8	2	8	—	—
ANNELIDA																
Syllis spenceri	5	16	58	41	39	1	53	43	82	24	35	17	39	37	—	—
Syllis vittata	3	28	29	1	2	2	22	14	1	13	19	7	—	—	—	—
Syllis armillaris	2	7	21	140	127	25	78	123	1	66	54	22	24	2	—	—
Perinereis monterea	—	—	6	3	3	—	3	4	—	2	1	1	—	—	—	—
Dexiospira spirillum	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Phragmatopoma californica	1	1	—	—	—	—	—	—	—	2	—	—	—	—	—	—
Nereis grubei	6	4	3	—	2	1	2	2	—	—	2	5	—	—	—	—
Syllidae (unident.)	—	2	—	1	8	1	4	—	—	—	—	—	—	1	5	—
Oligochaeta (unident.)	—	—	7	31	5	68	3	1	—	19	1	5	—	—	1	—
BRYOZOA																
Filicrisia franciscana	+	+	+	+	+	+	+	+	+	+	+	+	+	+	—	—
MOLLUSCA																
Pelecypoda																
Hiatella arctica	13	26	1	—	—	—	—	—	—	—	—	—	—	—	—	—
Lasaea cistula	117	193	6,400	11,100	3,700	4,700	7,400	7,600	5,500	6,600	6,800	7,600	5,600	1,100	66	805
Mytilus californianus	53	397	521	495	—	4	55	55	220	38	44	46	32	78	—	—
Musculus sp.	358	543	876	36	319	—	7	7	6	6	53	2,382	34	15	—	1

APPENDIX I (CONTINUED)

	L_1	L_2	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	H_1	H_2
Gastropoda																
Acmaea paradigitalis	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
Acmaea digitalis	1	2	18	43	36	11	6	11	39	32	2	8	31	5	5	2
Acmaea scabra	14	32	59	27	45	16	7	11	28	18	10	10	16	43	7	5
Acmaea pelta	16	25	21	22	21	2	3	3	6	15	1	—	3	11	—	—
Acmaea limatula	—	1	—	—	—	—	1	1	—	7	4	1	—	—	—	—
Ocenebra circumtexta	1	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Littorina scutulata	15	11	188	541	1,053	1,149	444	337	113	326	95	482	772	1,126	105	544
Littorina planaxis	—	—	10	33	12	106	7	—	545	8	1	94	808	—	46	46
Acanthina spirata	—	—	—	1	5	—	1	9	—	1	—	—	—	—	—	—
Thais emarginata	3	5	—	2	1	—	9	3	—	—	2	1	—	—	—	—
Tegula funebralis	1	28	—	1	1	—	3	21	—	—	5	—	—	—	—	—
Barleeia oldroydi	63	28	25	—	2	—	2	19	—	5	—	18	—	6	—	—
Tricolia pulloides	15	30	—	—	5	—	2	1	—	—	3	4	—	1	—	—
Unident. gastropods	—	3	5	13	49	1	9	63	34	54	4	6	5	3	—	—
Amphineura																
Cyanoplax dentiens	8	1	5	—	12	—	3	—	—	3	2	1	1	—	—	—
ECHINODERMATA																
Leptasterias pusilla	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
ARTHROPODA																
Crustacea																
Balanus glandula	255	304	372	150	116	519	38	138	320	94	35	1,619	1,232	1,043	239	495
Chthamalus dalli	1,197	231	706	14	8	32	11	45	77	5	13	162	18	240	46	33
Chthamalus microtretus												1	—	8	28	6
Tetraclita rubescens	35	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mitella polymerus	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—
Dynamenella glabra	32	56	129	122	194	1	229	262	10	41	95	290	12	117	—	—
Excirolana chiltoni	—	1	—	—	—	1	—	3	—	—	—	1	—	—	—	—
Chelifera (unident.)	2	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Allorchestes ptilocerus	73	86	21	—	—	—	18	1	—	—	15	7	—	2	—	—
Hyale sp.	23	50	1	—	2	31	—	18	46	—	1	15	15	44	8	12
Pontogeneia sp.	4	21	—	—	—	—	2	—	—	—	—	2	—	—	—	—
Pachygrapsus crassipes (juvenile)	1	—	2	2	1	—	—	8	—	3	2	—	—	—	—	—
Insecta																
Diaulota densissima	—	—	21	44	32	45	31	7	93	20	31	89	62	37	1	39
Tipulidae (unident.)	4	—	3	1	1	14	25	13	15	31	20	40	7	9	1	5
Ephydridae (unident.)	—	—	2	—	—	1	5	2	3	—	—	—	6	12	2	—
Arachnida																
Rhombognathus sp.	—	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Agauopsis sp.	4	3	71	14	13	1	7	76	5	63	13	160	49	11	9	3
Ameronothrus sp.	—	—	—	—	—	—	—	1	—	2	—	—	—	—	—	—
Parasitidae (unident.)	—	—	—	—	—	—	5	2	—	—	1	1	1	—	—	—
Suidasia sp.	—	—	+	+	+	+	+	+	+	+	+	209	1,115	+	242	+
Mesostigmata (unident.)	—	—	—	24	3	2	37	15	29	51	3	1	52	3	—	3

APPENDIX II

Dry weights (mg) of total number of each species collected from quadrat samples

Non-preserved samples of *Endocladia muricata* and *Gigartina agardhii* were weighed with a triple beam balance to the nearest 0.01 g, and have been converted to mg weights in this tabulation. *Gigartina agardhii* in Quadrats III, XI, and H_1, and *E. muricata* in Quadrat H_1, were weighed on a balance accurate to the nearest 0.1 mg.

The weights of the Cirripedia in each of the 14 quadrats were extrapolated from the relation between the known number of individuals in the five size-classes making up the sample and the mean weight of five individuals representative of each of these classes. For example, each barnacle in the quadrat sample belonging to the 2 mm size-class (range, 1.0—2.9) was calculated to have a dry weight of 3.8 mg, the mean dry weight of five individuals. For further explanation see text under *Balanus glandula.*

The weights of *Chthamalus dalli* and *C. microtretus* are combined in quadrats I through IX, because of the difficulty in separating these species in this phase of the study.

Species	Quadrats	L1	L2	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	H1	H2
ALGAE																	
Chlorophyta																	
Cladophora sp.		—	—	—	—	2.7	—	—	—	—	—	—	—	—	—	—	—
Rhodophyta																	
En..ocladia muricata		14,850	29,670	14,670	18,180	15,630	6,420	8,070	12,790	11,550	7,320	13,070	10,260	2,900	5,030	20.0	550
Gigartina agardhii		5,220	990	—	340	15.7	1,760	2,840	1,050	390	8,490	9,700	830	40.0	—	3.0	—
Gelidium coulteri		—	—	194.0	—	—	—	—	—	—	—	—	—	—	—	—	—
Porphyra schizophylla		—	—	8.2	3.3	6.1	—	—	—	—	—	10.6	0.1	—	—	—	—
Rhodoglossum affine		—	—	1,340.0	—	—	—	—	—	—	—	—	—	—	—	—	—
Phaeophyta																	
Pelvetiopsis limitata		—	—	—	—	1.4	—	—	—	—	—	—	—	1.5	0.7	—	—
ANGIOSPERMAE																	
Phyllospadix torreyi (seedling)		—	15.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—
COELENTERATA																	
Abietinaria sp.		—	0.4	0.1	0.1	0.2	0.2	—	0.1	0.1	1.1	3.7	—	<0.1	0.2	—	—
Sertularia sp.		—	0.1	—	—	<0.1	—	—	—	—	—	—	—	—	—	—	—
Anthopleura elegantissima		—	—	—	—	103.0	—	—	—	—	10.6	—	—	—	—	—	—
PLATYHELMINTHES																	
Notoplana acticola		—	—	7.8	—	—	—	22.0	—	—	—	2.1	0.9	—	—	—	—
NEMERTEA																	
Emplectonema gracile		7.7	39.4	4.7	37.6	38.2	1.0	58.3	—	—	21.5	5.6	20.0	19.5	61.2	—	—
Nemertopsis gracilis		1.0	—	54.1	86.1	64.0	0.8	5.5	20.5	23.2	6.8	1.0	17.5	4.3	5.3	—	—
ANNELIDA																	
Syllis spenceri		14.1	22.7	90.7	71.0	43.5	2.7	43.7	53.8	185.4	31.8	20.7	38.1	69.6	96.1	—	—
Syllis vittata		1.0	17.0	16.8	0.8	1.9	0.1	11.0	9.6	0.4	9.8	5.7	0.9	—	—	—	—
Syllis armillaris		1.8	1.1	5.2	4.9	8.1	3.4	7.4	8.0	0.1	3.2	3.2	3.3	4.7	0.1	—	—
Perinereis monterea		—	—	18.3	57.0	32.1	—	11.0	22.1	—	2.3	2.1	0.4	—	—	—	—
Dexiospira spirillum		1.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Phragmatopoma californica		0.7	1.0	—	—	—	—	—	—	—	<0.1	—	—	—	—	—	—
Nereis grubei		10.3	1.0	5.8	—	1.4	<0.1	2.8	4.0	—	—	0.4	0.2	—	—	—	—
Syllidae (unident.)		—	<0.1	—	0.7	1.0	<0.1	0.4	—	—	—	—	—	—	<0.1	—	—
Oligochaeta (unident.)		—	—	0.1	0.9	0.1	3.5	0.1	<0.1	—	0.2	<0.1	0.1	—	—	<0.1	—
BRYOZOA																	
Filicrisia franciscana		6.7	18.1	3.3	8.2	1.1	0.1	3.8	34.8	9.2	2.4	4.4	0.3	0.9	14.7	—	—
MOLLUSCA																	
Pelecypoda																	
Hiatella arctica		14.6	32.2	5.8	—	—	—	—	—	—	—	—	—	—	—	—	—
Lasaea cistula		63.3	80.1	3,025.1	2,777.2	1,814.8	1,607.1	2,393.3	2,215.6	1,562.8	1,923.0	3,601.9	1,718.1	2,160.1	362.7	17.7	271.1
Mytilus californianus		430.4	477.3	1,947.0	297.3	—	0.9	39.6	13.7	62.8	50.4	30.3	564.6	9.1	8.5	—	—
Musculus sp.		271.5	559.8	218.2	15.0	23.2	—	2.0	1.5	1.8	2.8	14.7	585.7	8.5	6.0	—	0.2

