PRE-EARTHQUAKE INTERTIDAL ECOLOGY OF THREE SAINTS BAY, KODIAK ISLAND, ALASKA

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INTRODUCTION

The intertidal zone of Alaska is very incompletely known, and the present study had as its major purpose the description, both qualitative and quantitative, of the intertidal zone of a protected bay on Kodiak Island. Three Saints Bay was chosen because it offered a variety of shores of differing aspect, slope, and substrate for comparative study.

Included in the major objective of this study were: (1) the enumeration of the major species of semi-sedentary and sedentary invertebrates present with data on their ecology; (2) delimitation of the tidal ranges of the aforementioned invertebrates and their variation in density with changing tidal level; (3) description of the horizontal belts or zones which existed on the various shores.

In addition to the major purpose, other goals were: to contrast the zonation of the shores of Three Saints Bay with published accounts of zonation at other points on the Pacific coast of North America and to compare the zonation of Three Saints Bay with a published scheme of universal zonation on the rocky shores of the world.

The study was restricted to the sedentary and semi-sedentary species of intertidal invertebrates; there was no attempt to sample highly motile invertebrates or very small invertebrates.

The Alaskan earthquake of Good Friday, 1964, and following land subsidence had a considerable effect on Kodiak Island where the land sank from 2 to 5 ft (Plafker and Kachadoorian, 1966). Since this is apparently the only quantitative study from the island before this major disturbance, it is thus important as a basis for comparison and evaluation of changes which may be described in any post-earthquake intertidal studies of the region.

The field work which forms the basis of this report was carried out during June, July, and August of 1963.

(Editor's note. The thesis which formed the basis for this paper was first reviewed by me in late 1965; most of the delay in publication is my responsibility. F.C.D.)

LITERATURE REVIEW

Descriptive ecological studies of selected intertidal areas on the Pacific

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Coast in terms of physiognomy and dominant organisms are reported only for areas south of Vancouver Island. The most recent study is that of Stephenson and Stephenson (1961 a, b) on Vancouver Island. Earlier studies were those of Rigg and Miller (1949) at Neah Bay, Washington, and Gislen (1943, 1944) on the California Coast. Quantitative intertidal studies in this area are those of Shelford et al. (1935) and Hewatt (1937), the former in Puget Sound and the latter in Monterey Bay.

The above studies were undertaken on rocky shores of open coasts. There have been other studies relating to other environments. MacGinitie (1935) has reported the ecology of Elkhorn Slough, an estuarine region; Gersbacher and Denison (1929) reported on organisms of tide pools; Packard (1918) has given data on San Francisco Bay. More recently Doty (1946) as well as Doty and Archer (1950) have contributed important experimental data concerning the existence of critical tide factors controlling zonation on shores.

Studies of the succession of animal associations and the recolonization of open surfaces in the tidal zone and shallow water areas of the Pacific Coast have been reported by Pieron and Huang (1926), Hewatt (1935), Scheer (1945), Graham and Gay (1945), and Reish (1961, 1963).

The vast kelp beds of the Pacific Coast have been subjected to ecological studies by Andrews (1945) and McLean (1962), while the algae distributional patterns have been summarized by Scagel (1963).

Autecologic studies of intertidal organisms are also uncommon. The ecology of the major Pacific Coast barnacles has been discussed by Towler (1930), Worley (1930), Rice (1930), and Henry (1942). Intertidal mollusks of the genus *Acmaea* have been studied by Test (1945), Shotwell (1950) and Frank (1966). Ecology of the more common pelecypod species has been the subject of papers by Mossop (1921), Fraser (1931), and Fraser and Smith (1928a, b). Smith (1962) has given some ecological data on the holothurian, *Cucumaria curata*. The major portions of the books of Ricketts and Calvin (1962) and MacGinitie and MacGinitie (1949) are also devoted to autecologic studies of West Coast invertebrates.

Although this summarizes to a very limited extent the intertidal ecological work published for the Pacific Coast, and emphasizes the neglect, extensive information relating to the intertidal zone is available for other parts of the world and particularly for the eastern Atlantic. Entrance into this extensive literature may be obtained through papers of Evans (1947a, b, 1949), Spooner and Moore (1940), Pyefinch (1943), Kitching (1935), Rees (1940), Sloane et al. (1957), Beanland (1940), and Lewis

(1953, 1954, 1957). Much of this early work is well summarized and combined with his own work in Lewis' (1964) book.

The arctic regions, particularly Greenland, have been the subject of extensive investigation by Danish workers. Lengthy papers by Sparck (1933), Thorson (1933, 1934), and Madsen (1936) have discussed this area thoroughly. There has also been considerable activity by the Russians. Much of this work has been available only in Russian, but a recent (1963) English translation of Zenkevitch's book *Biology of the Seas of the U.S.S.R.* has summarized a large portion of it.

On the American side of the Atlantic the most ambitious work has been that of Stephenson and Stephenson (1950, 1952, 1954) which covered the coast from Canada to Key West. Other studies on this Coast include Allee (1932a, b), Dexter (1947), Fahey (1947), Newcombe (1935), Pearse, Humm and Wharton (1942), and MacDougall (1943).

A surge of activity in intertidal ecology has come from the southern hemisphere where considerable lengths of shoreline of the Australian continent have been studied by Dakin, Bennett and Pope (1948), Bennett and Pope (1953), Womersley and Edmonds (1952, 1958), Endean, Stephenson and Kenny (1956a,b) and Hodgkin (1960). Similar studies have extended to Tasmania (Guiler, 1950; 1951; Bennett and Pope, 1960) and New Zealand (Knox, 1953; Dellow, 1950; and Dellow and Morrison, 1955).

Except for Australia tropical areas have received little attention. This gap has been partially filled for West Africa by the work of Lawson (1954, 1955, 1957a, b).

Finally, Doty (1957), Southward (1958) and Mokyevsky (1960) have provided comprehensive reviews of intertidal ecology.

GENERAL DESCRIPTION OF THE AREA

Kodiak Island is the largest of a group of islands which lie between 56°30′ and 58°40′ North latitude and 150°40′ and 154°50′ West longitude in the western reaches of the Gulf of Alaska. Geologically a submarine extension of the Kenai Peninsula from the mainland to the northeast, the Kodiak Island group is presently separated from this related area by about 40 miles of ocean at the nearest point on Shuyak Island, the most northerly island of the Kodiak Group. The island group is further separated from the rugged volcanic and geologically dissimilar Alaska Peninsula to the north by Shelikof Strait which varies in width from 20 to 40 miles.

Kodiak Island itself has an area of about 3,588 square miles and is about 100 miles long by 60 miles wide at its extremes. The following description of the geology is summarized from Capps (1937); a recent review of the 1964 earthquake may be found in Plafker and Kachadoorian (1966). The island is characterized by a highly dissected shoreline with deep bays or fjords which penetrate, in a few cases, nearly the width of the island (Fig. 1). The island itself has a very rough, rugged topography in the northern three-fourths where steep-sided mountains alternate with narrow valleys. In most instances the mountains rise abruptly from the bays and fjords. The mountains have an average height of 2,500 ft; the highest point, which occurs on the central mountainous spine of the island, reaches 4,200 ft. The southern quarter, in contrast, is more flattened and regular in outline.

Much of the rugged relief of the island, and surely the existence of the deep fjords, has resulted from Pleistocene glacial scouring action on what had been previously an island of more regular outline. During the height of the Late Pleistocene glaciation evidence indicates that Kodiak was nearly covered by ice. However, in spite of this extensive glaciation, glacial deposits are uncommon as most debris was moved out to sea.

The mountainous spine of the island, oriented northeast-southwest, from which rise the highest peaks, is composed of a large intrusive mass of diorite. Outliers of this granitic spine appear as dikes and sills forced up through the overlying Mesozoic and Tertiary rocks which lie in thick beds on either side of the central spine. Rocks of Triassic and Jurassic ages are the oldest recognized on the island and consist primarily of greenstone, cherts, and slates. Unconformably over these rocks is laid a thick series of Cretaceous slate, graywacke, and conglomerate. A final series of rocks overlying these includes a sedimentary series of freshwater sandstones and shales of Eocene age which are overlain unconformably, in turn, by a series of marine Pliocene or Miocene sandstones.
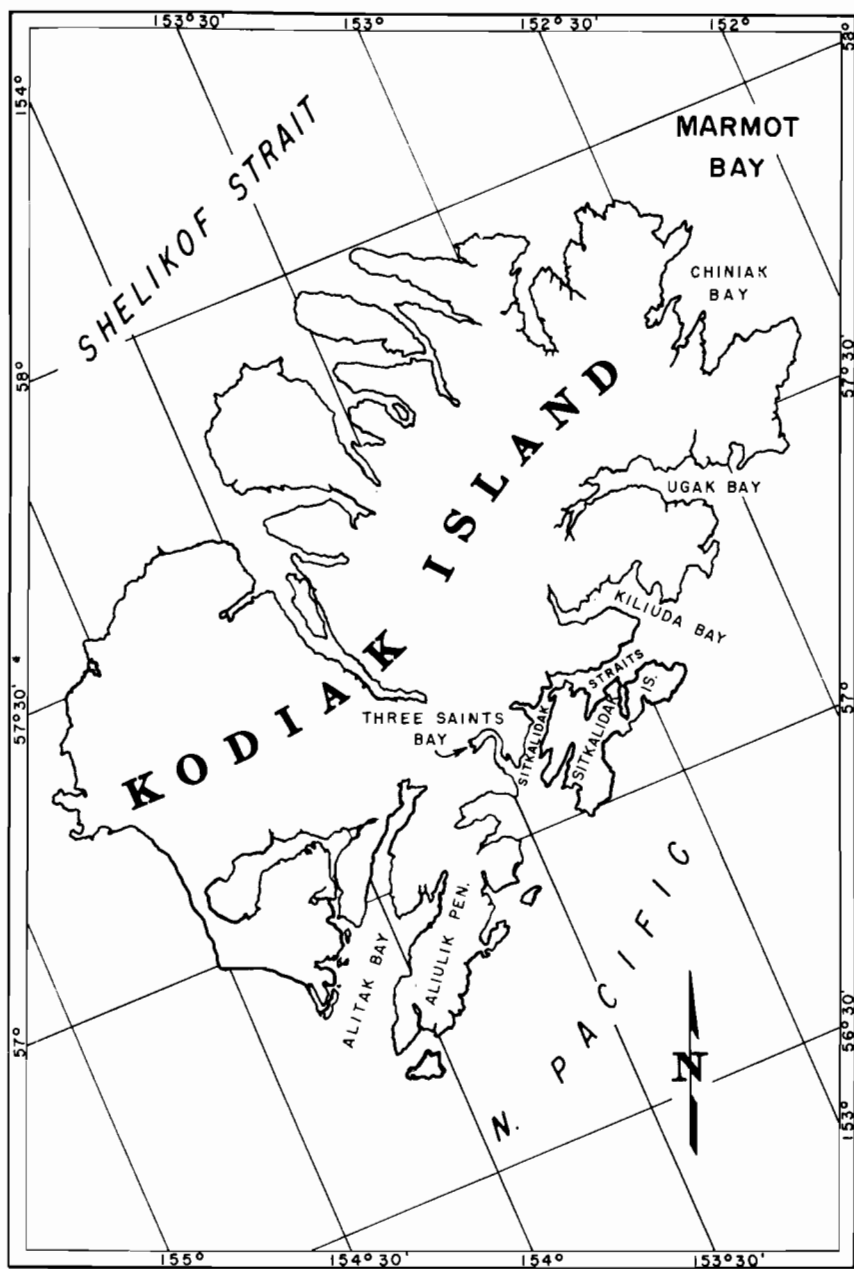
Figure 1. Kodiak Island and vicinity.
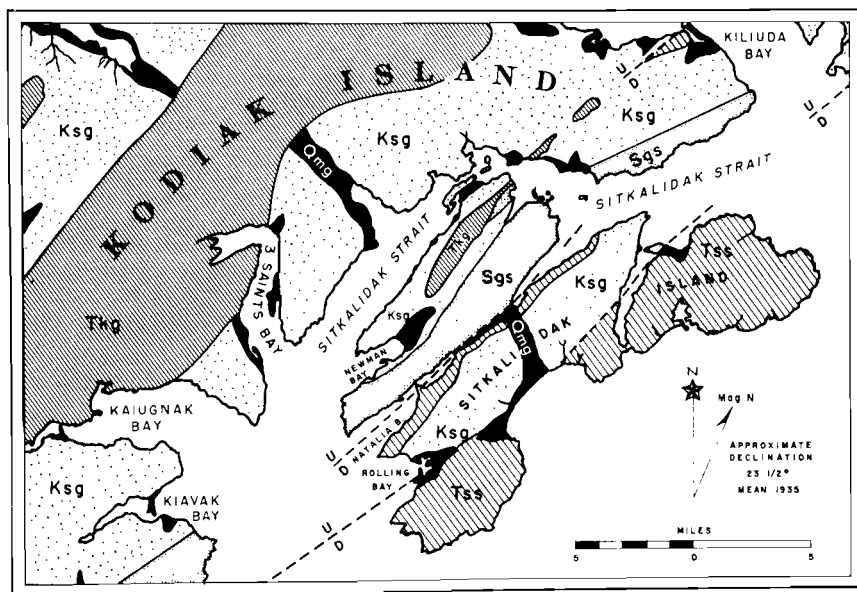
Figure 2.   Geologic Map of the Three Saints Bay Area, Kodiak Island, Alaska*

LEGEND

Faults: U = upthrow   D = downthrow

Granular intrusive rocks, mainly quartz diorite, with some diorite, and minor amounts of gabbro.

Present stream gravel, sand, and silt (low terrace gravel; alluvial fans; beach deposits. Glacial moranial material). Pleistocene and Recent.

Fresh water sandstone, shale, and conglomerate, locally containing coal seams. Eocene?

Mainly upper Cretaceous rocks (slate, argillite, graywacke, and conglomerate, thoroughly indurated and generally highly metamorphosed).

Mainly Triassic and Jurassic rocks possibly some Paleozoic or older rocks (A structurally complex group of rocks of great lithological diversity).

* This map and legend have been modified from Capps, 1937.

Figure 2.   Geologic map of the Three Saints Bay area, Kodiak Island, Alaska.*

Considerable faulting, primarily vertical but oriented in a northeast-southwest direction, has disturbed the above outlined sequences in many areas such that the beds no longer lie in correct sequence and young and old sediments are greatly offset against each other and against the dioritic spine (Fig. 2).

The shoreline of the island, at least that part from Chiniak Bay south to and including Three Saints Bay (Fig. 1), is formed of the above rock series. In part the unbroken faces meet the water; elsewhere fragments of varying sizes form the shoreline barrier or secondary alluvial deposits have accumulated. At the heads of bays and in protected lagoons the fine alluvial material, mixed with sand and gravel, forms the majority of the shore. Where the bays have cut into the mountains, and steep precipitous slopes drop into the water, exposed solid rock faces are found interspersed with talus slopes. Where more gentle slopes meet the sea, sorted cobble, gravel or sand shores are common. Boulders often characterize beaches where the shores border more gently sloping terrain; they are also major constituents at the base of talus slopes. In fully protected waters beaches of sand, gravel, and mud are common.

Although Kodiak Island is situated latitudinally in the subarctic, the climate is temperate maritime. This is due in great measure to the warming effect exerted on the island by the Alaska Stream, a warm current offshoot of the West Wind Drift which flows westward just offshore of the Kodiak group (Uda, 1963).

The maritime climate is sustained by the persistent year-around influence of the Alaska Stream which thus maintains fairly stable air temperatures on Kodiak, damping extremes in either direction. As a result the average difference in temperature between August, the warmest month (55.1°F. average), and January, the coldest (29°F. average), is only 26°F. (Reiger and Wunderlich, 1960). Summer temperatures are thus cool, fluctuating between 45° and 60°F, and temperatures in excess of 70°F are rare. The highest recorded temperature is 85°F (Rieger and Wunderlich, 1960). Similarly, the winter temperatures are warmer than those on the mainland at the same latitude and average between 28° and 34°F. Temperatures below 0°F occur only rarely, and the lowest temperature on record is –5°F.

Due to these weather conditions, the fjords, harbors, and bays of the island remain ice free throughout the year except locally during severe cold spells. Thus, the intertidal zone is never subjected to the scouring effect of annual ice accumulation which characterizes more arctic shores.

Precipitation on Kodiak averages nearly 60 inches per year and is distributed rather evenly such that no month averages less than 3.5

inches; considerably more than half of the annual average occurs during the fall and winter months. During the winter months precipitation consists of snow and rain. Snow is persistent throughout the winter at higher elevations but at the lower altitudes is very variable in presence and depth. Maximum annual snow depth near sea level in the city of Kodiak has varied from 35 inches to less than 2 inches; it is frequently less than 6 inches (Rieger and Wunderlich, 1960).

Kodiak is subject to strong winds; these winds, which may occur at any season, are most common during the winter months. Average wind velocities vary from a high of 13 mph in January to a low of 5.9 mph in July. Storm velocities may exceed these averages by several times and become particularly high in the winter storms. The prevailing wind direction is northwest during the winter and northeast to southeast during the summer months (Capps, 1937).

Cloudy, overcast days are common on Kodiak throughout the year, and fogs are very common. July and August are the foggiest months.

The major part of Kodiak Island is treeless; the vegetation consists primarily of extensive areas of dense, low shrubs with areas of grassland, heath, and wet meadow. The only extensive forests, almost exclusively of Sitka Spruce (*Picea sitkensis*), are found on the north end and terminate abruptly just south of the city of Kodiak on a line extending across the island from northwest to southeast just south of Chiniak Bay. Elsewhere on the island, fairly extensive stands of balsam poplar (*Populus balsamifera*) are found along the stream bottoms at the heads of most of the bays on the island.

The steep-sided mountains have an almost impenetrable, low shrub cover of alder (*Alnus crispus*), salmonberry (*Rubus spectabilis*), Devil's club (*Oplopanax horridus*), and elderberry (*Sambucus racemosa*) at lower and middle elevations. At higher elevations the mountains show a typical alpine-arctic heath vegetation of mosses, lichens, low ericaceous plants and dwarf willows.