Species Quadrats	L1	L2	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	H1	H2
Gastropoda																
Acmaea paradigitalis	1.4	—	—	—	2.1	—	—	—	—	—	—	—	—	—	—	—
Acmaea digitalis	19.6	50.7	821.8	1,249.5	783.1	339.1	187.5	363.4	1,151.8	748.8	389.7	72.4	1,693.7	843.8	524.3	173.3
Acmaea scabra	177.9	136.4	644.6	302.9	294.8	131.3	91.9	213.0	1,073.5	91.6	74.1	631.8	112.3	972.9	356.1	219.1
Acmaea pelta	36.5	48.6	44.4	64.8	38.6	8.5	12.5	35.3	32.7	35.1	0.5	—	28.0	87.9	—	—
Acmaea limatula	—	15.2	—	—	—	—	3.5	34.9	—	40.7	17.4	9.0	—	—	—	—
Ocenebra circumtexta	—	134.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Littorina scutulata	310.2	202.1	1,036.3	2,610.6	4,146.8	10,299.8	4,228.9	3,597.1	882.6	7,747.1	3,595.0	2,397.5	2,222.5	488.0	807.2	1,971.6
Littorina planaxis	—	—	235.1	1,261.7	50.3	1,055.1	52.9	—	431.0	626.0	33.6	73.6	1,197.8	—	1,143.3	1,478.3
Acanthina spirata	—	—	—	2,925.9	1,634.5	—	163.1	1,185.7	—	221.1	—	—	—	—	—	—
Thais emarginata	140.1	384.8	—	113.9	123.3	—	131.4	94.3	—	—	1.8	0.5	—	—	—	—
Tegula funebralis	102.6	282.2	—	2.5	50.3	—	57.7	6,214.3	—	—	1,565.5	—	—	—	—	—
Barleeia oldroydi	60.3	20.8	12.0	—	0.4	—	0.4	4.6	—	1.5	—	2.7	—	2.2	—	—
Tricolia pulloides	34.6	42.2	—	—	2.1	—	0.3	0.4	—	—	0.7	1.8	—	1.0	—	—
Gastropoda (unident.)	—	1.6	0.8	1.2	6.2	0.1	1.1	6.4	8.1	19.3	0.4	0.9	0.1	0.3	—	—
Amphineura																
Cyanoplax dentiens	18.9	8.8	4.9	—	9.2	—	21.9	—	—	25.0	3.1	0.1	<0.1	—	—	—
ECHINODERMATA																
Leptasterias pusilla	—	61.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
ARTHROPODA																
Crustacea																
Balanus glandula	+	+	105,000	46,000	19,400	187,000	32,000	42,000	151,000	35,000	8,300	113,000	154,000	114,000	49,000	107,000
Chthamalus dalli	+	+	1,920	380	45	400	83	420	2,700	142	210	4,600	230	2,200	1,610	280
Chthamalus microtretus	+	+										43	—	21	1,060	106
Tetraclita rubescens	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mitella polymerus	—	1.4	1.0	—	—	—	—	—	—	—	—	—	—	—	—	—
Dynamenella glabra	4.1	7.4	20.8	17.2	34.3	0.1	59.1	27.7	3.3	5.7	18.0	94.8	3.8	51.5	—	—
Excirolana chiltoni	—	12.0	—	—	—	1.1	—	1.1	—	—	—	0.8	—	—	—	—
Chelifera (unident.)	<0.1	—	—	0.1	—	—	—	—	—	—	—	—	—	—	—	—
Allorchestes ptilocerus	19.9	23.5	8.5	—	—	—	7.2	0.6	—	—	11.6	1.0	—	1.1	—	—
Hyale sp.	11.9	22.0	0.3	—	1.9	10.9	—	2.5	19.0	—	0.4	5.0	6.6	28.4	1.8	7.3
Pontogeneia sp.	4.3	6.9	—	—	—	—	1.1	—	—	—	—	0.4	—	—	—	—
Pachygrapsus crassipes (juvenile)	4.8	—	12.0	10.5	19.0	—	—	50.4	—	35.2	32.1	—	—	—	—	—
Insecta																
Diaulota densissima	—	—	1.5	3.5	2.1	4.1	2.9	0.4	9.3	1.3	2.6	7.6	4.8	3.2	0.1	4.3
Tipulidae (unident.)	7.5	—	0.9	0.3	0.2	7.7	27.4	23.3	25.7	38.7	11.3	8.1	5.9	1.4	0.4	3.5
Ephydridae (unident.)	—	—	1.8	—	—	0.1	<0.1	0.3	4.6	—	—	—	4.8	32.6	2.8	—
Arachnida																
Rhombognathus sp.	—	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Agauopsis sp.	<0.1	<0.1	0.9	0.3	<0.1	<0.1	0.2	0.9	<0.1	0.8	0.1	1.7	0.6	0.1	<0.1	<0.1
Ameronothrus sp.	—	—	—	—	—	—	—	+	—	+	—	—	—	—	—	—
Parasitidae (unident.)	—	—	—	—	—	—	+	+	—	—	+	+	+	—	—	—
Suidasia sp.	—	—	+	+	+	+	+	+	+	+	+	0.8	3.7	+	0.3	+
Mesostigmata (unident.)	—	—	—	0.4	0.1	<0.1	0.5	0.2	0.3	0.6	<0.1	<0.1	0.5	0.1	—	<0.1

Appendix III

Protein-nitrogen content of some members of the *Endocladia-Balanus* association

Dry weight refers to the minimum weight attained at 35—40° C for two days in partial vacuum (20—25 mm Hg). The desiccants used were anhydrous P_2O_5, 36 N H_2SO_4, and anhydrous $CaCl_2$.

All preserved material was pickled in 95% ethanol.

None of the animals in this tabulation was allowed to clear its gut for any constant or prolonged time prior to analysis. However, all of the material was collected at low water, when feeding activity for most species was at a minimum.

In arriving at the nitrogen content (mg), calculations were carried out to the second and sometimes the third decimal place. Often these figures were used in the statistical treatment of data, but the percent nitrogen values have been rounded off so that only significant figures remain.

Group	Species	Collection date	Size (mm)	Dry wt. (mg)	Nitrogen (mg)	Percent nitrogen	Remarks
Algae	*Endocladia muricata*	July 10, 1959	—	135.9	4.74	3.5	Each sample represented
				114.2	4.18	3.7	small sprigs from different
				127.0	4.54	3.6	plants.
		October 30, 1959	—	128.8	4.34	3.4	Not preserved.
				131.9	3.85	2.9	
				139.7	4.48	3.2	
		January 13, 1960	—	108.7	3.09	2.8	
				118.3	3.64	3.1	
				164.8	5.01	3.0	
		April 15, 1960	—	154.6	4.18	2.7	
				138.7	3.37	2.4	
				144.3	3.79	2.6	
	Gigartina agardhii	September 4, 1959	—	159.8	4.16	2.6	Each sample represented
				136.4	3.75	2.8	small sprigs from different
				82.7	1.92	2.3	plants.
		January 13, 1960	—	171.8	6.10	3.6	Not preserved.
				168.5	5.90	3.5	
				73.0	2.34	3.2	
		April 15, 1960	—	104.6	2.06	2.0	
				102.7	2.07	2.0	
				136.6	2.95	2.2	
		June 15, 1960	—	107.8	2.87	2.7	
				102.9	2.62	2.5	
				123.0	3.22	2.6	
Polycladida	*Notoplana acticola*	November 7, 1961	—	9.0	1.22	13.9	Sample of two individuals. Not preserved.
Nemertea	*Emplectonema gracile*	October 23, 1961	—	11.8	1.05	8.9	Not preserved.
				11.8	1.03	8.7	
				3.2	0.24	7.4	

Group	Species	Collection date	Size (mm)	Dry wt. (mg)	Nitrogen (mg)	Percent nitrogen	Remarks
	Nemertopsis gracilis	November 7, 1961	—	11.8	1.35	11.4	Sample of two individuals. Not preserved.
Polychaeta	*Syllis spenceri*	October 15, 1960	—	3.6	0.38	10.6	Preserved.
				2.5	0.27	10.7	
				3.7	0.36	9.8	
		April 9, 1960	—	3.0	0.38	12.7	
				1.2	0.15	12.5	
				1.6	0.26	16.2	
				3.6	0.45	12.5	
				2.1	0.27	12.9	
				1.7	0.24	14.1	
				3.6	0.46	12.8	
		January 16, 1961	—	4.9	0.63	12.9	
				1.7	0.24	14.1	
				5.0	0.61	12.2	
				3.8	0.50	13.2	
				2.1	0.32	15.2	
	Syllis vittata	November 7, 1961	—	8.8	1.04	11.8	Sample of five specimens. Not preserved.
	Perinereis monterea	March 19, 1959	—	18.3	2.46	13.4	Preserved.
Bryozoa	*Filicrisia franciscana*	January 13, 1960	—	34.8	0.25	0.7	Sample of many separate branches (different colonies). Preserved.
Mollusca	*Lasaea cistula*	April 9, 1960	0.65— 0.94	2.0	0.03	1.5	Samples in April, July,
			0.95— 1.24	4.7	0.06	1.3	October, and January pre-
			1.25— 1.54	5.8	0.07	1.2	served. February sample
			1.55— 1.84	5.1	0.07	1.4	not-preserved. The size of
			1.85— 2.14	10.1	0.14	1.4	each sample is indicated
			2.15— 2.44	13.4	0.20	1.5	by the limits within which
			2.45— 2.74	18.5	0.24	1.3	the greatest shell length

Group	Species	Collection date	Size (mm)	Dry wt. (mg)	Nitrogen (mg)	Percent nitrogen	Remarks
			2.75— 3.04	2.2	0.04	1.8	was measured with an ocular micrometer. Each of the two size-class samples from 0.65 to 1.24 mm was composed of 40 individuals. The 1.25 to 1.54 mm size-class contained 20 specimens; the four size-classes ranging from 1.55 to 2.74 mm were made up of 10 specimens each, and the last class represents one individual only.
		July 17, 1960	0.65— 0.94	1.9	0.03	1.6	
			0.95— 1.24	4.9	0.07	1.4	
			1.25— 1.54	5.2	0.09	1.7	
			1.55— 1.84	5.1	0.09	1.8	
			1.85— 2.14	10.1	0.17	1.7	
			2.15— 2.44	14.5	0.26	1.8	
			2.45— 2.74	21.1	0.36	1.7	
			2.75— 3.04	3.1	0.04	1.3	
		October 15, 1960	0.65— 0.94	2.1	0.03	1.4	
			0.95— 1.24	5.2	0.09	1.7	
			1.25— 1.54	5.4	0.09	1.7	
			1.55— 1.84	5.6	0.08	1.4	
			1.85— 2.14	8.9	0.14	1.6	
			2.15— 2.44	11.7	0.19	1.6	
			2.45— 2.74	18.0	0.27	1.5	
			2.75— 3.04	2.2	0.04	1.8	
		January 16, 1961	0.65— 0.94	2.1	0.03	1.4	
			0.95— 1.24	4.3	0.07	1.6	
			1.25— 1.54	4.9	0.08	1.6	
			1.55— 1.84	5.5	0.09	1.6	
			1.85— 2.14	9.2	0.15	1.6	
			2.15— 2.44	14.2	0.18	1.3	
			2.45— 2.74	21.7	0.33	1.5	
		February 18, 1961	0.65— 0.94	2.4	0.05	2.1	
			0.95— 1.24	5.6	0.10	1.8	
			1.25— 1.54	5.9	0.10	1.7	
			1.55— 1.84	5.0	0.08	1.6	
			1.85— 2.14	10.1	0.19	1.9	
			2.15— 2.44	16.9	0.30	1.8	
			2.45— 2.74	24.0	0.41	1.7	
			2.75— 3.04	2.8	0.05	1.8	

Group	Species	Collection date	Size (mm)	Dry wt. (mg)	Nitrogen (mg)	Percent nitrogen	Remarks
	Littorina scutulata	April 9, 1960	0.5 — 1.4	(0.3)	(0.004)	(1.3)	Samples in April, June. July, October, and January preserved from six months to one year. February sample not preserved. The size-classes represent the limits within which the greatest shell height was measured with a 0.5 mm rule. Since a balance weighing to the nearest 0.1 mg was used, the figures obtained for very small specimens are placed within brackets, indicating their uncertain reliability.
			1.5 — 2.4	(0.8)	(0.011)	(1.2)	
			1.5 — 2.4	1.6	0.02	1.2	
			2.5 — 3.4	3.0	0.04	1.3	
			3.5 — 4.4	7.7	0.07	0.9	
			4.5 — 5.4	19.1	0.16	0.8	
			5.5 — 6.4	36.9	0.22	0.6	
			6.5 — 7.4	46.8	0.34	0.7	
		June 13, 1960	0.5 — 1.4	(0.2)	(0.003)	1.5	
			1.5 — 2.4	1.3	0.01	1.1	
			2.5 — 3.4	1.4	0.02	1.8	
			2.5 — 3.4	3.7	0.05	1.3	
			2.5 — 3.4	6.2	0.07	1.1	
			3.5 — 4.4	14.5	0.12	0.8	
			3.5 — 4.4	14.5	0.12	0.8	
			4.5 — 5.4	25.9	0.15	0.6	
			4.5 — 5.4	22.2	0.19	0.9	
			4.5 — 5.4	17.3	0.15	0.9	
			5.5 — 6.4	40.6	0.26	0.6	
		July 17, 1960	2.5 — 3.4	2.2	0.02	0.9	
			3.5 — 4.4	8.9	0.08	0.9	
			3.5 — 4.4	6.2	0.05	0.8	
			3.5 — 4.4	8.7	0.07	0.8	
			4.5 — 5.4	21.6	0.16	0.7	
			5.5 — 6.4	23.7	0.18	0.8	
		October 15, 1960	2.5 — 3.4	5.4	0.07	1.3	
			3.5 — 4.4	6.4	0.08	1.2	
			4.5 — 5.4	23.6	0.19	0.8	
			5.5 — 6.4	65.7	0.43	0.7	
			5.5 — 6.4	34.2	0.26	0.8	
			5.5 — 6.4	33.4	0.25	0.7	
		January 16, 1961	0.5 — 1.4	(0.7)	(0.007)	(1.0)	