On the bars and low-lying, level areas of the shore between the dense shrub vegetation of the mountain sides and the intertidal zone, the vegetation loses many of the shrub species common to the hillsides and has a lower, more open physiognomy dominated by grasses (primarily *Elymus arenarius*) and sedges.

MARINE ENVIRONMENTAL CONDITIONS

The northeastern and southeastern coasts of Kodiak Island from Chiniak Bay at least as far as the Alitak Peninsula (Fig. 1) are influenced by mixed tides.

Using the *Tide Tables* it is possible to compute certain reference levels with respect to the tide for Three Saints Bay. This has been done, and these levels have been indicated on the right side of the graph in Figure 3. These levels will be used throughout this paper as reference points. The levels are: Mean Higher High Water (MHHW), Mean High Water (MHW), Mean Tide Level (MTL), Mean Low Water (MLW), and Mean Lower Low Water (MLLW). Mean Lower Low Water is the datum point for all charts and tidal heights and is therefore defined to be 0.00 feet. It is usually also important as the upper limit of most truly sublittoral animals, thereby delimiting a distinct faunal break. Mid Tide Level is nearly synonymous with Mean Sea Level and indicates a vertical level on the shore which is covered and uncovered by every oscillation of the tide. It is defined as the level midway between Mean High and Mean Low Water. Mean Higher High Water is the mean of the higher of the two high waters of a lunar day. Mean High Water is the mean of all high waters. Mean Low Water is the mean of all low waters.

The Three Saints Bay area has a maximum tidal range of slightly over 13 ft (13.2 ft in 1963). During the time of the field work in June, July, and August of 1963 the maximum range encountered was 12.8 ft (10.4 high to –2.4 low). The mean range, the difference between MHW and MLW, for Three Saints Bay is 6.5 ft. The diurnal range, the difference between MHHW and MLLW, is 8.3 ft. The time of occurrence of the lowest tides of the year, and hence the maximum tidal range, is variable. In 1963 the highest tide occurred in December, but tides within a few tenths of a foot of this maximum also occurred in May, June, and July.

Another important aspect of the tide is the time of its lowest ebb since precise ecological work in the tidal zone could only be done during the hours of daylight. Figure 4 shows the distribution of the lowest tides at Three Saints Bay for each day of the year as a function of time of day of their occurrence. This graph shows quite decisively that from October to early February the lowest tides occur during the night and hence would be difficult to work. However, in the spring and summer months nearly all lowest tides occur during hours of daylight.

Unfortunately, except for the tidal data, no long-term or even short-term environmental data are available for Three Saints Bay itself. Temperature and salinity measurements on a long-term basis are available
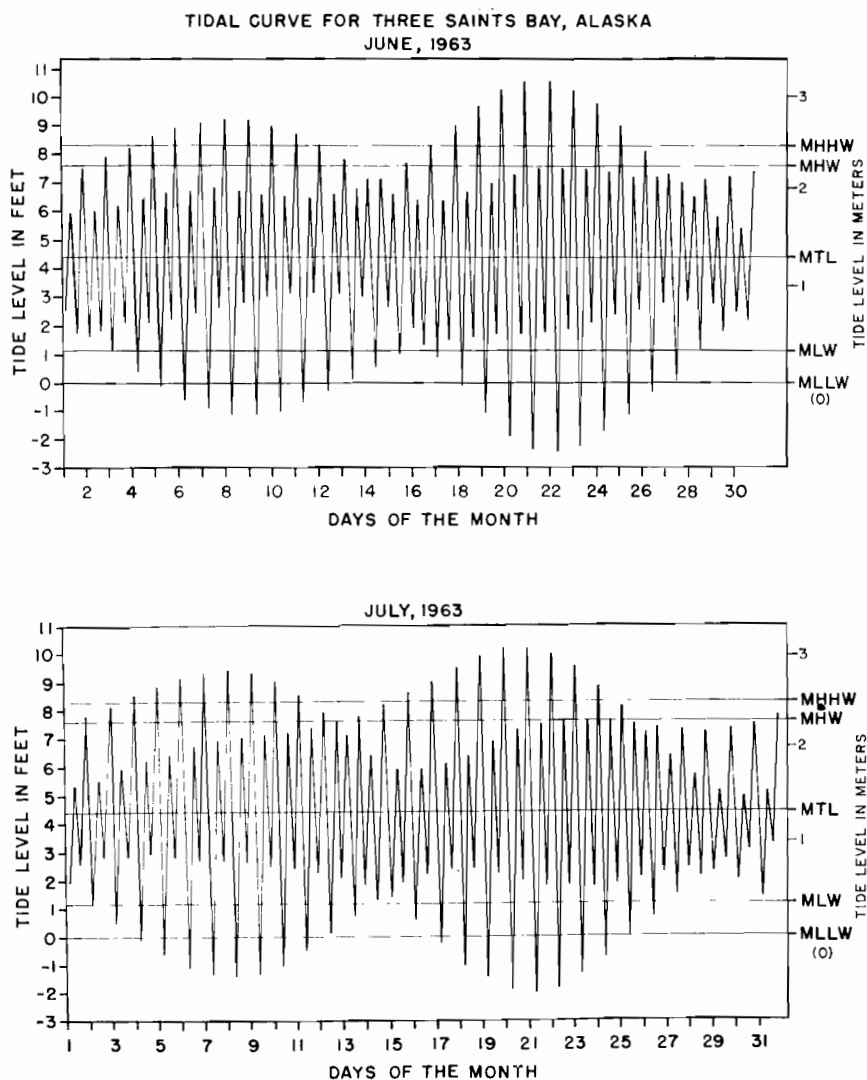
Figure 3.   Tidal curves for Three Saints Bay for June and July, 1963. Constructed from data given in the U.S. Dept. of Commerce, Coast and Geodetic Survey Tide Tables, West Coast North and South America, 1963.

only for Women's Bay, a much shallower body of water just south of the city of Kodiak and somewhat over 60 miles from Three Saints Bay. However since this study was concerned only with surface water, the data from that station should serve to give general trends which would also
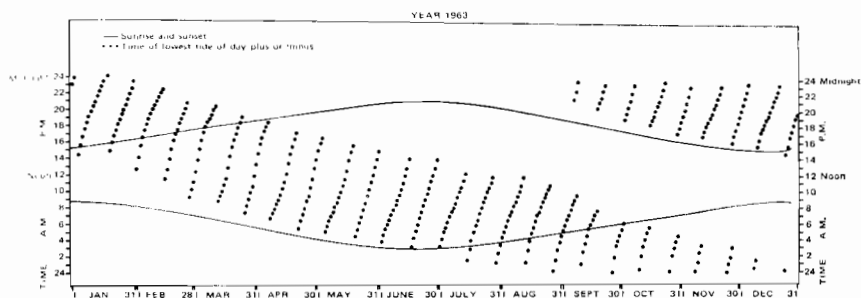
Figure 4. Time of occurrence, relative to daylight and darkness, of the lowest tide of each day of the year 1963 in Three Saints Bay.
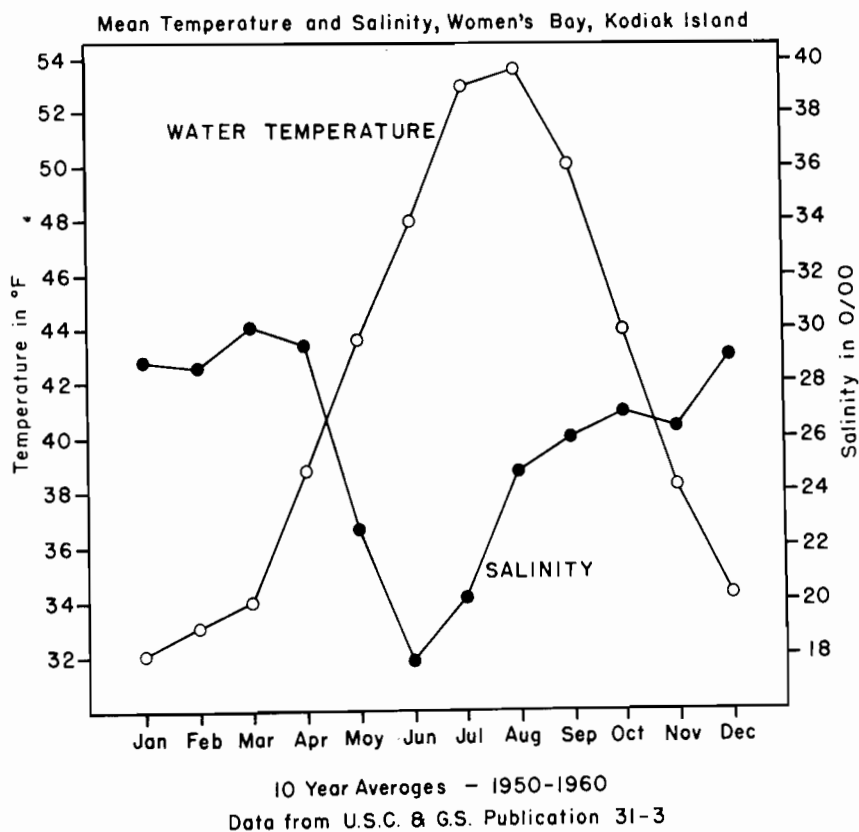
Figure 5. Mean water temperature and salinity, Women's Bay, Kodiak Island, Alaska.

be applicable to Three Saints Bay. These data are summarized in graphic form in Figure 5. It is important to note the great decrease in the salinity during May, June, and July. This fluctuation is probably due to the great influx of melt water from higher elevations at that time. Very similar salinity curves, with even greater reductions in surface salinity, are found at most tide stations in Southeastern Alaska (C & GS Publication 31-3, 1962a).

Actual field measurements taken several times in Three Saints Bay during June, July, and August of 1963 by members of the field party revealed an average surface temperature near shore of 51.8°F based on 15 measurements (J. Hubbard, personal communication), which correlates well with the mean temperature shown in Figure 5.

THREE SAINTS BAY

Three Saints Bay is located in the southern half of Kodiak Island about 60 miles from the city of Kodiak (Fig. 1). It has a unique shape among the other bays found on the island in that a right angle forms an inner "crook" or "arm," giving the bay an inverted "L" shape (Figs. 1, 6).

The bay is ringed with steep-sided mountains rising directly from the water (Fig. 6). The mountains fringing the west and north shores reach heights over 3,000 ft; those to the east have summits from 1,500 to 2,000 ft. Although there are few low lying or level land areas marginal to this bay, two alluvial fans have been formed where the streams enter the bay—one at the head, where a pair of streams enter, and another about half way up the west side of the bay. The remaining areas of low relief are two peninsulas, one on either side of the bay (Fig. 6). That on the west is a bar built up and maintained by the action of along shore currents; the origin of the one on the east is unknown. The west peninsula encloses a deep lagoon which affords a fine anchorage to small boats and hence became the site of our field camp (Fig. 6).

Three Saints Bay is a fjord-like bay of considerable depth. Not only is the bay deep (to 360 ft), but deep water extends very close to shore, particularly along the western shore (Fig. 6).

Several types of shore are found in the bay. The east shore of the bay from the east peninsula south as far as Cape Liakik is composed of gently sloping boulder beaches. North of the east peninsula on the east side of the bay gravel and cobble beaches prevail and extend as far as the head of the bay where the streams enter. The northern third of the west shore and the south shore of the inner "arm" are composed primarily of vertical rock faces with interspersed talus slopes. South of these vertical faces on the west side the shores are again cobble and gravel as far as the location of the campsite and the west peninsula (Fig. 6). From the west peninsula south to Cape Kasiak the shores have a similar composition at higher tidal levels but extensive boulder reefs are exposed at the lowest tidal levels.

Three Saints Bay is open to the ocean at its mouth and receives ocean swell from the south. This swell and its refracted waves have a profound effect on the shores near the mouth and as far into the bay as sample areas #4 and #6 (Fig. 6). The inner "arm" is subject only to local wind-formed waves.

Winds coming especially from the north are funneled by the local mountains resulting in winds of very high velocity which commonly
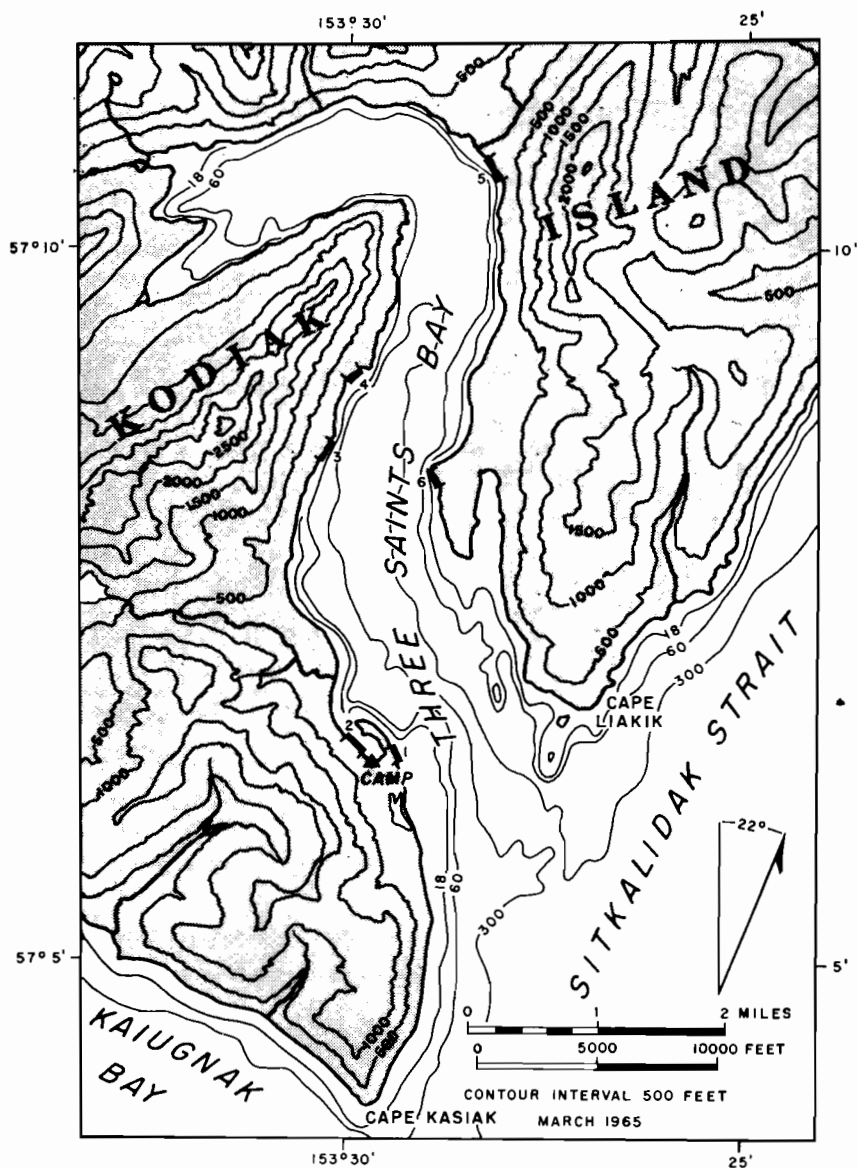
Figure 6.   Three Saints Bay, redrawn from a U.S.G.S. topographic map, showing the location of the sampling sites. 1 = West Reef; 2 = Beach Transects; 3 and 4 = Vertical Transects; 5 = Tide Pool; and 6 = East Reef.

DIAGRAMMATIC REPRESENTATION OF SUBSTRATE
OF THREE SAMPLING AREAS
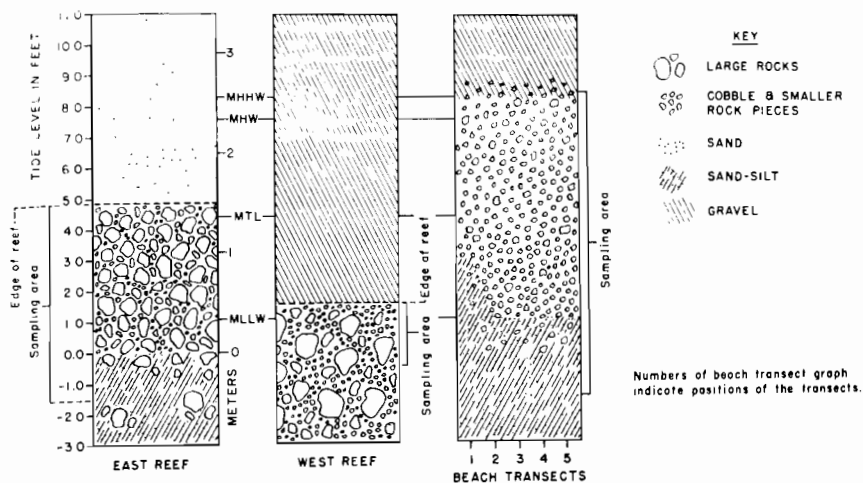
Figure 7. Diagrammatic representation of the substrates of three sampling areas.

pour down the bay raising waves and making boating treacherous. These winds can occur suddenly and, at least in summer, are frequent.

Three Saints Bay is thus representative of the many fjord-like bays which occur in the northern two-thirds of the island.

SAMPLING AREAS

Six areas within Three Saints Bay were worked intensively and form the basis of this paper. The location of each sampling area is designated in Figure 6. Numerical designation of each is purely arbitrary and indicates neither importance nor sequence of work.

Five areas were selected as representing the several types of shore in the bay. These were: the West Reef (Sample Area #1), which was representative of the low-lying boulder reefs on the west side of the bay south of camp; the Beach Transect Area (Sample Area #2) which was representative of the cobble beaches existing in protected water; the Vertical Transects (Sample Areas #3 & #4) which were representative of the sheer granite faces and talus areas of the northern third of the west shore of the bay; and the East Reef (Sample Area #6) which was characteristic of the rock and boulder beaches of the east side of the bay. The tide pool (Sample Area #5) served to test the applicability of the grid system of sampling to a subtidal environment. The only shore type which was not sampled was the mud-sand area existing as a very restricted zone bordering the two stream outlets entering the head of the bay.