Group	Species	Collection date	Size (mm)	Dry wt. (mg)	Nitrogen (mg)	Percent nitrogen	Remarks
			1.5 — 2.4	(0.9)	(0.014)	(1.6)	
			2.5 — 3.4	5.9	0.08	1.4	
			3.5 — 4.4	8.0	0.10	1.2	
			4.5 — 5.4	19.5	0.18	0.9	
			5.5 — 6.4	38.9	0.31	0.8	
			6.5 — 7.4	57.0	0.36	0.6	
			6.5 — 7.4	57.9	0.39	0.7	
			6.5 — 7.4	54.9	0.43	0.8	
		February 18, 1961	1.5 — 2.4	(0.3)	(0.003)	(1.0)	
			1.5 — 2.4	(0.8)	(0.014)	(1.8)	
			2.5 — 3.4	3.3	0.06	1.8	
			2.5 — 3.4	3.9	0.07	1.8	
			3.5 — 4.4	11.7	0.15	1.3	
			3.5 — 4.4	13.3	0.16	1.2	
			4.5 — 5.4	25.2	0.20	0.8	
			4.5 — 5.4	26.3	0.24	0.9	
			5.5 — 6.4	36.0	0.30	0.8	
			5.5 — 6.4	31.6	0.27	0.9	
			6.5 — 7.4	51.8	0.54	1.0	
			6.5 — 7.4	58.2	0.54	0.9	
	Littorina planaxis	October 23, 1961	—	32.6	0.33	1.0	Not preserved.
				45.9	0.44	1.0	
				23.8	0.26	1.1	
	Acmaea digitalis	April 9, 1960	2.5 — 3.4	1.6	0.03	1.9	April, July, October, and January preserved from about six months to one year. February not preserved.
			3.5 — 4.4	4.2	0.09	2.1	
			4.5 — 5.4	10.4	0.20	1.9	
			9.5 —10.4	76.9	1.43	1.9	
		July 17, 1960	3.5 — 4.4	7.2	0.15	2.1	
			5.5 — 6.4	18.0	0.35	1.9	
			12.5 —13.4	209.1	3.94	1.9	
		October 15, 1960	5.5 — 6.4	16.6	0.40	2.4	
			7.5 — 8.4	40.6	0.82	2.0	

Group	Species	Collection date	Size (mm)	Dry wt. (mg)	Nitrogen (mg)	Percent nitrogen	Remarks
			9.5 —10.4	105.3	1.85	1.8	
			11.5 —12.4	150.3	2.88	1.9	
		January 16, 1961	7.5 — 8.4	37.1	0.95	2.6	
			8.5 — 9.4	54.9	1.36	2.5	
			12.5 —13.4	196.0	4.95	2.5	
			14.5 —15.4	343.4	6.87	2.0	
		February 18, 1961	3.5 — 4.4	2.4	0.06	2.5	
			4.5 — 5.4	14.1	0.26	1.8	
			4.5 — 5.4	15.1	0.32	2.1	
			5.5 — 6.4	20.1	0.44	2.2	
			6.5 — 7.4	41.7	0.75	1.8	
			7.5 — 8.4	52.2	1.00	1.9	
			8.5 — 9.4	57.0	1.30	2.3	
			8.5 — 9.4	65.0	1.23	1.9	
			14.5 —15.4	254.5	4.91	1.9	
			15.5 —16.4	395.1	7.37	1.9	
	Acmaea scabra	November 7, 1961		93.8	2.10	2.2	Not preserved.
				38.4	0.97	2.5	
				36.3	1.01	2.8	
	Acmaea pelta	November 7, 1961	—	5.3	0.17	3.2	Not preserved.
	Mytilus californianus	October 23, 1961	—	14.2	0.33	2.3	Not preserved.
				16.7	0.36	2.2	
				26.8	0.56	2.1	
	Musculus sp.	October 23, 1961	0.7 — 3.4	23.2	0.75	3.2	Sample of 20 specimens. Greatest shell length ranged within the limits given. Not preserved.
	Cyanoplax dentiens	April 15, 1960	—	25.0	1.05	4.2	Preserved.
	Acanthina spirata	November 7, 1961	—	420.8	3.87	0.9	Not preserved.
				632.7	5.33	0.8	
	Thais emarginata	October 23, 1961	—	75.2	1.01	1.3	Not preserved.
				241.5	3.63	1.5	

Group	Species	Collection date	Size (mm)	Dry wt. (mg)	Nitrogen (mg)	Percent nitrogen	Remarks
				374.8	4.88	1.3	
	Tegula funebralis	October 23, 1961	—	386.7	4.42	1.1	Not preserved.
				574.7	6.77	1.2	
				575.7	7.39	1.3	
Arthropoda	*Balanus glandula*	April 9, 1960	3.0 — 5.9	23.5	0.14	0.6	April, July, October, and January specimens preserved from about six months to one year. February not preserved. Size-classes represent estimated limits of combined height and basal diameter.
			3.0 — 5.9	25.7	0.17	0.7	
			3.0 — 5.9	24.3	0.20	0.8	
			6.0 —11.9	293.7	1.32	0.4	
			6.0 —11.9	149.6	0.98	0.7	
			6.0 —11.9	207.3	1.44	0.7	
			12.0 —32.0	867.4	4.31	0.5	
			12.0 —32.0	1,076.2	5.64	0.5	
			12.0 —32.0	1,106.6	5.12	0.5	
		July 17, 1960	3.0 — 5.9	20.1	0.14	0.7	
			6.0 —11.9	60.4	0.49	0.8	
			12.0 —32.0	633.1	2.80	0.4	
		October 15, 1960	3.0 — 5.9	19.8	0.16	0.8	
			6.0 —11.9	463.0	2.89	0.6	
			12.0 —32.0	993.1	4.24	0.4	
		January 16, 1961	3.0 — 5.9	24.5	0.30	1.2	
			6.0 —11.9	320.2	2.59	0.8	
			12.0 —32.0	985.0	4.66	0.5	
		February 18, 1961	3.0 — 5.9	36.6	0.25	0.7	
			3.0 — 5.9	74.0	0.50	0.7	
			6.0 —11.9	255.6	1.69	0.7	
			6.0 —11.9	229.2	1.55	0.7	
			12.0 —32.0	920.2	3.87	0.4	
			12.0 —32.0	1,211.4	5.52	0.5	
	Chthamalus dalli	February 18, 1961	3.0 — 5.9	15.5	0.19	1.2	Not preserved.
			3.0 — 5.9	33.2	0.36	1.1	
			3.0 — 5.9	22.9	0.37	1.6	

Group	Species	Collection date	Size (mm)	Dry wt. (mg)	Nitrogen (mg)	Percent nitrogen	Remarks
			6.0 —11.9	92.4	0.62	0.7	
	Chthamalus microtretus	February 18, 1961	3.0 — 5.9	6.5	0.07	1.1	Not preserved.
			3.0 — 5.9	11.0	0.13	1.2	
			3.0 — 5.9	14.3	0.14	1.0	
			6.0 —11.9	20.7	0.18	0.9	
			6.0 —11.9	37.8	0.30	0.8	
			6.0 —11.9	34.4	0.28	0.8	
	Dynamenella glabra	October 23, 1961	1.4 — 3.0	12.9	0.66	5.1	Sample of 20 individuals Not preserved.
	Allorchestes ptilocerus	November 7, 1961	—	8.8	0.81	9.2	Sample of 5 individuals. Not preserved.
	Hyale sp.	November 7, 1961	—	8.2	0.78	9.5	Sample of 5 individuals. Not preserved.
	Pachygrapsus crassipes	April 15, 1960	—	35.2	2.11	6.0	Sample of 3 individuals. Preserved.
	Diaulota densissima	March 19, 1959 January 13, 1960 April 15, 1960 September 23, 1961 October 21, 1961	—	15.6	1.88	12.1	Combined sample of 199 individuals from the five months indicated. Preserved.
	Tipulidae	November 7, 1961	—	20.3	2.52	12.4	Sample of 4 individuals. Not preserved.
	Agauopsis sp.	March 19, 1959 January 13, 1960 April 15, 1960 September 23, 1961 October 21, 1961	—	4.9	0.61	12.4	Sample of 419 individuals. Preserved.

Appendix IV

Biomass and net production of *Endocladia muricata* as determined by harvesting studies, 1959—1960

Study site	Area covered by each individual sample strip (cm^2)	Initial harvest Date	Initial harvest Amount harvested (g dry weight) Total	Initial harvest Amount harvested (g dry weight) Per m^2	Second harvest Date	Second harvest Amount harvested (g dry weight) Total	Second harvest Amount harvested (g dry weight) Per m^2	Time between harvest for regrowth (months)	% of regrowth toward original harvest weight	Net production (g dry wt/month) Per sample strip	Net production (g dry wt/month) Per m^2
		29 April 1959	7.07	131	27 April '60	6.25	116	12	88	0.5	10
		28 May 1959	6.76	125		1.93	36	11	29	0.2	4
		25 June 1959	6.58	122		3.27	60	10	50	0.3	6
		25 July 1959	3.07	57		1.33	25	9	43	0.2	4
		25 Aug. 1959	4.02	74		0.03	< 1	8	1	<0.1	< 1
I	540	29 Sept. 1959	1.57	29		1.59	29	7	101	0.2	4
		30 Oct. 1959	7.47	138		6.82	126	6	91	1.1	21
		28 Nov. 1959	1.73	32		0.92	17	5	53	0.2	4
		28 Dec. 1959	1.19	22		0.67	12	4	56	0.2	4
		27 Jan. 1960	6.98	129		0.15	3	3	2	<0.1	< 1
		28 Feb. 1960	2.32	43		0.00	0	2	0	<0.1	< 1
		29 Mar. 1960	3.48	65		0.14	2	1	4	0.1	2
		29 April 1959	30.21	396	26 May '60	0.00	0	13	0	0.0	0
		28 May 1959	7.15	94		0.00	0	12	0	0.0	0
		25 June 1959	5.67	74		0.00	0	11	0	0.0	0
		25 July 1959	9.60	126		0.00	0	10	0	0.0	0
		25 Aug. 1959	4.42	58		0.08	1	9	2	<0.1	< 1
II	764	29 Sept. 1959	12.16	159		0.90	12	8	7	0.1	1
		30 Oct. 1959	7.41	97		0.00	0	7	0	0.0	0
		28 Nov. 1959	2.64	35		0.00	0	6	0	0.0	0
		28 Dec. 1959	2.68	35		0.27	4	5	10	<0.1	< 1
		27 Jan. 1960	1.18	15		0.05	1	4	4	<0.1	< 1
		28 Feb. 1960	2.08	27		0.04	< 1	3	2	<0.1	< 1
		29 Mar. 1960	4.80	63		1.38	18	2	29	0.7	9
		29 April 1959	7.58	104	21 June '60	11.81	162	14	156	0.8	11
		28 May 1959	21.79	299		9.58	131	13	44	0.7	10
		25 June 1959	22.50	308		10.38	142	12	46	0.9	13

			25 July	1959	18.28	250		5.17	71	11	28	0.5	7
			25 Aug.	1959	21.28	292		4.80	66	10	23	0.5	7
III	730		29 Sept.	1959	3.62	50		3.09	42	9	85	0.3	4
			30 Oct.	1959	10.98	150		0.28	4	8	3	<0.1	< 1
			28 Nov.	1959	14.59	200		1.45	20	7	10	0.2	3
			28 Dec.	1959	4.46	61		2.06	28	6	46	0.3	4
			27 Jan.	1960	15.79	216		5.37	74	5	34	1.1	16
			28 Feb.	1960	8.20	112		1.28	18	4	16	0.3	4
			29 Mar.	1960	3.46	47		1.81	25	3	52	0.6	9
			29 April	1959	7.45	123	22 June '60	5.30	87	14	71	0.4	7
			28 May	1959	6.40	106		3.97	65	13	62	0.3	5
			25 June	1959	10.05	166		0.00	0	12	0	0.0	0
			25 July	1959	17.42	288		17.12	282	11	98	1.6	28
			25 Aug.	1959	9.44	156		11.79	194	10	125	1.2	21
IV	606		29 Sept.	1959	9.87	163		5.27	87	9	53	0.6	10
			30 Oct.	1959	4.74	78		2.03	34	8	43	0.3	5
			28 Nov.	1959	10.05	166		6.57	101	7	65	1.3	22
			28 Dec.	1959	8.25	136		11.16	184	6	135	1.9	33
			27 Jan.	1960	10.69	176		9.03	149	5	85	1.8	31
			28 Feb.	1960	13.37	221		4.80	79	4	36	1.2	21
			29 Mar.	1960	12.95	214		4.50	74	3	35	1.5	26
		A	29 April	1959	16.57	256	23 June '60	0.00	0	14	0	0.0	0
		B	28 May	1959	34.36	505		8.01	118	13	23	0.6	9
		B	25 June	1959	36.17	531		8.00	118	12	22	0.7	10
	A = 647	B	25 July	1959	16.53	243		3.69	54	11	22	0.3	4
		A	25 Aug.	1959	2.35	36		0.00	0	10	0	0.0	0
V		A	29 Sept.	1959	7.26	112		0.00	0	9	0	0.0	0
			30 Oct.	1959	—	—		—	—	—	—	—	—
	B = 681		28 Nov.	1959	—	—		—	—	—	—	—	—
			28 Dec.	1959	—	—		—	—	—	—	—	—
		A	27 Jan.	1960	0.26	4		0.00	0	5	0	0.0	0
			28 Feb.	1960	—	—		—	—	—	—	—	—
			29 Mar.	1960	—	—		—	—	—	—	—	—

Appendix V

Measurements of volume, weight, and percent of various constituents found in the water washing over the *Endocladia-Balanus* association at high tide, April, 1959—May, 1960

Monthly averages follow each of the 14 months sampled. Collections were made at weekly intervals over this period (a) at two different stations (#1 sheltered, and #2 exposed to wave action) during both high tide cycles of the day, April 24, 1959—August 28, 1959, (b) at station #1 only, during both high tide cycles of the day, September 4, 1959—December 25, 1959, and (c) at station #1 only, during a single high tide cycle in the day, January 1, 1960—May 27, 1960. All collections were made at the predicted time of high water, and the time of day with respect to the observed luminosity of the sky is noted as light, crepuscular or dark. Where collections were made at both high tide cycles in a day, samples are listed in order from the first of these high-tide periods to the last to occur in the day.

Large pieces of algae (exceeding about 1 cm in length) were excluded from the values of wet settled volume. Samples with a wet settled volume of <0.1 ml/100 liters actually represent a value of <0.1 ml/30 liters, which was the volume of water filtered. The minimum value of <0.1 ml/100 liters was used in the calculations for arriving at the absolute volumes of the various materials present in a sample.

Dry weight values represent an average of usually four to five combined samples from each month except for April, 1959 where only a single sample was weighed. The various samples used in obtaining these values are marked with +. For further explanation pertaining to Appendix V see text („Quantitative community composition, Plankton and suspended detritus").

Date	Station	Time of day: light	Time of day: crepuscular	Time of day: dark	Wet settled vol (ml/100 l)	Dry weight (mg/100 l)	Plant fragments %	Plant fragments vol × %	Organic detritus %	Organic detritus vol × %	Phytoplankton %	Phytoplankton vol × %	Zooplankton %	Zooplankton vol × %	Inorganic detritus %	Inorganic detritus vol × %
Apr. 24, 1959	1	+			<0.1	—	—	—	—	—	—	—	—	—	—	—
” ”	2	+			0.3	40.7	—	—	—	—	—	—	—	—	—	—
” ”	1			+	0.3	—	81	0.24	10	0.03	3	0.01	5	0.02	1	<0.01
” ”	2			+	<0.1	—	—	—	—	—	—	—	—	—	—	—
Monthly average					0.2	40.7	81	0.24	10	0.03	3	0.01	5	0.02	1	<0.01
May 1, 1959	1	+			2.3	—	—	—	—	—	—	—	—	—	—	—
” ”	2	+			1.0	+	—	—	—	—	—	—	—	—	—	—
” ”	1		+		1.3	—	—	—	—	—	—	—	—	—	—	—
” ”	2		+		2.7	—	—	—	—	—	—	—	—	—	—	—
May 8, 1959	1	+			0.3	—	—	—	—	—	—	—	—	—	—	—
” ”	2	+			<0.1	+	—	—	—	—	—	—	—	—	—	—
” ”	1			+	0.7	—	—	—	—	—	—	—	—	—	—	—
” ”	2			+	<0.1	—	—	—	—	—	—	—	—	—	—	—
May 15, 1959	1		+		1.0	—	60	0.60	10	0.10	20	0.20	10	0.10	0	0
” ”	2		+		2.3	+	—	—	—	—	—	—	—	—	—	—
May 16, 1959	1		+		1.0	—	—	—	—	—	—	—	—	—	—	—
” ”	2		+		1.7	—	—	—	—	—	—	—	—	—	—	—
May 22, 1959	1	+			0.3	—	60	0.18	10	0.03	10	0.03	20	0.06	0	0
” ”	2	+			1.3	+	—	—	—	—	—	—	—	—	—	—
” ”	1			+	0.3	—	60	0.18	10	0.03	0	0	30	0.09	0	0
” ”	2			+	0.3	—	—	—	—	—	—	—	—	—	—	—
May 29, 1959	1		+		1.3	—	70	0.91	10	0.13	10	0.13	10	0.13	0	0
” ”	2		+		0.7	+	—	—	—	—	—	—	—	—	—	—
” ”	1	+			0.3	—	60	0.18	15	0.04	5	0.02	20	0.06	0	0
” ”	2	+			0.3	—	—	—	—	—	—	—	—	—	—	—
Monthly average					1.0	60.9	62	0.41	11	0.07	9	0.08	18	0.09	0	0
June 5, 1959	1	+			1.0	—	80	0.80	10	0.10	5	0.05	5	0.05	0	0
” ”	2	+			1.0	+	—	—	—	—	—	—	—	—	—	—
” ”	1			+	1.0	—	75	0.75	10	0.10	10	0.10	5	0.05	0	0
” ”	2			+	0.7	—	—	—	—	—	—	—	—	—	—	—