The substrate classification employed throughout this paper is arbitrary and can only be used to indicate the relative sizes of the particles. No absolute numerical dimensions can be attached to the classification, but indicative figures and descriptions can be given. The classification in ascending order of size in this scheme is mud-sand (or sand-silt), sand, gravel, cobble, rock, and boulder. The substrate was considered to be mud-sand when in rubbing it between the fingers the sand grains could be easily felt among the soft smooth organic matrix of the mud, sand when the grains were estimated to be less than .1 mm in size, gravel when the particle size was 1 mm to 15 mm in size, cobble when the particle size was 2 cm to 10 cm, rocks when the size was 15 to 25 cm, and boulders when the size was above 25 cm. Figure 7 compares diagrammatically the substrates found on the East Reef, Beach Transects, and West Reef.

SAMPLE AREA #1: WEST REEF

This sample area was the most northerly part of a much more extensive reef system which extends intermittently south toward Cape Kasiak. The sampled reef was separated from the rest of the system by a 30-yard-wide, cobbly shelf which was covered with about 6 inches of water at a –2.0 tide and was nearly free of large algae. This separating shelf had a
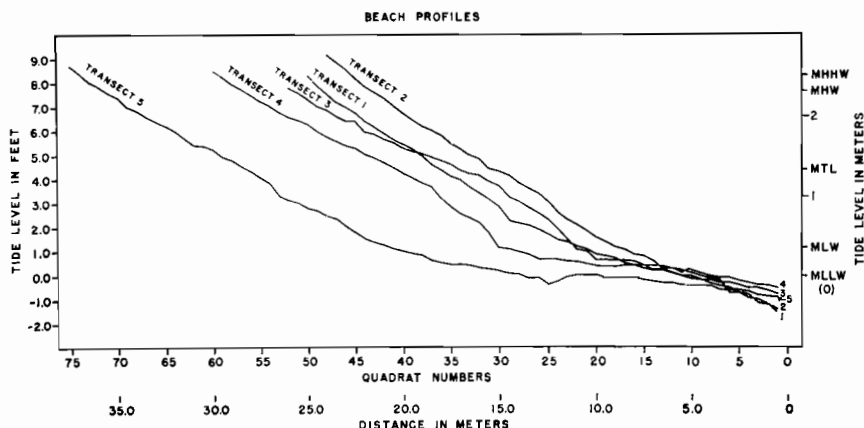
Figure 8.   Beach profiles of each of the five transects taken in sample area #2.

considerable population of the sea urchin *Strongylocentrotus drobachiensis* and in this respect was similar to the pool sampled in area #5.

The West Reef extended out from the base of a sharply sloping, unstable, gravel beach which harbored a highly depauperate fauna made up primarily of amphipods. The reef itself, extending 150 ft along the shore and 200 ft out from shore on a –2.0 tide, was composed primarily of rock boulders 30 to 40 cm in diameter separated by areas of cobble and rock of smaller sizes. Underneath the surface pavement of rocks and fragments, the substrate was a mixture of sand, mud, rock pieces, and shell debris (Fig. 7). No definite edge existed within the tidal range on the seaward side. The entire reef system was very low lying and was exposed only at the lowest tides. It sloped seaward very gradually (in the sample area a drop of 1.3%). Thus, the entire reef system was uncovered late in the tidal ebb cycle and covered early in the tidal flow cycle resulting in no zonal differentiation.

SAMPLE AREA #2:   BEACH TRANSECTS

The steeply sloping shore (Fig. 8) around the lagoon on which camp was situated consisted of partially consolidated pieces of rock varying in size from a few centimeters up to 10 cm with most pieces between 5 and 7 cm in diameter. These rock pieces, hereafter referred to as cobble, formed a surface pavement overlying a finer substrate beneath (Fig. 7).

The pronounced slope continued down to about the level of MLLW (Fig. 8). At this point the shore became nearly flat and ran toward the center of the lagoon with a substrate of mud or sandy mud. This mud flat

varied in width but terminated on a steep dropoff to the deeper water of this lagoon. The steepness of the dropoff can be appreciated when it is considered that the water went from –2.0 ft to –50.0 ft in a matter of 10 horizontal feet.

This beach was well protected from direct wave action; water level on the beach was determined almost entirely by tidal action.

Another important feature of this sampling area was the presence of the outlet of a freshwater stream adjacent to transect #1. The stream varied in width from 4 to 20 ft. The volume of outflow was never measured, but did diminish as the summer progressed. It was most probably highest during the spring months. This influx of fresh water was assumed to have a great effect on the distribution and abundance of organisms in transect #1 and a lesser effect as the distance from the stream increased toward transect #5.

SAMPLE AREAS #3 AND #4: VERTICAL TRANSECTS

These areas were studied by means of a series of vertical belt transects. Transects #1, #3 and #4 (Area #3) and #5 to #7 (Area #4) were made on slopes which faced the open end of the bay to the south and hence were open to the sea swell and direct wave action from that quarter. Transect #2 (Area #3) faced to the north, toward the closed end of the bay and was subject to swell but little direct wave action. •

The shore was formed of a nearly vertical series of massive dioritic rock faces which dropped off very abruptly into the water. There were no beaches, and the water depth immediately next to shore was 60 ft or more.

The vertical faces had but a limited number of ledges or horizontal fracturing with the result that few animals were found of the type which did not have mechanisms for attachment to vertical surfaces. Those which were found were necessarily confined to the few surface cracks.

SAMPLE AREA #5: TIDE POOL

The sampled tide pool lay at the upper edge of the *Fucus* zone in a small isolated reef area and was assumed on the basis of its vegetation to be at or near mid-tide level. The pool itself, about 100 ft long and 50 ft wide was shaped roughly as an inverted mushroom with the stem opening out into the bay. Although the pool had a direct tidal outlet to the bay the outlet was higher than the main body of the pool; thus the pool never drained completely even at very low tides. The level of the outlet barrier did permit reduction of the water level in the pool to only a foot or two at low tide.

Within the pool the bottom substrate of unconsolidated cobble was not completely uniform. Scattered piles of larger rock up to 2 ft in width were found extending to the surface. Macroscopic algae were absent from the pool.

The reef area surrounding the tide pool was also of the same cobble and supported a community dominated by *Mytilus edulis* and *Fucus distichus* which superficially resembled that sampled in the beach transects of Sample Area #1 except that *Mytilus* seemed much more abundant.

Sample Area #6: East Reef

The East Reef was on the northern edge of an extensive peninsula formed of rocks and boulders.

The sampling area itself consisted primarily of rock boulders 25 to 30 cm in diameter separated by cobble and smaller rock fragments. This substrate sloped off toward the bay, terminating with a modified substrate of sand-silt (Fig. 7). Shoreward the reef originated at the base of a gently sloping sand beach. The pronounced slope of this reef (3.1%) was considerably greater than that of the West Reef (1.3%). The East Reef also extended higher in the intertidal zone (+5.00 ft vs. +1.65 ft). Development of definite horizontal bands of zonation was a pronounced feature of this reef. The reef extended for about 800 ft along the shore and 150 ft to seaward measured at a –1.5 tide. At the seaward end of the reef there was no definite edge in the tidal zone; it continued sub-tidally as an extensive eelgrass bed. Part of this eelgrass bed was exposed at low tides at the bay end of the reef from the –1.32 level to the –.5 level.

The upper edge of the reef (about +5.0 ft tide level) was very abrupt where it met the sand of the upper beach. From this point to and beyond the high tide level on the shore the substrate was loose sand. The fauna was very depauperate and consisted almost entirely of amphipods.

METHODS

The methods used in this study were adaptations of those which have been used, primarily by plant ecologists, to survey and quantify vegetation. The restriction of this study to sedentary and semisedentary species of macro-invertebrates allowed such methods to be used. The belt transect method has, in addition, been commonly used in previous intertidal studies (Hewatt, 1937; Rees, 1940; Spooner and Moore, 1940).

Requisite equipment for use throughout the study consisted of a surveyor's transit, 16.5 ft level rod, measuring tapes, ropes, quadrats, an accurate watch, and a copy of *Tide Tables West Coast North and South America* (U.S. Dept. Comm. C. & G. S., 1962b).

Quadrat sampling was always related to tide level by means of standard levelling procedure using a transit and level rod. Base readings were taken before and after each series of quadrat levels to relate the level line to actual tide level.

On the vertical transects tidal levels were determined without the aid of the transit. The near verticality of the faces permitted the level rod alone to be used. Computation of the level from the *Tide Tables* was similar to the method used on the other quadrats. In all sampling areas reference specimens of algae and invertebrates were taken.

Belt Transects

The belt transect method, that is a series of adjacent .25 m^2 quadrats in a line providing the described belt, was used to sample the vertical granite faces and the sloping cobble beach (Sample Areas #2, #3 and #4, Fig. 6).

Beach Transects: On the beach near camp five parallel transects were laid out 10 m apart and were numbered 1 through 5 running from south to north. At the highest part of each transect a stake was erected marking the transect station. A second tall stake perpendicular to the beach line and seaward of the first provided a visual sighting system by which the remainder of the transect was aligned.

When these two stakes had been erected, sampling along each transect was begun at the edge nearest the lagoon at the level of lowest tide. Since the several transects were not begun on the same day and tide nor necessarily at the time of lowest water, the five transects show some variation of the tide level of their starting point.

A wooden .25 m^2 quadrat was used in all sampling in the bay. This size was determined since its initial use on the beach transects demon-

strated it to be of sufficient size to pick up all macro-invertebrate species present. Smaller sizes did not sample all species while larger sizes of 1 m² obscured the obvious vegetational belts on the shore.

Each quadrat of each transect was described in turn as to vegetation, obvious niches of organisms, substrate, presence of large rocks or other attachments, and any unusual features such as clumping of barnacles on a single rock or attachment of all algae to a single rock. Per cent of the quadrat covered with algae or eel grass was estimated. This estimate was made independently by each member of the work party (from two to four individuals); these estimates were averaged by the recorder. This same method of assessing per cent cover was used throughout the study in all areas. A level reading was taken in the center of each quadrat. The quadrat was systematically examined and the number of individuals of each species of invertebrate found were recorded on tally sheets. All macro-invertebrates were enumerated except amphipods. The rapid movement of these crustaceans did not permit accurate counting.

Finally the lower, left hand quarter of the quadrat (1/16 m²) on the seaward side was excavated to a depth of 15 cm and the substrate screened on a 3 mm screen. The organisms found in this quarter were also counted and recorded. No one transect was completed on any single tide sequence.

Vertical Transects: On all vertical faces, the transects were delimited by the use of the level rod alone, placed against the face to be sampled. Next to the upright rod sampling was begun at the water's edge. The .25 m² frame was held against the face by an assistant and the quadrat was described as with those taken on the beach. An estimate of cover was obtained; the number of each invertebrate species in the quadrat was recorded; the upper and lower limits of distribution of most invertebrates were noted; and changes in presence and physiognomy of vegetation were measured and described. Successive quadrats were taken progressing upwardly on the rock face. Sampling continued up to the black lichen band which usually had its lower limit between the +9.0 and +10.0-ft tide level. Each completed transect usually consisted of six or seven quadrats. The data obtained by this method are presented in this paper by plotting the presence of each species in succeeding quadrats against the tide level for each transect. For the organisms which appear to dominate the shore zones the graphs illustrate measured points above or below which the organism does not appear. In some instances with the abundant organisms and often with the less common organisms a specific uppermost or lowermost tidal limit was not measured. The data recorded were the

lowest and uppermost quadrats of occurrence. In these cases the limits were considered to be the midpoints of the terminal quadrats. Where an organism was found only once or in a single quadrat the organism was considered present in the entire quadrat unless actual observation indicated presence in only a fraction; in these latter cases only that fraction was plotted. Where either an upper or lower limit was measured but the other was unmeasured, the latter limit was considered as the midpoint of the quadrat or as a fraction of the quadrat if that was indicated. All of these levels which were not specifically measured have been plotted on the presence graphs as "inferred" levels. At the extreme, that is when the upper and lower "inferred" limits are plotted at quadrat midpoints, the accuracy of plotted tidal distribution is within .8 ft of the true measure. For certain species occurring rarely, such as *Henricia leviuscula*, this obscures the narrowness of the ecological limits of the organism.

Secondly, abundance relative to tidal level was obtained for the major faunal constituents. Individual density within a quadrat is represented by a single point graphed at the center of its vertical span. In the case of the three barnacle species and *Mytilus edulis*, all of which occurred in very large numbers on the faces, actual counts of individuals were made only up to 500. In the common event that more than this number occurred in the quadrat it was merely noted as "over 500", "many hundreds", or "thousands" depending on the relative density. The resultant graphs of these species indicate numbers only up to 500. If the lines indicating density reach this point, it means that at least 500 were present, but the density may be far greater than that. In the case of the small barnacle *Chthamalus dalli* this is especially misleading as within their narrow band of distribution they completely covered the rocks at densities often in excess of 1,000 per .25 m².

It is important to note that the absence of *C. dalli* from transects one and two is due to the fact that this small species was not recognized and differentiated until after these two transects had been sampled. Previously they had been thought to be spat of *Balanus glandula*. Fortunately, spat of no species were counted so the count of adult *Balanus glandula* has not been invalidated. It is almost certain that *C. dalli* was present on these transects.

Algal cover is presented as a percentage of the total area. Variation in the vertical distribution of the major species among the seven transects is demonstrated through center of presence plots for each.

Random Sampling

The second basic method, employed on the West Reef, the East Reef,

and the tide pool, involved the random establishment of sampling stations on a surveyed grid system. At each station a .25 m² quadrat was analyzed.

At each sample area, a 100-ft base line was staked next to the reef (or pool) and approximately parallel to the interface between rocky reef area and the sand-gravel upper beach. This base line was set in using standard surveying methods with monumented stations 10 ft apart. For sighting purposes, a duplicate base line was staked parallel to the first but offset 15 ft in a shoreward direction.

Stations on the grid were established on the reef coordinate using a nylon rope marked with paint at 15-ft intervals. These paint marks represented the stationing on the reef when the rope was laid out parallel to the slope on the reef from a base line station and perpendicular to the station. Laying out of the rope to delimit reef stationing was accomplished by sighting over the two base line stations, drawing the rope taut, aligning it, and then laying it down on the reef. The rope could then be moved from station to station along the base line. Sampling points were selected from a table of random numbers. At least 50 samples were taken on each of the reefs but only 24 in the pool.

The methods for describing and censusing each sample quadrat were the same as described for the belt transect method except that, instead of excavating only one quarter of the quadrat, the entire quadrat was excavated to a depth of 20 cm and screened for animals.

The calculations of frequency, observed density and abundance made for each species in each area subjected to random sampling were made as discussed by Grieg-Smith (1957). The calculated density figures for all species indicate the density to be expected for a random distribution and are based on the observed frequency; they were obtained from tables in Grieg-Smith (1957). The aggregation measure is merely the ratio between observed and calculated densities and thus measures the departure from randomness.

Standard statistical techniques described in Steele and Torrie (1960) were used throughout.

BIASES

In using these sampling methods certain biases were unavoidable. 1) In the few cases where the tide overtook us in a quadrat such that it was necessary to finish work under water, excavation of substrate became much less accurate and certain of the subsurface fauna were probably missed. 2) Screening the substrate on a 3 mm screen undoubtedly allowed many small invertebrates to escape. 3) Counting of very abundant

forms such as barnacles probably did not record every adult individual, while for less abundant or rare forms extra effort was often put into obtaining every last individual. 4) Motile forms such as isopods and hermit crabs were counted first in each quadrat, but it is certain that many moved out (or in) before the counts were finished. 5) Only barnacles which could be positively identified were counted. In practice this meant counting *Balanus cariosus* above a diameter of ¼ inch, *Balanus glandula* above ¼ inch, and *Chthamalus dalli* above ⅛ inch in size. No spat were ever counted.

RESULTS

The results are presented separately for each sample area; within each section appear the following: a) description of the zonation in a qualitative way, and b) documentation of observed zonation by quantitative data for each species. Finally, the results are summarized, principally in graphs and tables.

Additional ecological and behavioral data on most invertebrate species encountered in this study have been summarized in a series of species accounts (Appendix).

The term "dominant organisms" will be used frequently and is here defined to mean those organisms which, by their individual abundance, size, growth form, or by some combination of these characters give a characteristic appearance to large areas on the shore.

Results on Belt Transects

Zonation on beach transects (Sample Area #2): The five belt transects provided data on the presence of organisms, abundance of organisms, and per cent cover relative to tide level (Figs 9 to 28).

On a low tide of –2.0 ft, the beach sample area was obviously subdivided into a series of three principal horizontal bands which succeeded each other vertically. These bands will henceforth be considered zones named according to the dominant organisms. The lowest zone, green in color, was formed by a carpet of eelgrass (*Zostera marina*) which was continuous horizontally except near the outlet of the stream. No large surface dwelling invertebrates were visible on the surface. The substrate was soft mud-sand. The eelgrass zone reached its upper limit near the +.5 tide level.

The second obvious zone on the shore, up the beach from the eelgrass and dark yellow-brown in color, was composed of *Fucus distichus* as the dominant component but with *Ectocarpus* in the lower levels and occasional specimens of *Odonthalia floccosa*. Numbers of *Littorina sitkana* were visible on the fronds of the *Fucus*. The *Fucus* zone ended quite abruptly slightly above MTL (4.4 ft) between 4.4 and 5.0 ft and from a distance stood out as the most marked line on the beach (Fig. 22). It was less easy to define a single lower limit for this zone which varied from about +2 ft in transect #1 to +.6 ft in transect #3 (Fig. 22). Sharp limits of distribution were not expected at this level.