Date	Station	Time of day: light	Time of day: crepuscular	Time of day: dark	Wet settled vol (ml/100 l)	Dry weight (mg/100 l)	Plant fragments %	Plant fragments vol × %	Organic detritus %	Organic detritus vol × %	Phytoplankton %	Phytoplankton vol × %	Zooplankton %	Zooplankton vol × %	Inorganic detritus %	Inorganic detritus vol × %
June 12, 1959	1			+	3.3	—	60	1.98	20	0.66	10	0.33	10	0.33	0	0
„ „	2			+	2.3	+	—	—	—	—	—	—	—	—	—	—
„ „	1	+			3.3	—	73	2.41	20	0.66	5	0.16	2	0.07	0	0
„ „	2	+			1.7	—	—	—	—	—	—	—	—	—	—	—
June 19, 1959	1	+			6.7	—	20	1.34	15	1.00	60	4.02	5	0.34	0	0
„ „	2	+			6.7	+	—	—	—	—	—	—	—	—	—	—
„ „	1			+	4.3	—	10	0.43	20	0.86	65	2.80	5	0.22	0	0
„ „	2			+	4.0	—	—	—	—	—	—	—	—	—	—	—
June 26, 1959	1			+	0.3	—	85	0.26	10	0.03	0	0	5	0.02	0	0
„ „	2			+	1.0	+	—	—	—	—	—	—	—	—	—	—
„ „	1	+			0.3	—	70	0.21	20	0.06	0	0	10	0.03	0	0
„ „	2	+			0.3	—	—	—	—	—	—	—	—	—	—	—
Monthly average					2.4	45.3	59	1.02	16	0.43	19	0.93	6	0.14	0	0
July 3, 1959	1	+			6.7	—	35	2.34	15	1.00	40	2.68	10	0.67	0	0
„ „	2	+			6.3	+	—	—	—	—	—	—	—	—	—	—
„ „	1			+	1.3	—	70	0.91	15	0.20	10	0.13	5	0.06	0	0
„ „	2			+	1.3	—	—	—	—	—	—	—	—	—	—	—
July 10, 1959	1			+	0.3	—	78	0.23	15	0.04	2	0.01	5	0.02	0	0
„ „	2			+	0.3	+	—	—	—	—	—	—	—	—	—	—
„ „	1	+			0.7	—	68	0.48	20	0.14	2	0.01	10	0.07	0	0
„ „	2	+			0.3	—	—	—	—	—	—	—	—	—	—	—
July 17, 1959	1	+			<0.1	—	70	<0.01	20	<0.01	5	<0.01	5	<0.01	0	0
„ „	2	+			0.3	+	—	—	—	—	—	—	—	—	—	—
„ „	1			+	0.7	—	69	0.48	20	0.14	5	0.04	1	0.01	5	0.04
„ „	2			+	0.3	—	—	—	—	—	—	—	—	—	—	—
July 24, 1959	1			+	0.7	—	60	0.42	15	0.10	5	0.04	20	0.14	0	0
„ „	2			+	0.7	+	—	—	—	—	—	—	—	—	—	—
„ „	1	+			1.0	—	65	0.65	20	0.20	5	0.05	10	0.10	0	0
„ „	2	+			0.7	—	—	—	—	—	—	—	—	—	—	—
July 31, 1959	1	+			0.3	—	85	0.26	5	0.02	5	0.02	5	0.02	0	0
„ „	2	+			0.7	+	—	—	—	—	—	—	—	—	—	—

Date	Station	Time of day: light	Time of day: cre-puscu-lar	Time of day: dark	Wet settled vol (ml/ 100 l)	Dry weight (mg/ 100 l)	Plant fragments %	Plant fragments vol × %	Organic detritus %	Organic detritus vol × %	Phyto-plankton %	Phyto-plankton vol × %	Zoo-plankton %	Zoo-plankton vol × %	Inorganic detritus %	Inorganic detritus vol × %
” ”	1		+		0.3	—	75	0.22	15	0.04	5	0.02	5	0.02	0	0
” ”	2		+		0.3	—	—	—	—	—	—	—	—	—	—	—
Monthly average					1.2	56.3	68	0.60	16	0.19	8	0.30	8	0.11	0.5	<0.01
Aug. 7, 1959	1			+	1.0	—	65	0.65	20	0.20	5	0.05	10	0.10	0	0
” ”	2			+	0.7	+	—	—	—	—	—	—	—	—	—	—
” ”	1	+			0.7	—	75	0.52	15	0.10	5	0.04	5	0.04	0	0
” ”	2	+			0.7	—	—	—	—	—	—	—	—	—	—	—
Aug. 14, 1959	1	+			0.3	—	60	0.18	20	0.06	0	0	20	0.06	0	0
” ”	2	+			0.7	+	—	—	—	—	—	—	—	—	—	—
” ”	1		+		0.7	—	75	0.52	20	0.14	0	0	5	0.04	0	0
” ”	2		+		0.7	—	—	—	—	—	—	—	—	—	—	—
Aug. 21, 1959	1			+	0.7	—	70	0.49	20	0.14	0	0	10	0.07	0	0
” ”	2			+	0.3	+	—	—	—	—	—	—	—	—	—	—
” ”	1	+			0.3	—	80	0.24	10	0.03	0	0	10	0.03	0	0
” ”	2	+			0.3	—	—	—	—	—	—	—	—	—	—	—
Aug. 28, 1959	1	+			<0.1	—	25	<0.01	5	<0.01	0	0	70	<0.01	0	0
” ”	2	+			0.3	+	—	—	—	—	—	—	—	—	—	—
” ”	1		+		0.7	—	70	0.49	20	0.14	0	0	10	0.07	0	0
” ”	2		+		0.7	—	—	—	—	—	—	—	—	—	—	—
Monthly average					0.6	38.3	65	0.39	16	0.10	1	0.01	18	0.05	0	0
Sept. 3, 1959	1			+	1.3	—	60	0.78	20	0.26	10	0.13	10	0.13	0	0
” ”	1			+	1.3	—	—	—	—	—	—	—	—	—	—	—
Sept. 4, 1959	1	+			0.7	—	76	0.53	20	0.14	2	0.01	2	0.01	0	0
” ”	1	+			1.3	+	—	—	—	—	—	—	—	—	—	—
Sept. 11, 1959	1	+			0.7	—	65	0.46	15	0.10	0	0	20	0.14	0	0
” ”	1	+			0.7	+	—	—	—	—	—	—	—	—	—	—
” ”	1		+		1.0	—	—	—	—	—	—	—	—	—	—	—
” ”	1		+		1.0	—	70	0.70	20	0.20	5	0.05	5	0.05	0	0
Sept. 17, 1959	1			+	0.7	—	75	0.52	20	0.14	0	0	5	0.04	0	0

Date	Station	Time of day light	Time of day cre-puscu-lar	Time of day dark	Wet settled vol (ml/ 100 l)	Dry weight (mg/ 100 l)	Plant fragments %	Plant fragments vol × %	Organic detritus %	Organic detritus vol × %	Phyto-plankton %	Phyto-plankton vol × %	Zoo-plankton %	Zoo-plankton vol × %	Inorganic detritus %	Inorganic detritus vol × %
Sept. 18, 1959	1			+	0.7	+	—	—	—	—	—	—	—	—	—	—
” ”	1	+			0.7	—	70	0.49	20	0.14	0	0	10	0.07	0	0
” ”	1	+			0.7	—	—	—	—	—	—	—	—	—	—	—
Sept. 25, 1959	1	+			0.3	—	80	0.24	15	0.04	0	0	5	0.02	0	0
” ”	1	+			0.7	+	—	—	—	—	—	—	—	—	—	—
” ”	1	+			1.7	—	—	—	—	—	—	—	—	—	—	—
” ”	1	+			1.7	—	80	1.36	15	0.26	0	0	5	0.08	0	0
Monthly average					1.0	28.7	72	0.64	18	0.16	2	0.02	8	0.07	0	0
Oct. 2, 1959	1	+			0.7	—	91	0.64	5	0.04	0	0	2	0.01	2	0.01
” ”	1	+			0.7	+	—	—	—	—	—	—	—	—	—	—
” ”	1			+	0.7	—	86	0.60	10	0.07	0	0	2	0.01	2	0.01
” ”	1			+	0.7	—	—	—	—	—	—	—	—	—	—	—
Oct. 9, 1959	1			+	0.3	—	81	0.24	15	0.04	0	0	2	0.01	2	0.01
” ”	1			+	0.7	+	—	—	—	—	—	—	—	—	—	—
” ”	1	+			1.0	—	—	—	—	—	—	—	—	—	—	—
” ”	1	+			1.3	—	75	0.98	20	0.26	0	0	5	0.06	0	0
Oct. 16, 1959	1	+			1.0	—	—	—	—	—	—	—	—	—	—	—
” ”	1	+			1.0	+	—	—	—	—	—	—	—	—	—	—
” ”	1			+	0.3	—	80	0.24	20	0.06	0	0	0	0	0	0
Oct. 17, 1959	1			+	0.3	—	—	—	—	—	—	—	—	—	—	—
Oct. 23, 1959	1			+	0.3	—	88	0.26	10	0.03	0	0	2	0.01	0	0
” ”	1			+	0.3	+	—	—	—	—	—	—	—	—	—	—
” ”	1	+			0.3	—	—	—	—	—	—	—	—	—	—	—
” ”	1	+			0.7	—	81	0.57	15	0.10	0	0	2	0.01	2	0.01
Oct. 30, 1959	1	+			0.7	—	86	0.60	10	0.07	0	0	2	0.01	2	0.01
” ”	1	+			0.7	+	—	—	—	—	—	—	—	—	—	—
” ”	1			+	0.7	—	83	0.58	15	0.10	0	0	2	0.01	0	0
” ”	1			+	0.7	—	—	—	—	—	—	—	—	—	—	—
Monthly average					0.7	101.6	83	0.52	13	0.09	0	0	2	0.01	1	0.01

Date	Station	Time of day: light	cre-puscu-lar	dark	Wet settled vol (ml/100 l)	Dry weight (mg/100 l)	Plant fragments %	vol × %	Organic detritus %	vol × %	Phyto-plankton %	vol × %	Zoo-plankton %	vol × %	Inorganic detritus %	vol × %
Nov. 6, 1959	1			+	<0.1	—	—	—	—	—	—	—	—	—	—	—
,, ,,	1			+	0.3	—	70	0.21	15	0.04	0	0	15	0.04	0	0
,, ,,	1	+			0.3	—	83	0.25	15	0.04	0	0	2	0.01	0	0
,, ,,	1	+			0.3	+	—	—	—	—	—	—	—	—	—	—
Nov. 13, 1959	1	+			<0.1	—	—	—	—	—	—	—	—	—	—	—
,, ,,	1	+			<0.1	—	85	<0.01	10	<0.01	0	0	5	<0.01	0	0
,, ,,	1			+	0.3	+	—	—	—	—	—	—	—	—	—	—
,, ,,	1			+	0.3	—	83	0.25	15	0.04	0	0	2	0.01	0	0
Nov. 20, 1959	1			+	0.7	—	83	0.58	10	0.07	5	0.04	2	0.01	0	0
,, ,,	1			+	0.7	+	—	—	—	—	—	—	—	—	—	—
,, ,,	1	+			0.7	—	85	0.60	10	0.07	0	0	5	0.04	0	0
,, ,,	1	+			0.7	—	—	—	—	—	—	—	—	—	—	—
Nov. 27, 1959	1	+			0.3	+	—	—	—	—	—	—	—	—	—	—
,, ,,	1	+			0.3	—	83	0.25	10	0.03	2	0.01	5	0.02	0	0
,, ,,	1			+	0.3	—	—	—	—	—	—	—	—	—	—	—
,, ,,	1			+	0.3	—	89	0.27	10	0.03	0	0	1	<0.01	0	0
Monthly average					0.3	71.8	83	0.30	12	0.04	0.9	0.01	5	0.02	0	0
Dec. 4, 1959	1			+	0.3	+	—	—	—	—	—	—	—	—	—	—
,, ,,	1			+	0.3	—	89	0.27	10	0.03	0	0	1	<0.01	0	0
,, ,,	1	+			<0.1	—	90	<0.01	10	<0.01	0	0	0	0	0	0
,, ,,	1	+			<0.1	—	—	—	—	—	—	—	—	—	—	—
Dec. 11, 1959	1	+			<0.1	+	—	—	—	—	—	—	—	—	—	—
,, ,,	1	+			<0.1	—	84	<0.01	15	<0.01	0	0	1	<0.01	0	0
,, ,,	1			+	<0.1	—	84	<0.01	15	<0.01	0	0	1	<0.01	0	0
,, ,,	1			+	<0.1	—	—	—	—	—	—	—	—	—	—	—
Dec. 18, 1959	1			+	<0.1	—	90	<0.01	10	<0.01	0	0	0	0	0	0
,, ,,	1			+	<0.1	—	—	—	—	—	—	—	—	—	—	—
,, ,,	1	+			<0.1	+	—	—	—	—	—	—	—	—	—	—
,, ,,	1	+			<0.1	—	79	<0.01	20	<0.01	0	0	1	<0.01	0	0
Dec. 25, 1959	1		+		0.3	+	—	—	—	—	—	—	—	—	—	—
,, ,,	1		+		0.7	—	69	0.48	10	0.07	20	0.14	1	0.01	0	0

Date	Station	Time of day: light	Time of day: crepuscular	Time of day: dark	Wet settled vol (ml/100 l)	Dry weight (mg/100 l)	Plant fragments %	Plant fragments vol × %	Organic detritus %	Organic detritus vol × %	Phytoplankton %	Phytoplankton vol × %	Zooplankton %	Zooplankton vol × %	Inorganic detritus %	Inorganic detritus vol × %
Dec. 25, 1959	1			+	0.3	—	90	0.27	5	0.02	5	0.02	0	0	0	0
” ”	1			+	0.3	—	—	—	—	—	—	—	—	—	—	—
Monthly average					0.1	60.3	84	0.13	12	0.02	3	0.02	0.6	<0.01	0	0
Jan. 1, 1960	1	+			<0.1	—	87	<0.01	10	<0.01	2	<0.01	1	<0.01	0	0
” ”	1	+			<0.1	+	—	—	—	—	—	—	—	—	—	—
Jan. 8, 1960	1			+	<0.1	—	84	<0.01	10	<0.01	1	<0.01	0	0	5	<0.01
” ”	1			+	0.7	+	—	—	—	—	—	—	—	—	—	—
Jan. 15, 1960	1	+			0.7	—	84	0.59	5	0.04	1	0.01	0	0	10	0.07
” ”	1	+			0.7	+	—	—	—	—	—	—	—	—	—	—
Jan. 22, 1960	1			+	<0.1	—	93	<0.01	5	<0.01	0	0	2	<0.01	0	0
” ”	1			+	<0.1	+	—	—	—	—	—	—	—	—	—	—
Jan. 29, 1960	1	+			<0.1	—	94	<0.01	5	<0.01	1	<0.01	0	0	0	0
” ”	1	+			<0.1	+	—	—	—	—	—	—	—	—	—	—
Monthly average					0.2	70.8	88	0.12	7	0.01	1	<0.01	0.6	<0.01	3	0.01
Feb. 5, 1960	1			+	<0.1	—	89	<0.01	10	<0.01	0	0	1	<0.01	0	0
” ”	1			+	<0.1	+	—	—	—	—	—	—	—	—	—	—
Feb. 12, 1960	1	+			0.3	—	84	0.25	5	0.02	5	0.02	1	<0.01	5	0.02
” ”	1	+			0.3	+	—	—	—	—	—	—	—	—	—	—
Feb. 19, 1960	1	+			1.0	—	89	0.89	5	0.05	0	0	1	0.01	5	0.05
” ”	1	+			1.7	+	—	—	—	—	—	—	—	—	—	—
Feb. 26, 1960	1	+			<0.1	—	88	<0.01	2	<0.01	10	<0.01	0	0	0	0
” ”	1	+			<0.1	+	—	—	—	—	—	—	—	—	—	—
Monthly average					0.4	59.8	88	0.28	6	0.02	4	<0.01	0.8	<0.01	2	0.02
Mar. 4, 1960	1		+		<0.1	—	83	<0.01	2	<0.01	10	<0.01	5	<0.01	0	0
” ”	1		+		0.3	+	—	—	—	—	—	—	—	—	—	—
Mar. 11, 1960	1	+			1.0	—	63	0.63	15	0.15	20	0.20	2	0.02	0	0
” ”	1	+			0.7	+	—	—	—	—	—	—	—	—	—	—
Mar. 18, 1960	1	+			<0.1	—	93	<0.01	5	<0.01	2	<0.01	0	0	0	0