Above the *Fucus*, the last zone extended up to the level reached by the highest tides. This band was very dark, almost black, due to the visible bare cobble substrate. Except for occasional small white patches of
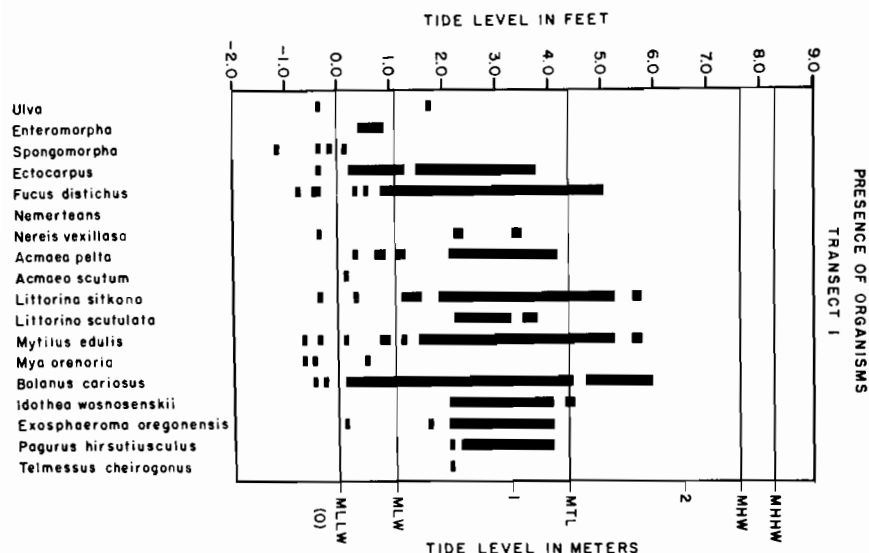
Figure 9.   Presence of organisms in Transect #1, Beach Transects.

barnacles nothing else was visible superficially in this zone. It has been designated as the barnacle zone.

A transition area, often present between the eelgrass and *Fucus* zones, was not well marked except in transect #5 where a reef of *Mytilus edulis* occurred (Fig. 25). In the other transects the transition zone was often a bare area. In no instance did the *Zostera-Fucus* zones meet in a sharp line as at the *Fucus*-barnacle interface (Fig. 22).

The substrate of the eelgrass (*Zostera*) zone was soft mud or sand mixed with much mud which gave way to a surface pavement of small bits of rock, considered as gravel or cobble depending on the size, near the +1.0 tide level; in transect #1 however the soft substrate extended up to +3.0 ft (Fig. 7). The substrate types were, however, not completely pure or isolated. Bits of rock or shell which formed a nucleus for attachment of organisms were occasionally found in areas of silt, mud, or sand, thus allowing the existence there of organisms which were otherwise restricted to hard surfaces. For example, *Fucus distichus* was found in areas which were designated as mud-sand in transect #1 (Fig 22). Since this species needs a hard surface for attachment, its presence implied that such surface was available. Another example is provided by *Mytilus edulis*, which can anchor in the soft substrate, thereby providing a hard surface to be used by *Balanus cariosus* and

TIDE LEVEL IN FEET

Ulva
Spongomorpha
Ectocarpus
Fucus distichus
Zostera marina
Nemerteans
Nereis vexillosa
Acmaea pelta
Acmaea scutum
Littorina sitkana
Littorina scutulata
Mytilus edulis
Clinocardium nuttalli
Balanus coriosus
Idothea wosnasenskii
Exosphaeroma oreganensis
Pagurus hirsutiusculus

PRESENCE OF ORGANISMS TRANSECT 2

TIDE LEVEL IN METERS
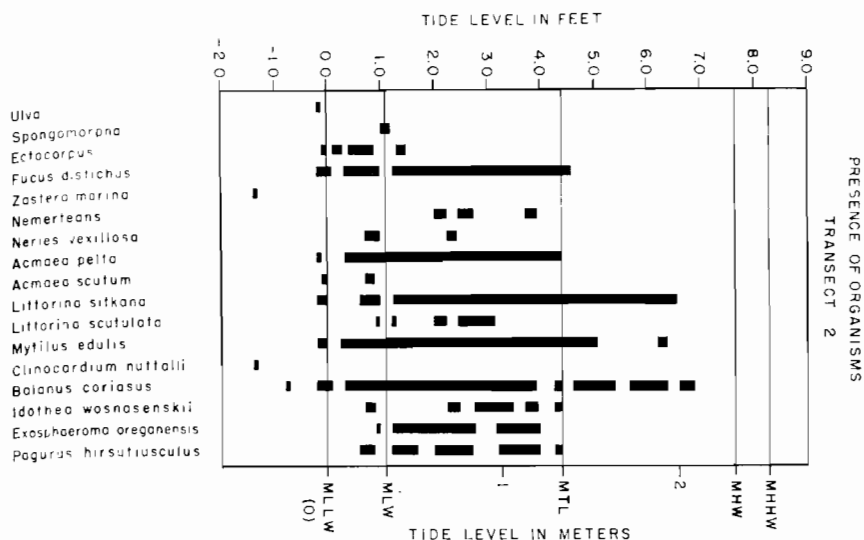
Figure 10. Presence of organisms in Transect #2, Beach Transects.

Acmaea pelta. Mytilus edulis showed a definite peak presence in the mud-sand substrate (Fig. 25) which corresponded in this case to the *Mytilus* reef of transect #5 (Fig. 25). At the same level *Acmaea pelta*, dependent

TIDE LEVEL IN FEET

Ectocarpus
Fucus distichus
Zostera marina
Nemerteans
Nereis vexillosa
Nephthys caeca
Acmaea pelta
Littorina sitkana
Littorina scutulata
Mytilus edulis
Clinocardium nuttalli
Macoma balthica
Mya arenaria
Balanus cariosus
Idothea wosnasenskii
Mesodotea
Exosphaeroma oreganensis
Pagurus hirsutiusculus
Cancer magister

PRESENCE OF ORGANISMS TRANSECT 3

TIDE LEVEL IN METERS

Figure 11. Presence of organisms in Transect #3, Beach Transects.
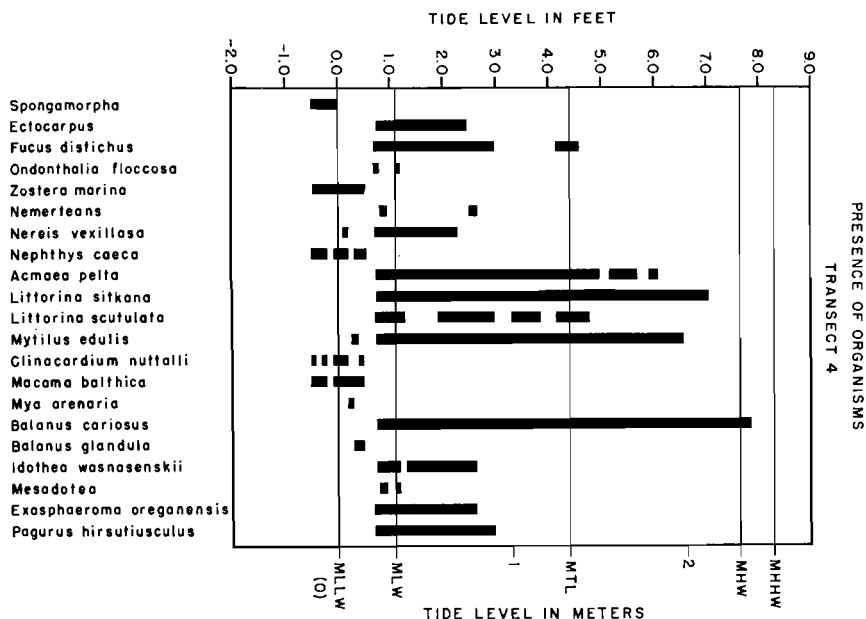
Figure 12.   Presence of organisms in Transect #4, Beach Transects.

on a hard substrate, also showed a peak (Fig. 25). These grouped data substantiate the general observation that A. *pelta* was very commonly observed on *Mytilus*; thus the importance of the most obvious substrate as a determinant of species may be obscured by such exceptional instances but not the importance of what the organism selects as its substrate.

Distribution and abundance of species on beach transects (Sample Area #2):   The three zones found on the beaches have been described and have been delimited by tidal levels. Data on the distribution and abundance of the component invertebrate species further verify the reality of these zones by demonstrating the aggregation of species in one or more of these zones (Figs. 14 to 21 and 23 to 27).

The eelgrass (*Zostera*) zone was most conspicuous by the near absence of surface-dwelling animals. Of the 15 species of invertebrates recorded more than once from the beach transects only the subsurface forms were commonly found. Thus *Clinocardium nuttalli, Nephthys caeca,* and *Macoma balthica* were restricted to this zone and did not extend above +1.0 ft (Figs. 21 and 23). No surface dwelling invertebrate species were encountered here except as scattered individuals.

Most of the species found on the beaches demonstrated strong aggre-
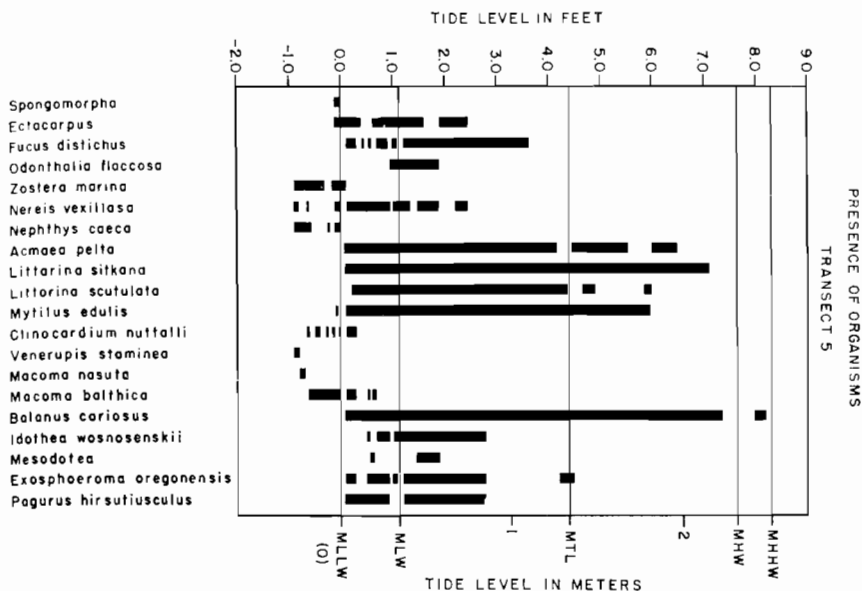
Figure 13. Presence of organisms in Transect #5, Beach Transects.

gation within the *Fucus* zone (Figs. 24, 25, and 26). The existence of a sharp break in the presence and densities of species between +4.4 and +5.0 ft, corresponding to the upper edge of the *Fucus* belt, is well marked (Figs. 9 to 20, and 28). *Balanus cariosus, Mytilus edulis, Littorina sitkana*, and *Acmaea pelta* extended above +5.0 (Figs. 14, 15, 16,
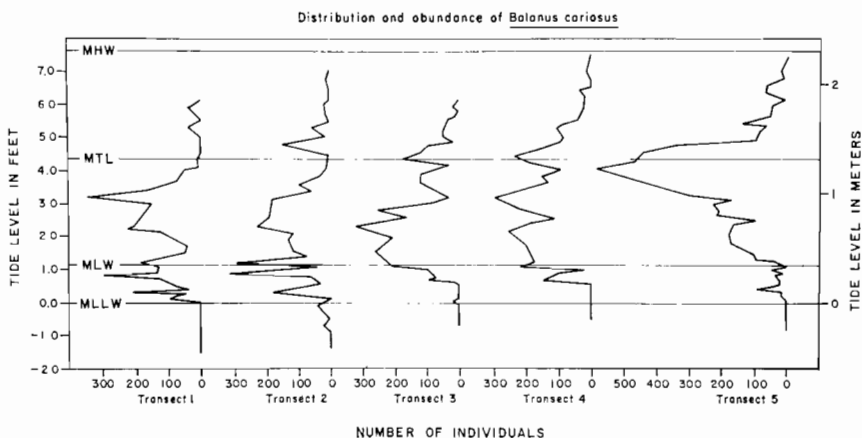
Figure 14. Distribution and abundance of *Balanus cariosus*, Beach Transects.
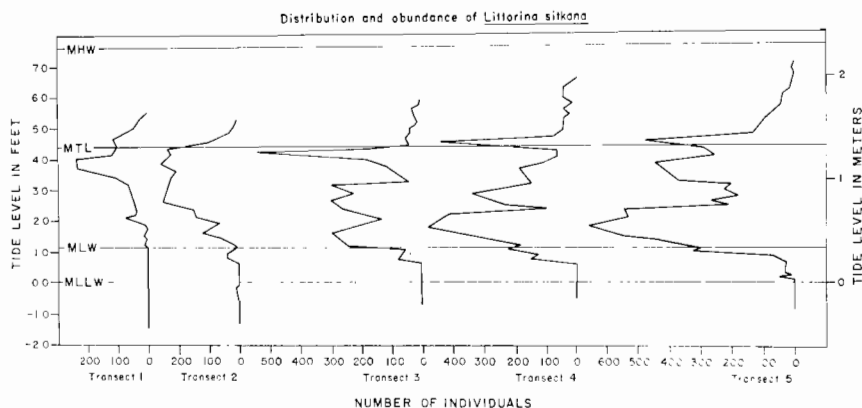
Figure 15. Distribution and abundance of *Littorina sitkana*, Beach Transects.

18, and 28), but all showed their maximum abundances below that level in the *Fucus* zone. *Idothea wosnosenskii*, *Nereis vexillosa*, and *Pagurus hirsutiusculus* did not even reach the upper border (Figs. 17, 20, 25, and 26). All species except *Nereis vexillosa*, *Acmaea pelta*, and *Littorina scutulata* reached their highest densities within the *Fucus* zone from +1.0 to +5.0 tide level (Figs. 24, 25).

The final band, the barnacle zone, was characterized, as was the eel-grass, by the reduction of the number of species inhabiting it. Further, all species which were found to inhabit this zone were also found in the *Fucus* zone below. The superficial observation that the zone had a small fauna is borne out. *Acmaea pelta* was present only as scattered individ-
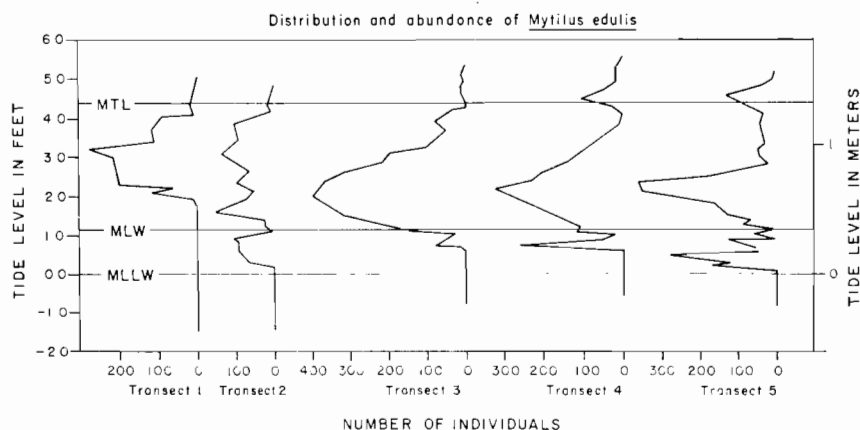
Figure 16. Distribution and abundance of *Mytilus edulis*, Beach Transects.
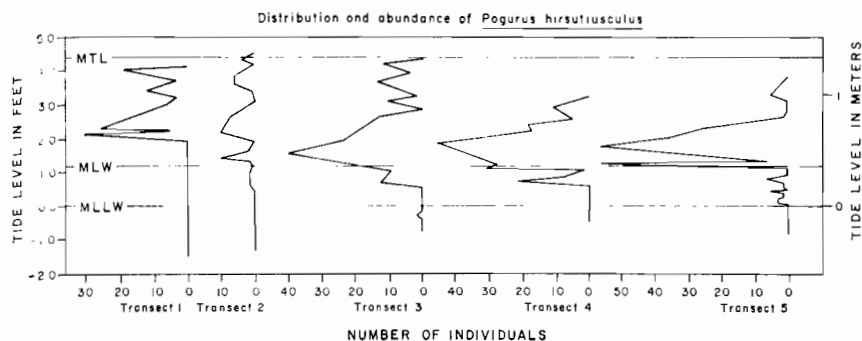
Figure 17.   Distribution and abundance of *Pagurus hirsutiusculus*, Beach Transects.

uals (Fig. 18) while *Littorina sitkana, Mytilus edulis,* and *Balanus cario-sus*, which apparently are more resistant to dessication or less dependent on cover, were present in small numbers (Figs. 14, 15, and 16).

Results on Vertical Transects

Sampling on the vertical faces of Areas #3 and #4 in the seven belt transects with their contiguous quadrats provided information on the presence of organisms, density (for a few of the species), and per cent cover as a function of tidal level (Figs. 29 to 38).

Zonation on vertical transects (Sample Areas #3 and #4): Initial observation of the vertical surfaces did not reveal the very sharp, distinct banding at all levels which was observed on the beach transects (Figs. 29
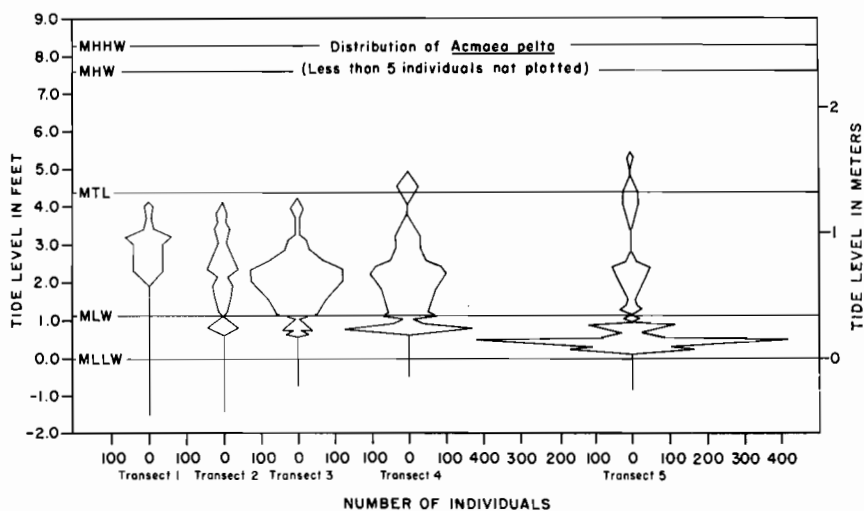
Figure 18.   Distribution and abundance of *Acmaea pelta*, Beach Transects.
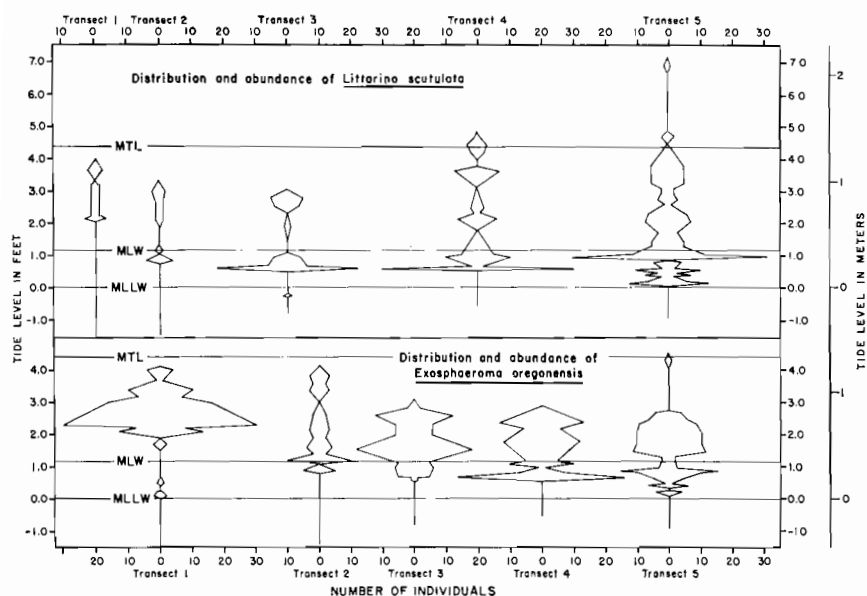
Figure 19. Distribution and abundance of *Littorina scutulata* and *Exosphaeroma oregonensis*, Beach Transects.

to 32). It was still possible, however, to discern three major zones on these faces.

The lowest zone, which was continuous subtidally, was dark in color and dominated by the algae *Alaria pylaii, Odonthalia floccosa,* and *Laminaria platymeris* and has been termed the *Odonthalia-Laminaria* zone.

Above this lowest zone occurred another dark colored zone dominated by *Fucus distichus.* The lower limit of this *Fucus* zone was usually around +1.0 to +2.0 ft, but there was no definite break between it and the *Odonthalia-Laminaria* zone below. This boundary was made increasingly obscure by the presence of very large amounts of the alga *Odonthalia floccosa* which extended from a subtidal position through the lowest laminarian zone well into the area of *Fucus* cover (Fig. 39). *Fucus distichus* reached its upper limit around the +7.5 ft tide level and formed at this level visually the most obvious line on these faces. The *Fucus* was dark and this line was emphasized by the existence of large numbers of light colored barnacles immediately above. This line was also emphasized by a narrow band of the bright green alga *Enteromorpha intestinalis* existing just above the *Fucus.* This area of barnacles formed a distinct zone, the barnacle zone, which, on these surfaces, graded off above within the distinct prominent band formed by the black (*Verru-*
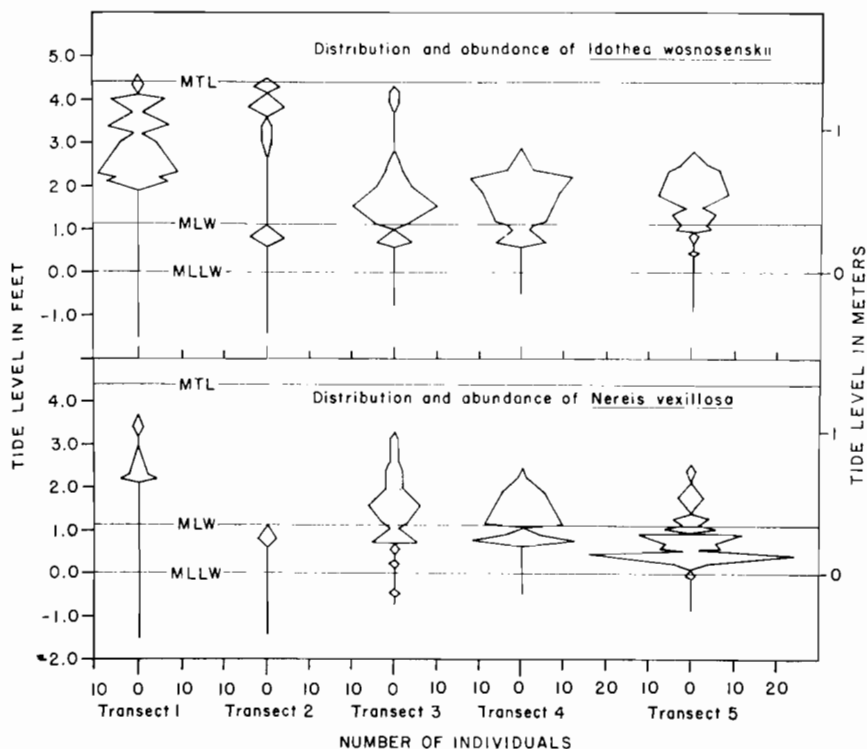
Figure 20.   Distribution and abundance of *Idothea wosnosenskii* and *Nereis vexillosa*, Beach Transects.

caria) lichens. This black lichen band was itself delimited above by the light color of the rocks. Lichens of the genus *Verrucaria* have been reported as a common feature of the highest levels of rocky shores in various parts of the world (Stephenson and Stephenson, 1949). This lichen band was not always continuous, however, and varied in width and in height above tidal datum. Where the band was found, its upper edge marked the upper limit of marine organisms and also was considered the upper limit of the barnacle zone.

The rock substrate in all seven transects was dioritic granite and thus cannot be considered in a fundamental way as a factor in the distribution of organisms. Differences in substrate material were not as fundamental here to species distributions as were variations in the surface microtopography. The presence or absence of cracks in the rock face was very important in the determining presence, absence, and abundance of several invertebrates. *Mytilis edulis*, for example, usually attached between
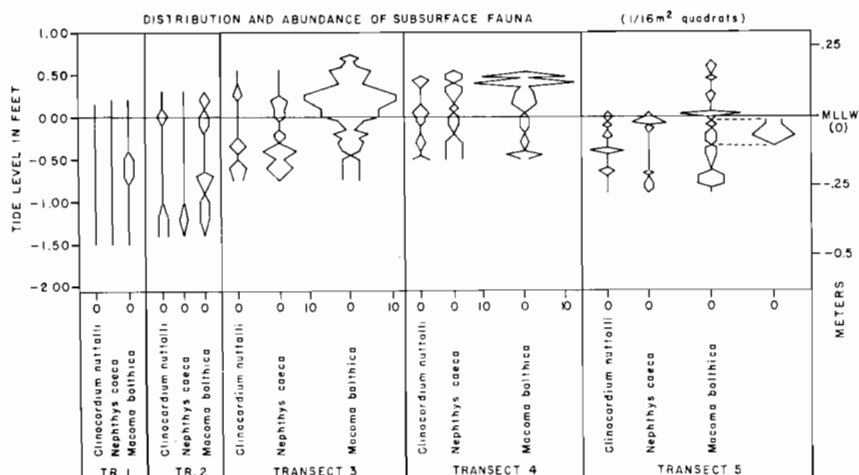
Figure 21. Distribution and abundance of the subsurface fauna, Beach Transects.

established barnacles or within rock fissures. *Leptasterias* was often found in such cracks while *Acmaea digitalis* and *Littorina sitkana* were nearly confined to them. The presence of numerous large barnacles with their hard, irregular surfaces and with crevices and ledges between individuals, constituted a secondary, but characteristic, substrate type. Species such as *Leptasterias, Henricia leviuscula,* and *Katharina tunicata* seemed to prefer this organic microtopography and their distribution in part followed the presence of large barnacles, particularly *Balanus cariosus.*

Distribution and abundance of species on vertical transects (Sample
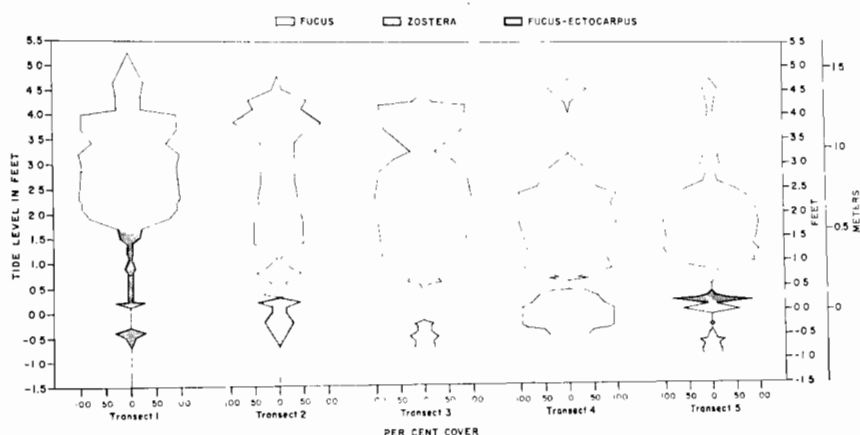
Figure 22. Per cent cover on five transects, Beach Transects.
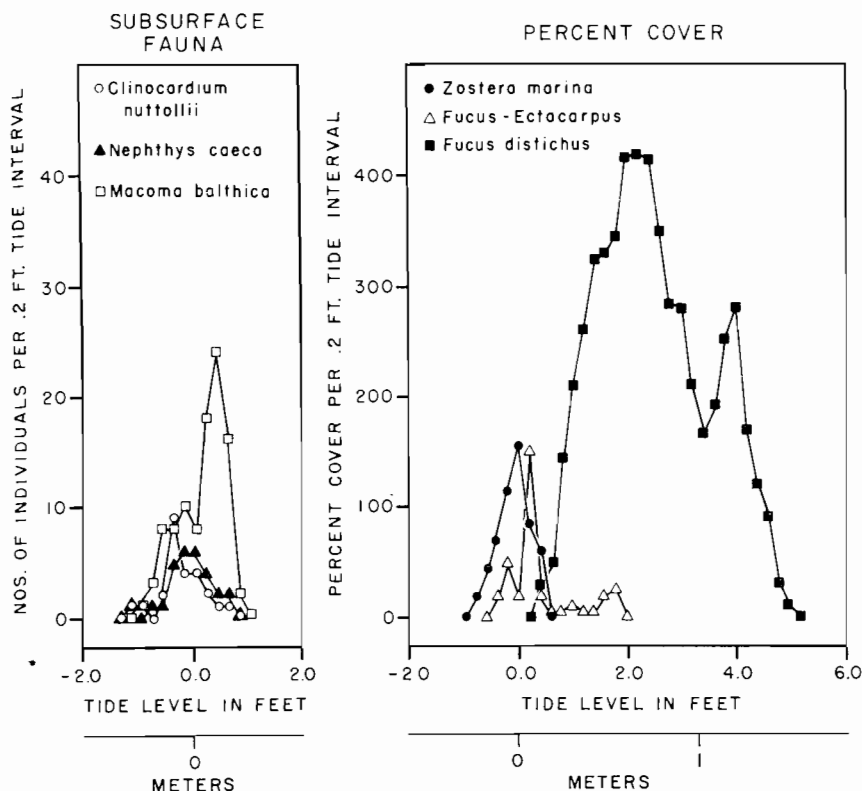
Figure 23.   Per cent cover and distribution and abundance of the subsurface fauna grouped over all five transects for each .2 ft tide interval, Beach Transects.

Areas #3 and #4):   The zones existing on the vertical surfaces have been qualitatively described. The data on presence of organisms demonstrate the reality of these zones and the tendency toward aggregation or restriction of species within their boundaries (Fig. 39).

The *Odonthalia-Laminaria* zone included the greatest number (13) of invertebrate species, but none could be considered dominant forms (Fig. 39); this zone was dominated entirely by algae.

The dominant invertebrate species, *Balanus cariosus* and *Mytilus edulis*, were nearly restricted to the *Fucus* zone and helped to characterize it although obscured by the surface cover of *Fucus*. Other species strongly concentrated in this zone included *Katharina tunicata*, *Acmaea pelta*, *Acmaea scutum*, and *Leptasterias* (Fig. 39).

The barnacle zone contained the fewest species of which only *Chtha-*
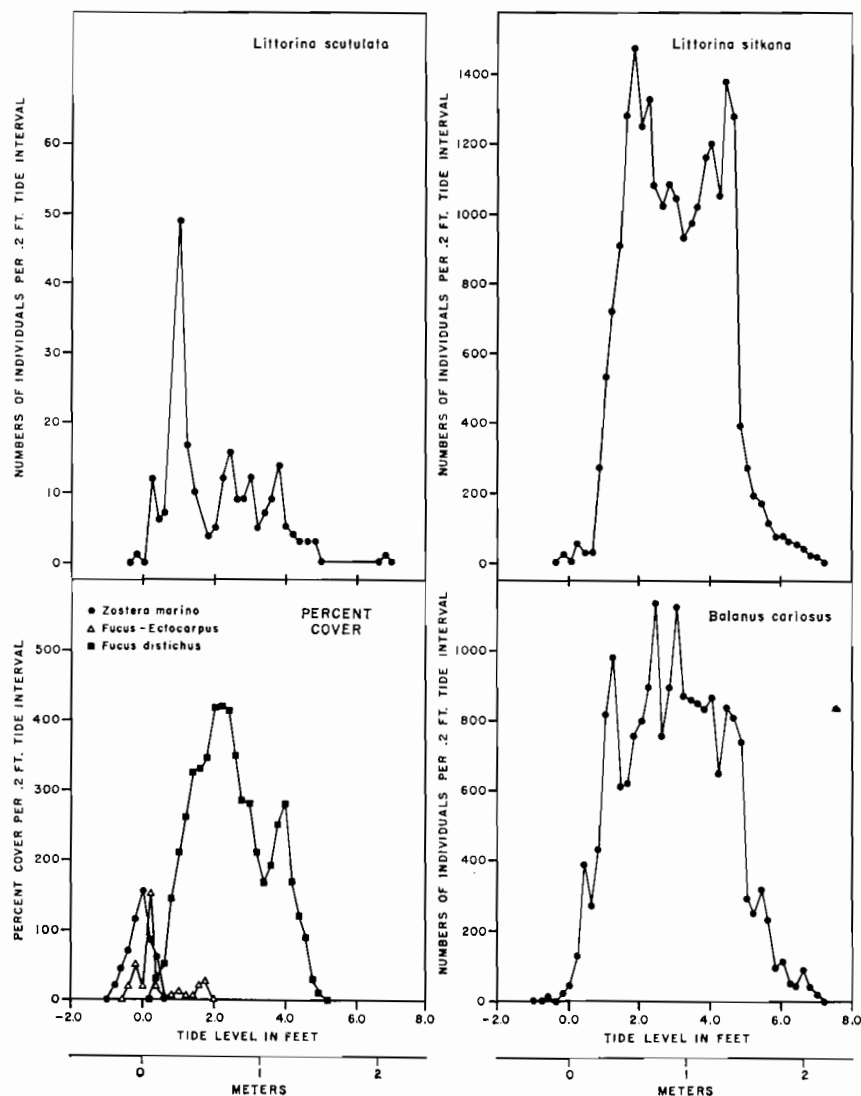
Figure 24.   Per cent cover and distribution and abundance of *Littorina sitkana*, *Littorina scutulata*, and *Balanus cariosus* grouped over all five transects for each .2 ft tide interval, Beach Transects.

malus dalli and *Acmaea digitalis* were distributed wholly within it (Fig. 39).