Date	Station	Time of day: light	Time of day: crepuscular	Time of day: dark	Wet settled vol (ml/ 100 l)	Dry weight (mg/ 100 l)	Plant fragments %	Plant fragments vol × %	Organic detritus %	Organic detritus vol × %	Phyto-plankton %	Phyto-plankton vol × %	Zoo-plankton %	Zoo-plankton vol × %	Inorganic detritus %	Inorganic detritus vol × %
Mar. 18, 1960	1	+			0.3	+	—	—	—	—	—	—	—	—	—	—
Mar. 25, 1960	1	+			<0.1	—	78	<0.01	10	<0.01	10	<0.01	0	0	2	<0.01
,, ,,	1	+			<0.1	+	—	—	—	—	—	—	—	—	—	—
Monthly average					0.3	60.5	79	0.16	8	0.04	10	0.05	2	<0.01	0.5	<0.01
Apr. 1, 1960	1	+			<0.1	—	75	<0.01	15	<0.01	10	<0.01	0	0	0	0
,, ,,	1	+			<0.1	+	—	—	—	—	—	—	—	—	—	—
Apr. 8, 1960	1			+	0.3	—	84	0.25	5	0.02	10	0.03	1	<0.01	0	0
,, ,,	1			+	0.7	+	—	—	—	—	—	—	—	—	—	—
Apr. 15, 1960	1	+			0.7	—	87	0.61	5	0.04	5	0.04	1	0.01	2	0.01
,, ,,	1	+			0.7	+	—	—	—	—	—	—	—	—	—	—
Apr. 22, 1960	1			+	3.7	—	65	2.40	5	0.18	20	0.74	10	0.37	0	0
,, ,,	1			+	4.0	+	—	—	—	—	—	—	—	—	—	—
Apr. 30, 1960	1	+			<0.1	—	78	<0.01	20	<0.01	0	0	2	<0.01	0	0
,, ,,	1	+			<0.1	+	—	—	—	—	—	—	—	—	—	—
Monthly average					1.0	77.1	78	0.65	10	0.05	9	0.16	3	0.08	0.4	<0.01
May 6, 1960	1			+	0.3	—	64	0.19	15	0.04	20	0.06	1	<0.01	0	0
,, ,,	1			+	0.7	+	—	—	—	—	—	—	—	—	—	—
May 13, 1960	1	+			0.3	—	57	0.17	20	0.06	20	0.06	1	<0.01	2	0.01
,, ,,	1	+			0.3	+	—	—	—	—	—	—	—	—	—	—
May 20, 1960	1			+	0.3	—	70	0.21	15	0.04	10	0.03	5	0.02	0	0
,, ,,	1			+	0.7	+	—	—	—	—	—	—	—	—	—	—
May 27, 1960	1	+			1.3	—	53	0.69	2	0.03	40	0.52	5	0.06	0	0
,, ,,	1	+			1.3	+	—	—	—	—	—	—	—	—	—	—
Monthly average					0.6	36.8	61	0.32	13	0.04	22	0.17	3	0.02	0.5	<0.01

ABSTRACT

Studies of the community composition, structure and species interrelationships of the *Endocladia-Balanus* association were carried out on the rocky shores at the Hopkins Marine Station, Pacific Grove, California, over the period 1959—1961. The organisms making up this biotic association form a horizontal band approximately two feet wide on intertidal rocks. The center of this belt averaged 4.6 ft in surveyed height above tidal datum, but field observations showed that the periods of exposure and submersion actually experienced under a variety of conditions at this level are those predicted for a level of about 3.8 ft above tidal datum. Selected aspects of the relatively mild marine and terrestrial climates were studied in relation to the high and low water periods.

The composition of the association was determined from quadrat samples, qualitative collections and field observations. A total of at least 93 benthic and transient species was enumerated, belonging to 15 major groups. Samples taken near the center of the association in different areas and at different seasons demonstrated great similarity and stability in species composition. Thirty-five of the species present in the assemblage were of common occurrence, and where feasible the following aspects of the biology of each were studied: (a) habitat niche, (b) activity patterns, (c) organic matter content of the body (based on the dry weight and nitrogen content), (d) seasonal occurrence, (e) population structure, (f) reproductive activity, (g) food relationships, and (h) growth rate. The most characteristic species were: Rhodophyta- *Endocladia muricata, Gigartina agardhii;* Platyhelminthes- *Notoplana acticola*; Nemertea- *Emplectonema gracile, Nemertopsis gracilis*; Annelida- *Syllis spenceri, S. vittata, S. armillaris, Nereis grubei, Perinereis monterea*; Bryozoa- *Filicrisia franciscana*; Mollusca (8 gastropods, 1 chiton, and 3 bivalves)- *Acmaea digitalis, A. scabra, A. pelta, Littorina scutulata, L. planaxis, Acanthina spirata, Thais emarginata, Tegula funebralis, Cyanoplax dentiens, Lasaea cistula, Mytilus californianus, Musculus* sp.; Arthropoda (7 crustaceans, 2 insects, and 3 mites)- *Balanus glandula, Chthamalus dalli, C. microtretus, Dynamenella glabra, Allorchestes ptilocerus, Hyale* sp., *Pachygrapsus crassipes, Diaulota densissima, Limonia marmorata, Agauopsis* sp., a mesostigmatid mite, and *Suidasia* sp.

A study of space relations shows that a multitude of species live among the holdfast branchlets and along the blades of *E. muricata,* and in the spaces formed by the tests of both living and dead *B. glandula.* Food studies of the 34 commoncst animal species show that seven are filter feeders, ten are herbivorous browsers and scrapers feeding on encrusting forms, six are herbivores feeding on the large benthic algae, five are omnivores and scavengers, and six are carnivores which prey mostly on filter feeders and scraping herbivores. Pelagic materials present during high tide periods, in order of decreasing absolute volume, were: (a) large plant fragments, (b) phytoplankton,

(c) other organic detritus, (d) zooplankton, and (e) inorganic detritus. Approximately 570 mg dry weight was available per m^3 of sea water throughout the year.

For the center of the *Endocladia-Balanus* zone the mean number of individuals above microscopic size of all species present at any time was 210,000/m^2, the mean dry weight biomass was 2,640 g/m^2, and the mean nitrogen content was 25 g/m^2. In quantitative as well as qualitative terms, the *Endocladia-Balanus* association shows considerable similarity with the *Gloiopeltis-Chthamalus* association in the Sea of Japan and with the *Chthamalus-Pygmaea* zone on English rocky shores.

Analysis of the association in terms of the protein content of the standing crop for the major trophic groups shows the following: filter feeding animals, 84 g/m^2; larger red algae and their attached epiphytes, 58 g/m^2; resident herbivores, 12 g/m^2; a transient herbivore, 1.2 g/m^2; resident carnivores, 0.9 g/m^2; transient carnivores, 0.8 g/m^2; omnivores and scavengers, 1.3 g/m^2. Although the scraping and grazing herbivores feed on algae produced in the zone, much of the food consumed in the association is derived by import of suspended detritus and plankton at high water.

Dr. PETER W. GLYNN
University of Puerto Rico
Institute of Marine Biology
Mayagüez - Puerto Rico