The pattern of distribution of the three *Acmaea* species (A. mitra is not considered since only one specimen was found) is somewhat less rigid.
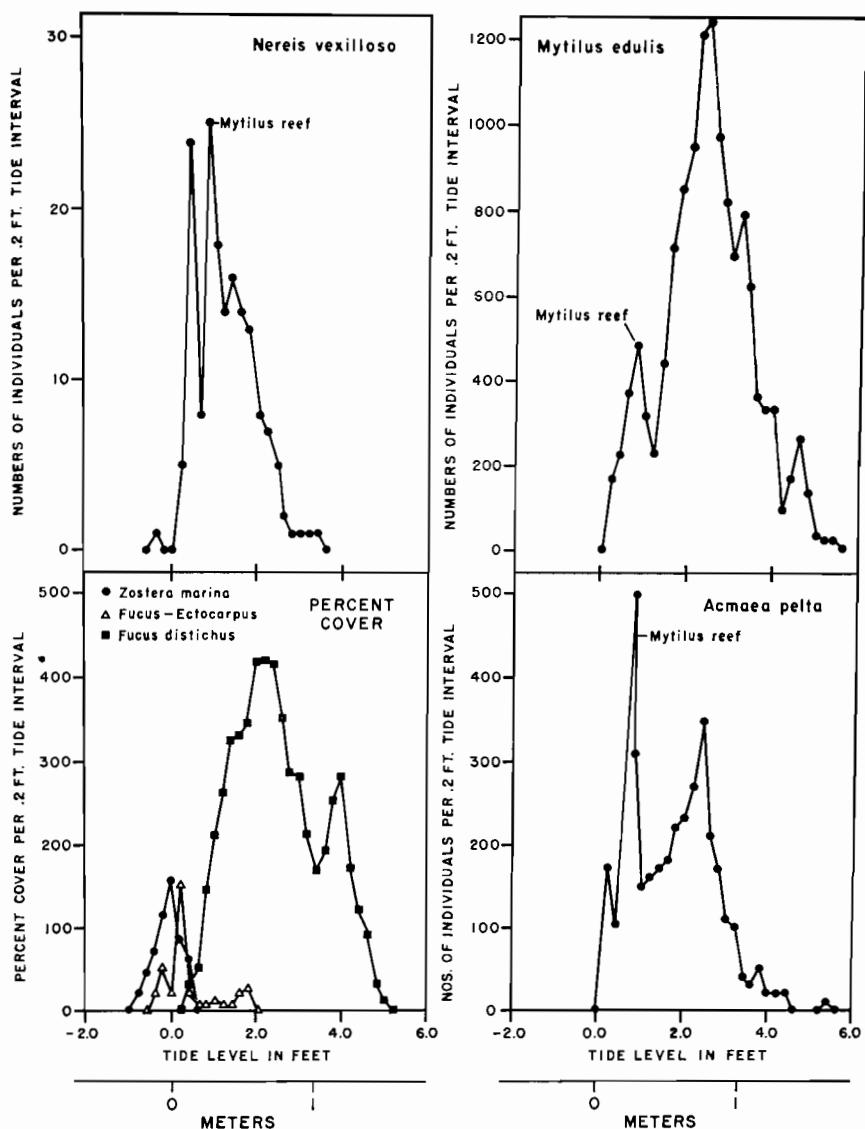
Figure 25. Per cent cover and distribution and abundance of *Nereis vexillosa,*
Mytilus edulis, and *Acmaea pelta* grouped over all five transects for each .2 ft
tide interval, Beach Transects.
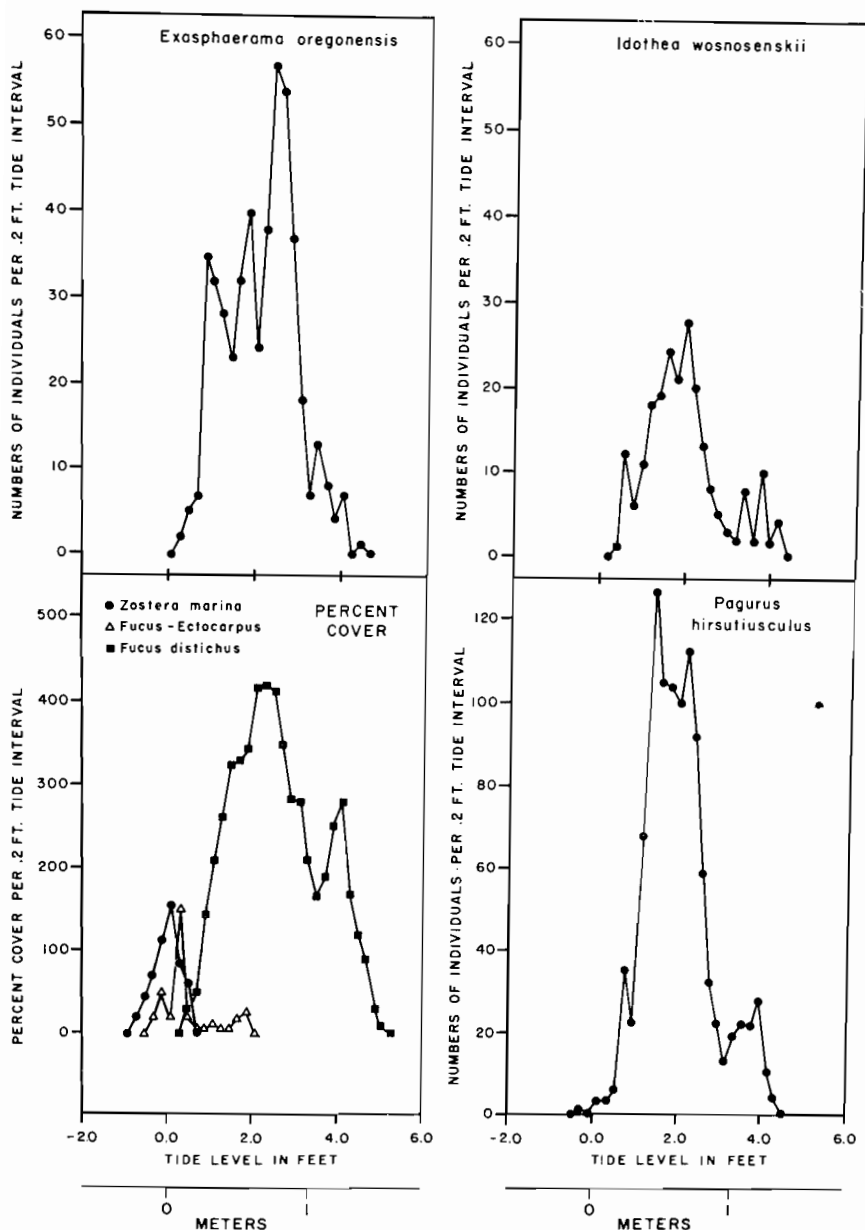
Figure 26. Per cent cover and distribution and abundance of *Exosphaeroma oregonensis*, *Idothea wosnosenskii*, and *Pagurus hirsutiusculus* grouped over all five transects for each .2 ft tide interval, Beach Transects.

PLOT OF MEDIAN INDIVIDUAL OF EACH TRANSECT
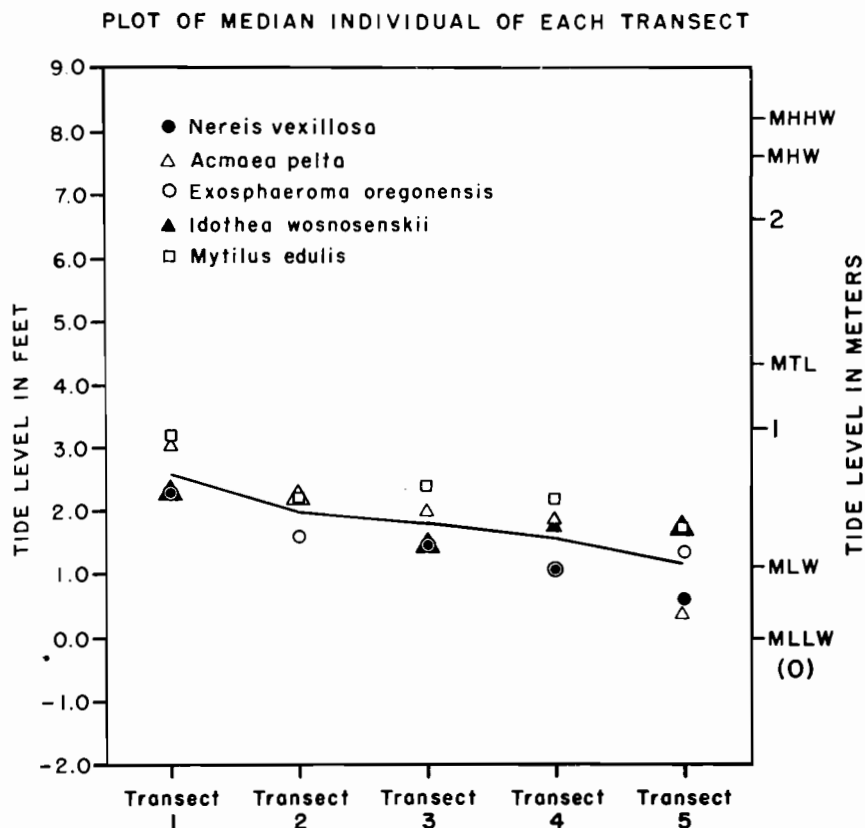
Figure 27.   Distribution of the median individual with tide level for each transect of Sample Area #2. Plotted only for those transects having more than five individuals of the species.

A. *digitalis* always occurred highest on the transect (Fig. 35). A. *scutum* was more often a creature of mid-tide levels here, but was distributed over a very wide tidal range, being found in other areas of the bay at the lowest levels. Not enough A. *pelta* were found to establish precisely its center of abundance. Compared to the distributions of the barnacle species, the three *Acmaea* species did not often show specific vertical replacement (Fig. 35, Transects #4 and #6).

Results of Random Sampling

Results on East Reef (Sample Area #6):   Three distinct bands or zones, much as were seen on the beach transects, were distinguishable on the East Reef. The lowest band, dark green in color, was dominated by a
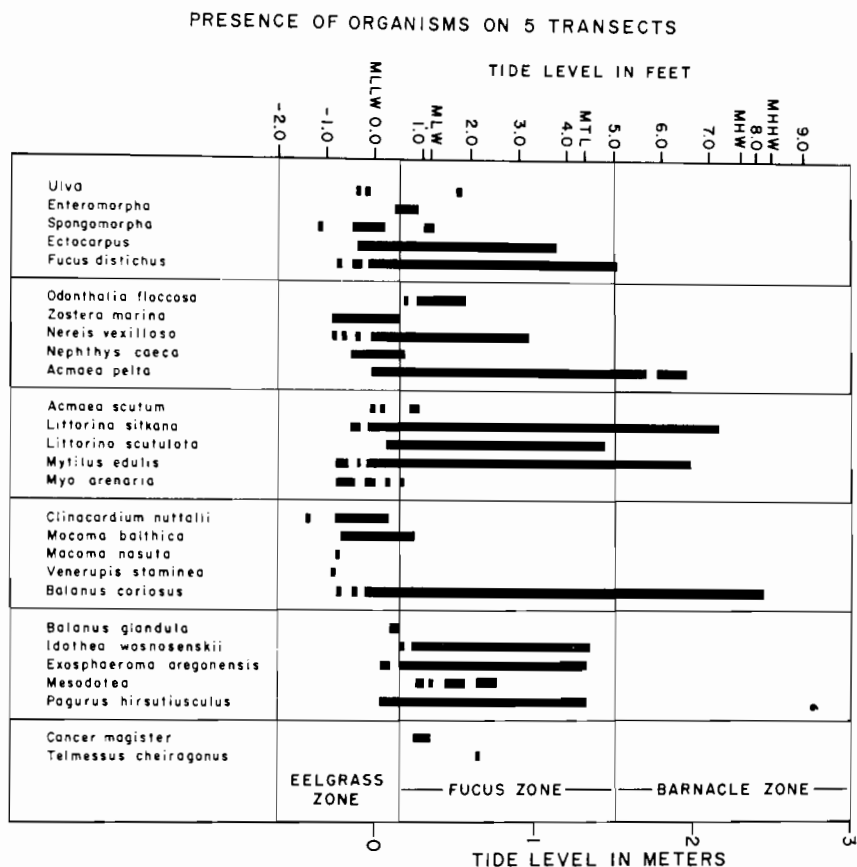
Figure 28. Grouped presence over all five transects of all organisms encountered in the Beach Transects with limits of the three observed zones marked.

heavy cover of eelgrass (*Zostera marina*); brown patches, due to the presence of the red alga *Rhodomela larix*, surrounded the occasional rocks. This zone, considered as an eelgrass (*Zostera*) zone, was continuous subtidally and extended upward to between the −.5 and 0.0 tide levels. Aside from the occasional large rocks the substrate was soft mud-sand (Fig. 7).

Extending shoreward from between 0.0 and +1.0, a second, dark brown band was dominated by the alga *Fucus distichus* with the associated brown alga, *Ectocarpus*. Other less common algae of this band were *Cryptosiphonia woodii*, *Enteromorpha* sp., *Rhodomela larix* and *Spongomorpha* sp. This narrow vertical band reached its upper limit between
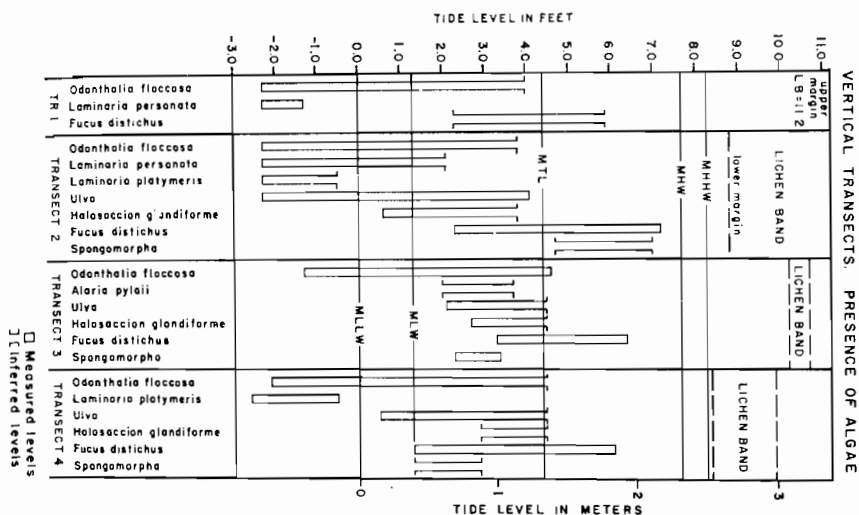
Figure 29. Presence of algae on four vertical transects. For an explanation of measured and inferred levels, see text.

+1.0 and +1.8 ft. Near the lower edge of the *Fucus* zone the substrate changed from the soft mud-sand of the *Zostera* bed to the rock and boulder substrate which extended from the lower edge of the *Fucus* zone to the uppermost levels reached by the reef (Fig. 7).
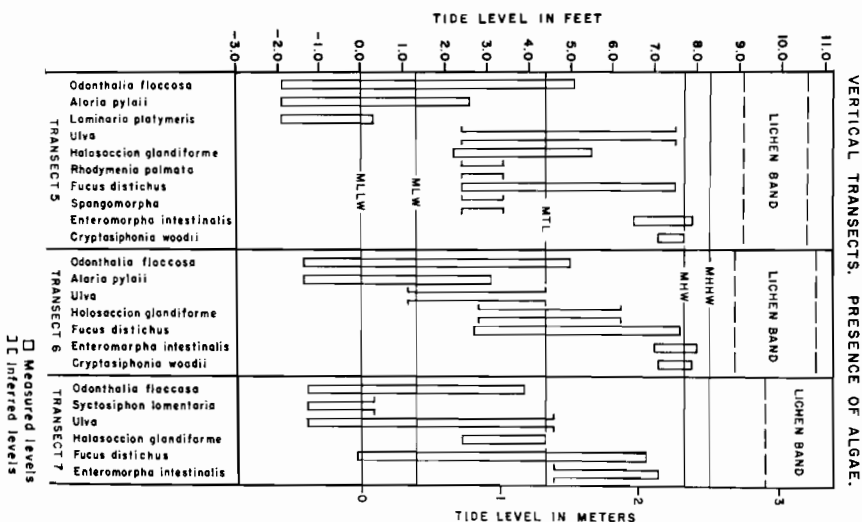
Figure 30. Presence of algae on three vertical transects. For an explanation of measured and inferred levels, see text.
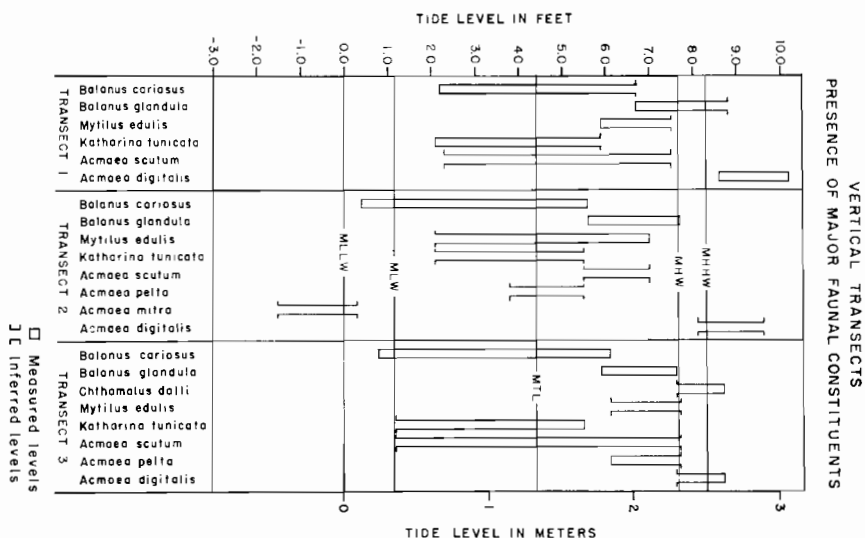
Figure 31.   Presence of major faunal constituents on three vertical transects.   For an explanation of measured and inferred levels, see text.   See also Figure 32.
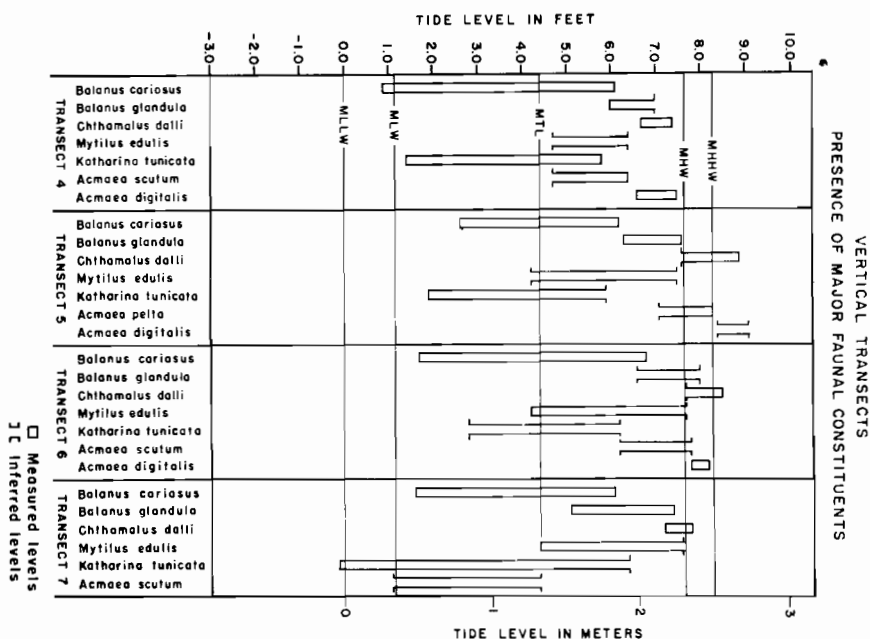
Figure 32.   Presence of major faunal constituents on four vertical transects.   For an explanation of measured and inferred levels, see text.   See also Figure 31.
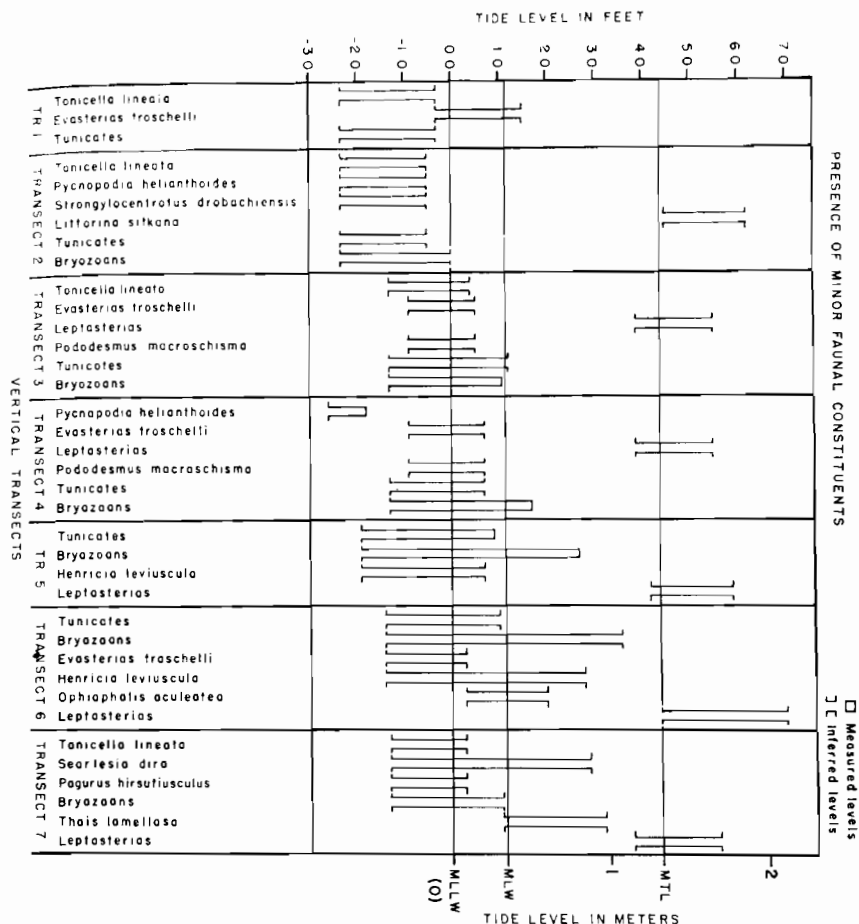
Figure 33.   Presence of minor faunal constituents on seven vertical transects. For an explanation of measured and inferred levels, see text.

Above +1.8 ft, open or bare substrate was the prominent feature of the uppermost zone; no large algae were present. This zone was characteristically dark, gray-black, the color of the rocky substrate, speckled with patches of barnacles of contrasting lighter color. The upper boundary of this barnacle zone occurred at an abrupt interface between the reef edge and the sandy shore at a tidal level of about +5.0 ft.

Results of quantitative sampling of this reef further document the observed zonation by demonstrating aggregation of species within one or more zones. For each of the three observed zones Table 1 presents
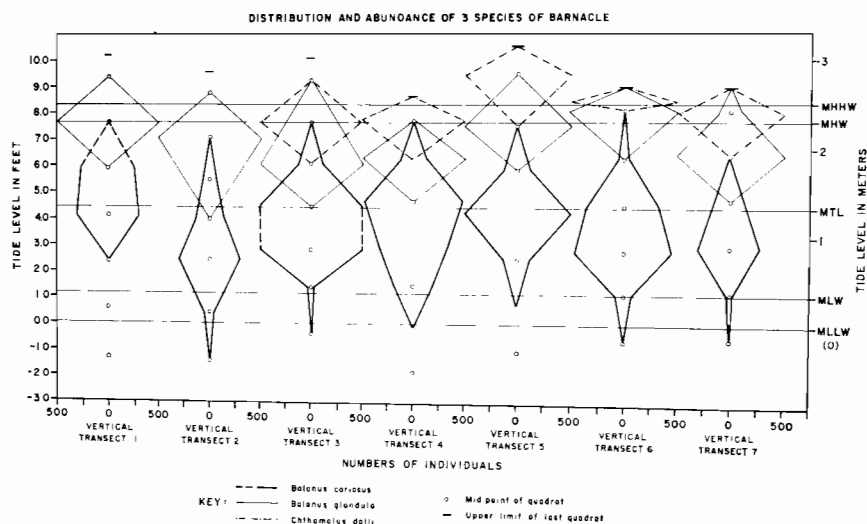
Figure 34. Distribution and abundance of three species of barnacles on seven vertical transects. Abundances plotted at the midpoint of the quadrat. For an explanation of the 500 limit, see text.
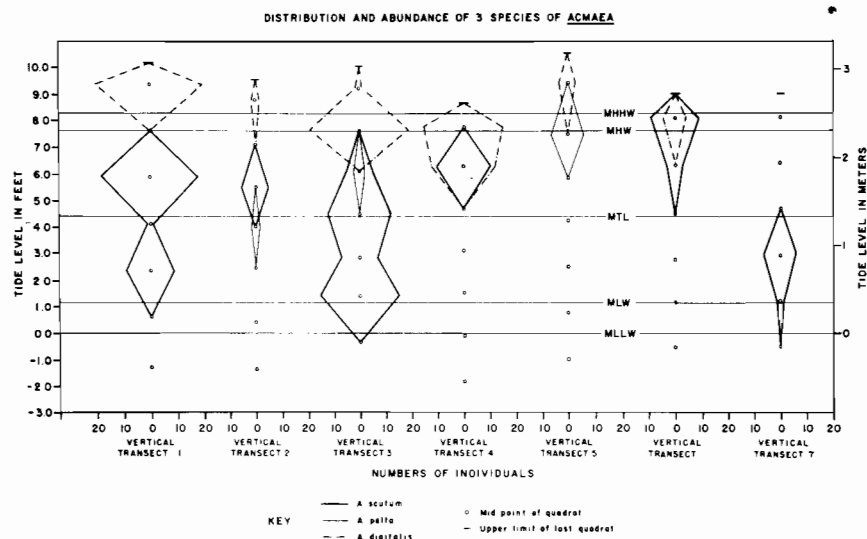
Figure 35. Distribution and abundance of three species of *Acmaea* on seven vertical transects. Abundance plotted at the midpoint of the quadrat.

TABLE 1. PER CENT OF TOTAL QUADRATS OF OCCURRENCE AND PER CENT OF TOTAL NUMBER OF INDIVIDUALS OF EACH SPECIES OF INVERTEBRATE IN EACH OF THE THREE OBSERVED ZONES ON THE EAST REEF

Species	Barnacle		Fucus		Zostera	
	% of total quadrats of occurrence	% of total # of individuals	% of total quadrats of occurrence	% of total # of individuals	% of total quadrats of occurrence	% of total # of individuals
Littorina sitkana	100.0	100.0	0	0	0	0
Idothea wosnosenskii	100.0	100.0	0	0	0	0
Buccinum baeri	100.0	100.0	0	0	0	0
Thais lima	93.33	96.51	6.67	3.49	0	0
Littorina scutulata	92.0	99.79	8.0	.21	0	0
Exosphaeroma oregonensis	92.59	97.71	7.41	2.29	0	0
Balanus glandula	88.23	98.56	11.77	1.44	0	0
Nerine foliosa	87.50	90.91	12.50	9.09	0	0
Mytilus edulis	83.33	98.56	16.67	1.44	0	0
Acmaea pelta	83.33	95.86	16.67	4.16	0	0
Balanus cariosus	76.47	86.84	23.53	13.16	0	0
Echiurus echiurus*	66.67	36.36	33.33	63.64	0	0
Pagurus hirsutiusculus	63.64	82.65	24.24	16.33	12.12	1.02
Venerupis staminea*	53.33	53.49	40.0	44.96	6.67	1.55
Saxidomus giganteus*	50.0	51.52	25.0	33.33	25.0	15.15
Nephthys caeca*	40.0	40.0	60.0	60.0	0	0
Macoma balthica*	33.33	43.86	66.67	57.14	0	0
Glycera nana*	25.0	20.0	50.0	40.0	25.0	40.0
Pugettia gracilis	0	0	28.57	20	71.42	80.0
Pycnopodia helianthoides	0	0	20.0	10.0	80.0	90.0
Dermasterias imbricata	0	0	0	0	100.0	100.0
Strongylocentrotus drobachiensis	0	0	0	0	100.0	100.0

* subsurface form.

TABLE 2. DISTRIBUTION, FREQUENCY, DENSITY, ABUNDANCE AND AGGREGATION OF THE INVERTEBRATE SPECIES OF THE EAST REEF.

| Species | No. quad-rats* of occur-rence | No. of indi-viduals | Fre-quency | Density | | Abun-dance | Aggre-gation measure |
				Ob-served	Calcu-lated		
Balanus cariosus	34	6733	61.82	122.41	.9676	197.0	126.50
Balanus glandula	17	275	30.91	5.00	.3711	16.18	13.47
Mytilus edulis	30	1810	54.54	32.91	.7765	60.33	42.38
Littorina sitkana	25	2661	45.45	48.38	.5978	106.44	80.93
Littorina scutulata	27	2822	49.09	54.95	.6733	104.51	81.61
Acmaea pelta	30	4805	54.54	87.36	.7765	160.17	112.50
Idothea wosnosenskii	6	27	10.91	.49	.2108	4.5	2.32
Exosphaeroma oregon-ensis	27	700	49.09	12.73	.6733	25.93	18.90
Pagurus hirsutiusculus	33	490	60.0	8.91	.9163	14.85	9.72
Thias lima	15	86	27.45	1.75	.3147	5.73	5.56
Venerupis staminea	15	249	27.45	4.53	.3147	16.6	14.40
Saxidomus giganteus	8	33	14.54	.60	.1508	4.12	3.98
Pycnopodia helian-thoides	10	20	18.18	.36	.1984	2.0	1.81
Echiurus echiurus	10	24	18.18	.44	.1984	2.40	2.22
burrowing anemone	12	27	21.82	.49	.2357	2.25	2.08
Nerine foliosa	8	16	14.54	.29	.1508	2.0	1.92
Pugettia gracilis	7	10	12.73	.18	.1278	1.43	1.41
Glycera nana	4	5	7.45	.091	.0726	1.25	1.25
Nephthys caeca	5	5	9.09	.091	.0943	1.0	.97
Buccinum baeri	2	4	3.82	.073	.0409	2.0	1.78
Macoma balthica	3	14	5.45	.25	.0512	4.67	4.88
Dermasterias imbricata	2	2	3.82	.036	.0409	1.0	.88
Cerebratulus sp.	2	3	3.82	.054	.0409	1.5	1.32
Telmessus cheiragonus	2	2	3.82	.036	.0409	1.0	.88
Acmaea scutum	1	1	1.82	.018	.0202	1.0	.89
Strongylocentrotus drobachiensis	1	1	1.82	.018	.0202	1.0	.89
Tonicella lineata	1	1	1.82	.018	.0202	1.0	.89
Phyllodoce groenlandica	1	1	1.82	.018	.0202	1.0	.89
Pectinaria sp.	1	1	1.82	.018	.0202	1.0	.89
Clinocardium nuttalli	1	1	1.82	.018	.0202	1.0	.89
Abarenicola pacifica	1	1	1.82	.018	.0202	1.0	.89
Mya arenaria	4	5	7.45	.091	.0726	1.25	1.25
Saxicava sp.	2	8	3.82	.15	.0409	4.0	3.67

* Based on 55 total quadrats.

the per cent of the total number of quadrats of occurrence for each species within each zone, as well as per cent of the total number of counted individuals per zone.

Species presence, frequency, density and abundance on this reef are presented in Table 2 and demonstrate the importance of each species
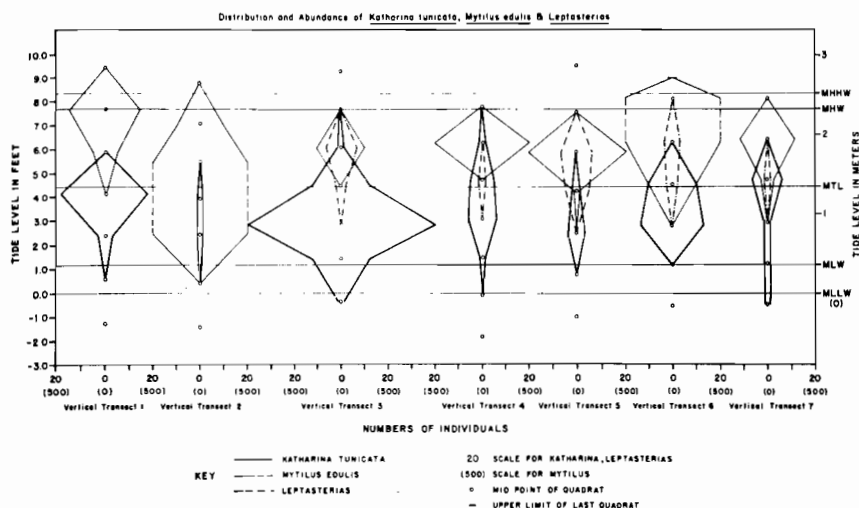
Figure 36.   Distribution and abundance of *Katharina tunicata*, *Mytilus edulis*, and *Leptasterias* sp. on seven vertical transects. Abundance plotted at the midpoint of the quadrat. For an explanation of the 500 limit for *Mytilus edulis*, see text.

TABLE 3.   CONFIDENCE LIMITS OF THE ABUNDANCE FIGURES FOR THE INVERTEBRATE SPECIES OF THE EAST REEF

Species	Abundance	Variance	Std. error	df	95% confidence limits
Balanus cariosus	198.0	27,408	28.39	33	198 ± 57.91
Balanus glandula	16.18	137.12	2.84	16	16.18 ± 6.02
Mytilus edulis	60.33	4,276	11.93	29	60.33 ± 24.33
Littorina sitkana	106.44	6,639	16.29	24	106.44 ± 33.55
Littorina scutulata	104.51	6,239	15.2	27	104.51 ± 31.16
Acmaea pelta	160.17	19,841	25.71	29	160.17 ± 52.44
Idothea wosnosenskii	4.5	22.0	1.91	5	4.5 ± 4.90
Exosphaeroma oregonensis	25.93	484.46	4.23	23	25.93 ± 8.87
Pagurus hirsutiusculus	14.85	224.13	2.64	32	14.85 ± 5.38
Thais lima	5.73	52.5	1.87	14	5.73 ± 4.00
Venerupis staminea	16.6	541	6.0	14	16.6 ± 12.84
Saxidomus giganteus	4.12	5.14	.801	7	4.12 ± 1.88
Pycnopodia helianthoides	2.0	.78	.279	9	2.0 ± .63
Echiurus echiurus	2.40	5.22	.72	9	2.4 ± 1.62
burrowing anemone	2.25	1.27	.325	11	2.25 ± .70
Nerine foliosa	2.0	3.71	.68	7	2.0 ± 1.6
Pugettia gracilis	1.43	1.28	.427	6	1.43 ± 1.03
Glycera nana	1.25	.25	.25	3	1.25 ± .79
Saxicava sp.	4.0	18.0	3.0	1	4.0 ± 38.1
Macoma balthica	4.67	10.5	1.87	2	4.67 ± 8.04
Buccinum baeri	2.06	2.0	1.0	1	1.78 ± 12.7
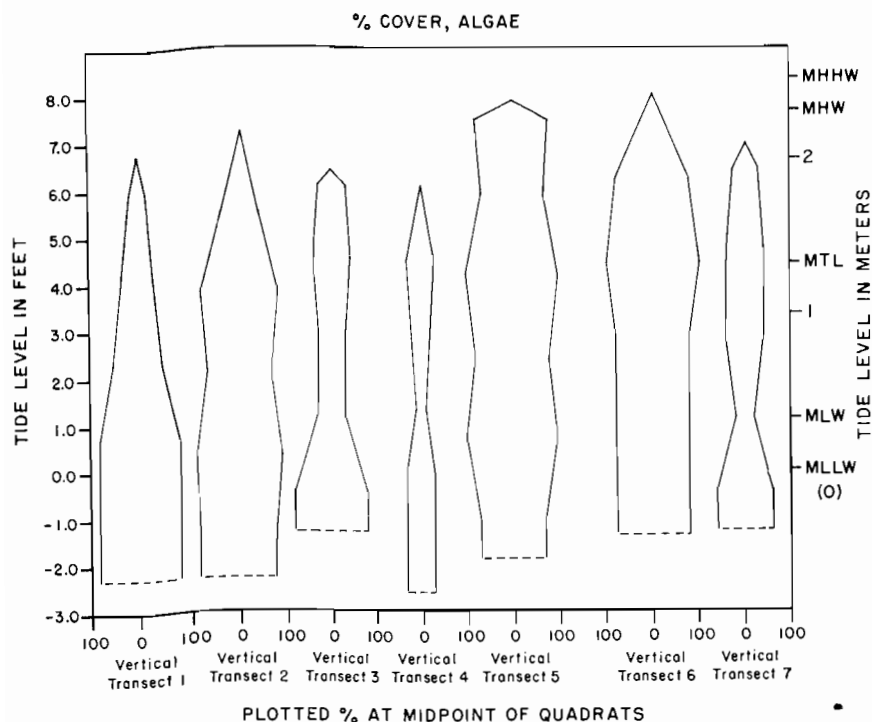
Figure 37.   Per cent cover on seven vertical transects.

on the reef. Table 3 presents, for those species which occurred more than once, the variance, standard error, and 95% confidence limits for the abundance figures of Table 2. Figure 40 shows the per cent cover and dominant algae on East Reef.

Results on West Reef (Sample Area #1): The contrast between the East Reef and the West Reef was particularly marked. The West Reef was low lying and of much reduced vertical range. It therefore did not support communities which ordinarily were found at high tide levels.

In contrast to the East Reef, sharply defined horizontal bands were not present. Closer observation and sampling demonstrated the reef to include but a single zone; this, however, was markedly more heterogeneous in species composition than the zones described on the East Reef or vertical transects. The reef was dominated, but not completely covered, by a mat of *Alaria pylaii*. Beneath the *Alaria* mat, but also extending out over the large rocks and open cobble, was a conspicuous green encrusting sponge which often covered rather extensive areas on the reef. On the tops of large rocks, whether or not surrounded by *Alaria*, was established

TABLE 4. DISTRIBUTION, FREQUENCY, DENSITY, ABUNDANCE AND AGGREGATION OF THE INVERTEBRATE SPECIES OF THE WEST REEF

Species	No. quadrats* of occurrence	No. of individuals	Frequency	Density Observed	Density Calculated	Abundance	Aggregation measure
Balanus cariosus	43	3854	86.0	77.08	1.9661	89.63	39.2
Chthamalus dalli	4	1502	8.0	30.04	.0844	375.50	355.92
Mytilus edulis	1	2	2.0	.40	.0202	2.0	1.98
Acmaea scutum	40	323	80.0	6.46	1.6094	8.07	4.01
Idothea wosnosenskii	31	145	62.0	2.90	.9676	4.68	3.00
Exosphaeroma oregonensis	15	321	30.0	6.42	.3567	21.4	17.94
Pagurus hirsutiusculus	29	143	58.0	2.86	.8675	4.93	3.29
Thais lamellosa	18	32	36.0	.64	.4463	1.78	1.43
Venerupis staminea	43	497	86.0	9.94	1.9661	11.56	5.05
Saxidomus giganteus	27	137	54.0	2.70	.7765	5.07	3.47
burrowing anemone	41	262	82.0	5.24	1.7148	6.39	3.05
Leptasterias sp.	37	126	74.0	2.52	1.3471	3.41	1.87
Katharina tunicata	36	146	72.0	2.92	1.2730	4.06	2.29
Pugettia gracilis	27	88	54.0	1.76	.7765	3.26	2.26
Strongylocentrotus drobachiensis	27	105	54.0	2.10	.7765	3.89	2.70
Nephthys caeca	22	42	44.0	.84	.5798	1.91	1.45
Cirratulus cirratus	20	69	40.0	1.38	.5108	3.45	2.70
Nerine foliosa	19	46	38.0	.92	.4780	2.42	1.92
Mopalia ciliata	19	45	38.0	.90	.4780	2.37	1.88
Glycera nana	20	28	40.0	.56	.5108	1.40	1.10
Nereis vexillosa	17	47	34.0	.94	.4155	2.76	2.26
Buccinum baeri	9	19	18.0	.38	.1984	2.11	1.92
Saxicava sp.	5	8	10.0	.16	.1053	1.6	1.52
Cancer magister	5	7	10.0	.14	.1053	1.4	1.33
Telmessus cheiragonus	5	7	10.0	.14	.1053	1.4	1.33
Natica clausa	4	4	8.0	.08	.0844	1.0	.95
Thelepus crispus	2	2	4.0	.04	.0409	1.0	.98
Arctönoe pulchra	1	2	2.0	.04	.0202	2.0	1.98
Echiurus echiurus	1	1	2.0	.02	.0202	1.0	.99
Fusitriton oregonensis	1	1	2.0	.02	.0202	1.0	.99
octopus	1	1	2.0	.02	.0202	1.0	.99
Cucumaria curata	33	149	66.0	2.98	1.0788	4.51	2.76

* Based on 50 total quadrats.

a growth of *Fucus distichus, Ulva, Halosaccion glandiforme,* and *Spongomorpha. Fucus* was not dominant here and was relatively smaller in size than plants of that species on the other sample areas.

Treatment of data for this reef was similar to that discussed for the East Reef, and the data are presented in Tables 4 and 5. Figure 41 shows per cent cover and dominant algae on the West Reef. Precise statements

TABLE 5. CONFIDENCE LIMITS OF THE ABUNDANCE FIGURES FOR THE INVERTEBRATE SPECIES OF THE WEST REEF

Species	Abundance	Variance	Std. error	df	95% confidence limits	
Balanus cariosus	89.63	5,315	11.12	42	89.63 ±	22.46
Chthamalus dalli	375.50	20,667	71.8	3	375.50 ±	228.32
Acmaea scutum	8.07	50.6	1.124	39	8.07 ±	2.26
Idothea wosnosenskii	4.68	51.0	1.29	30	4.68 ±	2.63
Exosphaeroma oregonensis	21.4	948.57	7.95	14	21.4 ±	17.01
Pagurus hirsutiusculus	4.93	25.79	.94	28	4.93 ±	1.93
Thais lamellosa	1.78	3.94	.467	17	1.78 ±	.99
Venerupis staminea	11.56	137.36	1.78	42	11.56 ±	3.6
Saxidomus giganteus	5.07	24.8	.958	26	5.07 ±	1.97
burrowing anemone	6.39	26.72	.807	40	6.39 ±	1.63
Leptasterias sp.	3.41	4.77	.36	36	3.41 ±	.73
Katharina tunicata	4.06	11.54	.56	35	4.06 ±	1.13
Cucumaria curata	4.51	19.75	.773	32	4.51 ±	1.57
Pugettia gracilis	3.26	7.04	.51	26	3.26 ±	1.04
Strongylocentrotus dro-bachiensis	3.89	48.46	1.339	26	3.89 ±	2.74
Nephthys caeca	1.91	.86	.197	21	1.91 ±	.41
Cirratulus cirratus	3.45	4.68	.483	19	3.45 ±	1.0
Nerine foliosa	2.42	2.64	.383	18	2.42 ±	.79
Mopalia ciliata	2.37	1.72	.30	18	2.37 ±	.62
Glycera nana	1.40	.42	.145	19	1.40 ±	.29
Nereis vexillosa	2.76	2.69	.37	16	2.76 ±	.78
Buccinum baeri	2.11	2.63	.54	8	2.11 ±	1.24
Saxicava sp.	1.6	1.75	.65	4	1.6 ±	1.80
Cancer oregonensis	1.4	.667	.308	4	1.4 ±	.86
Telmessus cheiragonus	1.4	.75	.39	4	1.4 ±	1.08

concerning the significance of observed dissimilarities in abundance on the two reefs are presented in Table 6.

Results in the Tide Pool (Sample Area #5): Tide pools were of infrequent occurrence within Three Saints Bay but they did present a very different environment from other intertidal habitats and were therefore sampled. The tide pool study did allow (1) assessment of the tide pool fauna and (2) sampling of an area where *Strongylocentrotus drobachiensis* was abundant. This species had previously been noted to exist in what appeared to be very high densities in the few tidal pools which were investigated. Thus it was possible to compare the abundance of *S. drobachiensis* in a subtidal situation with that measured in an intertidal environment on the West Reef.

Data from this sampling area were taken and treated in a manner similar to that used on the East and West Reefs (Tables 7 and 8). However, only 24 quadrats were taken as opposed to 50 and 55 on the West and East Reefs respectively.

CENTER OF PRESENCE OF 7 MAJOR ORGANISMS ON 7 TRANSECTS
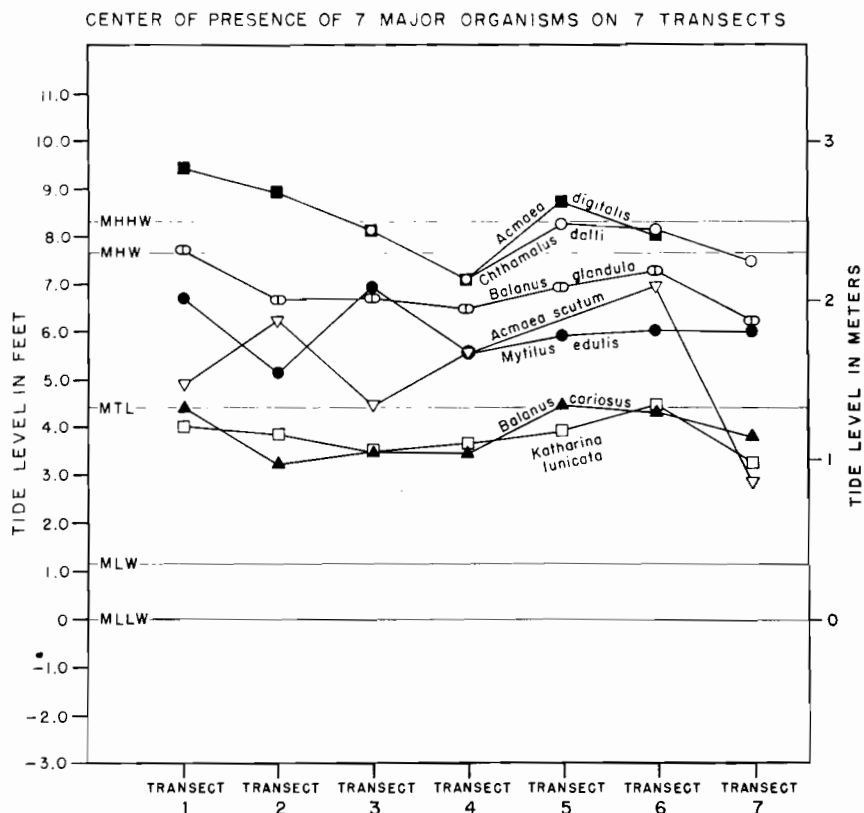
Figure 38.   Center of presence of seven major organisms on seven vertical transects.

The superficial observation that the pool was dominated by the presence of *Strongylocentrotus drobachiensis* was borne out by the quantitative data; this urchin appeared in every quadrat sampled. Not only were these animals much larger than the next most abundant organism, *Acmaea scutum*, but they were almost twice as abundant as well (30.46 as opposed to 17.46).

SUMMARY OF RESULTS

In order to summarize concisely the various invertebrate and algal species uncovered in the course of sampling and their distribution among the five sample areas, Table 9 and Figures 42 and 43 have been prepared.

Table 9 summarizes the number of species found and their distribu-

TABLE 6.   STATISTICAL COMPARISONS BETWEEN ABUNDANCES OF
SPECIES COMMON TO BOTH EAST AND WEST REEFS

Species	West Reef		East Reef		Std. error differ- ence	t	Signifi- cance
	df	Sums of squares	df	Sums of squares			
Balanus cariosus	42	223,242	33	904,460	28.1	3.86	**
Idothea wosnosenskii	30	1,557	5	110	3.06	.58	n.s.
Exosphaeroma ore- gonensis	14	13,280	26	12,596	8.19	.553	n.s.
Pagurus hirsutiusculus	28	722	32	6,948	2.9	3.42	**
Venerupis staminea	42	5,769	14	7,578	4.6	1.095	n.s.
Saxidomus giganteus	26	645	7	36	1.8	.53	n.s.
burrowing anemone	40	1,069	11	14	1.51	2.74	**
Glycera nana	19	8	3	.75	.35	.428	n.s.
Nephthys caeca	21	18	4	0	.41	2.22	*
Pugettia gracilis	26	183.19	6	7.71	1.03	1.78	n.s.
Buccinum baeri	8	21	1	2	1.27	.26	n.s.
Saxicava sp.	4	7	1	18	1.87	1.28	n.s.
Nerine foliosa	18	45	7	26	.71	.59	n.s.

** = highly significant (.01 level)
* = significant (.05 level)
n.s. = not significant

tion among the sample areas. It also provides data on the tidal range
worked and the total area sampled.   •

In this table it is of interest to note the very high number of quadrats
taken on the beach transects compared to the other areas and yet the

TABLE 7.   DISTRIBUTION, FREQUENCY, DENSITY, ABUNDANCE AND
AGGREGATION OF THE INVERTEBRATE SPECIES OF THE TIDE POOL

Species	No. quad- rats* of occur- rence	No. of indi- viduals	Fre- quency	Density		Abun- dance	Aggre- gation mea- sure
				Ob- served	Calcu- lated		
Strongylocentrotus drobachiensis	24	731	100.0	30.46	6.9078	30.46	4.409
Acmaea scutum	24	419	100.0	17.46	6.9078	17.46	2.53
Margarites pupillus	12	29	50.0	1.21	.6931	2.42	1.745
Stichopus californicus	6	8	25.0	.33	.2877	1.33	1.15
Searlesia dira	6	7	25.0	.29	.2877	1.17	1.01
Acmaea mitra	5	6	20.83	.08	.2357	1.20	.34
Pycnopodia helian- thoides	2	2	8.33	.08	.0844	1.00	.95
Fusitriton oregonensis	2	6	8.33	.25	.0844	3.0	2.96
Buccinum baeri	1	2	4.17	.08	.0409	2.0	1.95
Evasterias troschelli	1	1	4.17	.04	.0409	1.0	.98

* Based on 24 total quadrats.

PRESENCE OF ORGANISMS ON 7 VERTICAL TRANSECTS
TIDE LEVEL IN FEET

Balanus cariosus
Balanus glandula
Chthamalus dalli
Mytilus edulis
Katharina tunicata
Acmaea pelta

Acmaea scutum
Acmaea mitra
Acmaea digitalis
Tonicella lineata
Littorina sitkana
Searlesia dira

Thais lamellosa
Pododesmus macroschisma
Evasterias troschelii
Pycnopodia helianthoides
Henricia leviuscula
Leptasterias

Ophiopholis aculeata
Strongylocentrotus drobachiensis
Pagurus hirsutiusculus
Bryozoans
Tunicates
Odonthalia floccosa

Laminaria personata
Laminaria platymeris
Alaria pylaii
Fucus distichus
Ulva
Halosaccion glandiforme

Spongomorpha
Enteromorpha intestinalis
Cryptosiphonia woodii
Scytosiphon lomentaria
Rhodymenia palmata
Black lichen (Verrucaria)

ODONTHALIA–LAMINARIA ZONE   – – –FUCUS ZONE   BARNACLE ZONE

TIDE LEVEL IN METERS

Figure 39. Grouped presence over all seven transects of all organisms encountered on the vertical transects.

TABLE 8. CONFIDENCE LIMITS OF THE ABUNDANCE FIGURES FOR THE INVERTEBRATE SPECIES OF THE TIDE POOL

Species	Abundance	Variance	Std. error	df	95% confidence limits
Strongylocentrotus dro- bachiensis	30.46	1,128	6.8	23	30.46 ± 14.0
Acmaea scutum	17.46	101.26	2.05	23	17.46 ± 4.22
Margarites pupillus	2.42	1.09	.95	11	2.42 ± 2.09
Stichopus californicus	1.33	.28	.215	5	1.33 ± .55
Searlesia dira	1.17	.16	.163	5	1.17 ± .42
Acmaea mitra	1.20	.20	.179	4	1.20 ± .5
Pycnopodia helianthoides	1.00	0	0	1	
Fusitriton oregonensis	3.0	8.0	2.0	1	3.0 ± 25.4

% Cover and Dominant Algae at each Sampling Point   East Reef
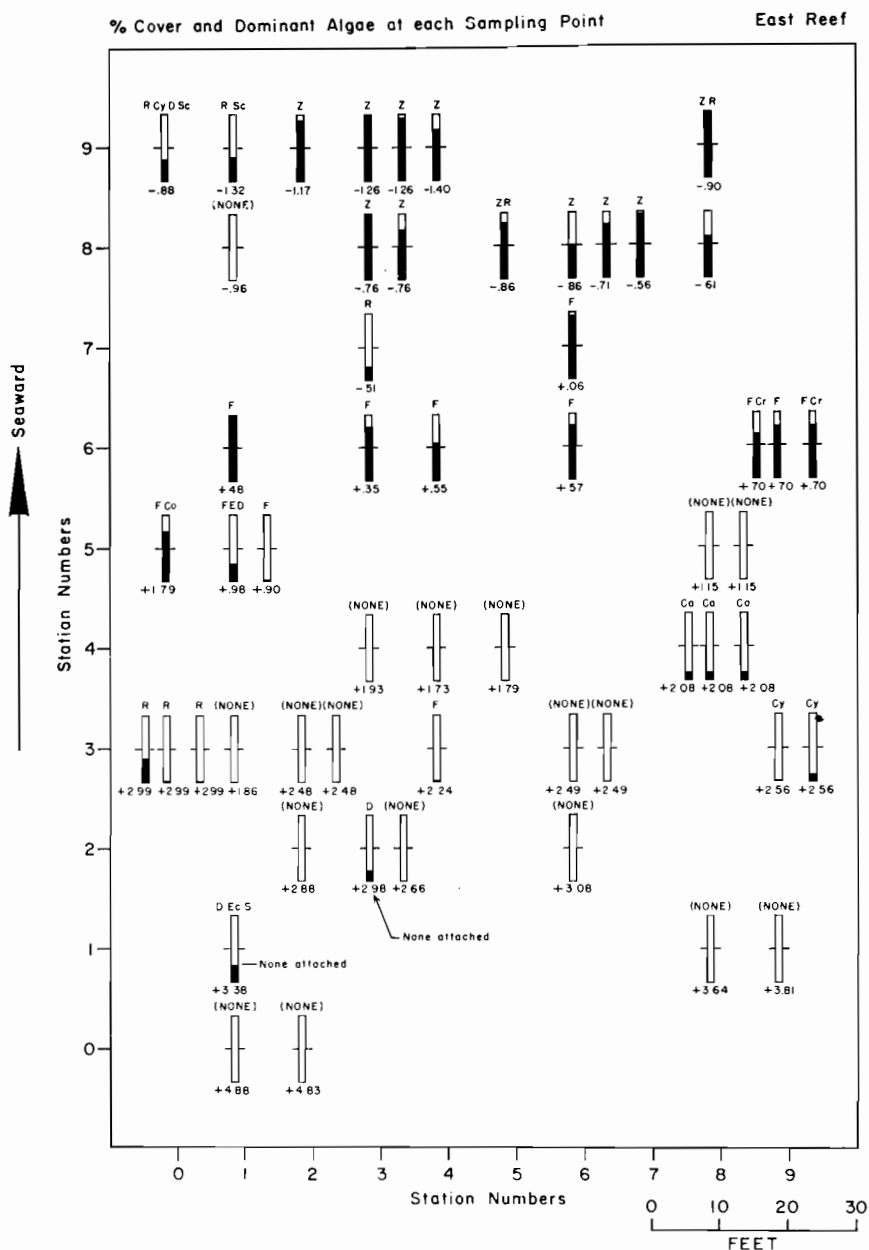
Figure 40. Per cent cover and dominant algae at each sampling point, East Reef. Each bar represents a sampling point. Amount of blackening of the bar indicates the per cent cover. Numbers below each bar indicate the tide level of the sampling point. Letters indicate the dominant algae at the sampling point: Z = *Zostera marina* (eelgrass); F = *Fucus distichus*; Co = *Colpomenia sinuosa*; Cr = *Cryptosiphonia woodii*; D = *Dictyosiphon foeniculacens*; Ec = *Ectocarpus*; S = *Spongomorpha*; R = *Rhodomela larix*; Sc = *Scytosiphonia lomentaria*; Cy = *Cystoseira germinata*.
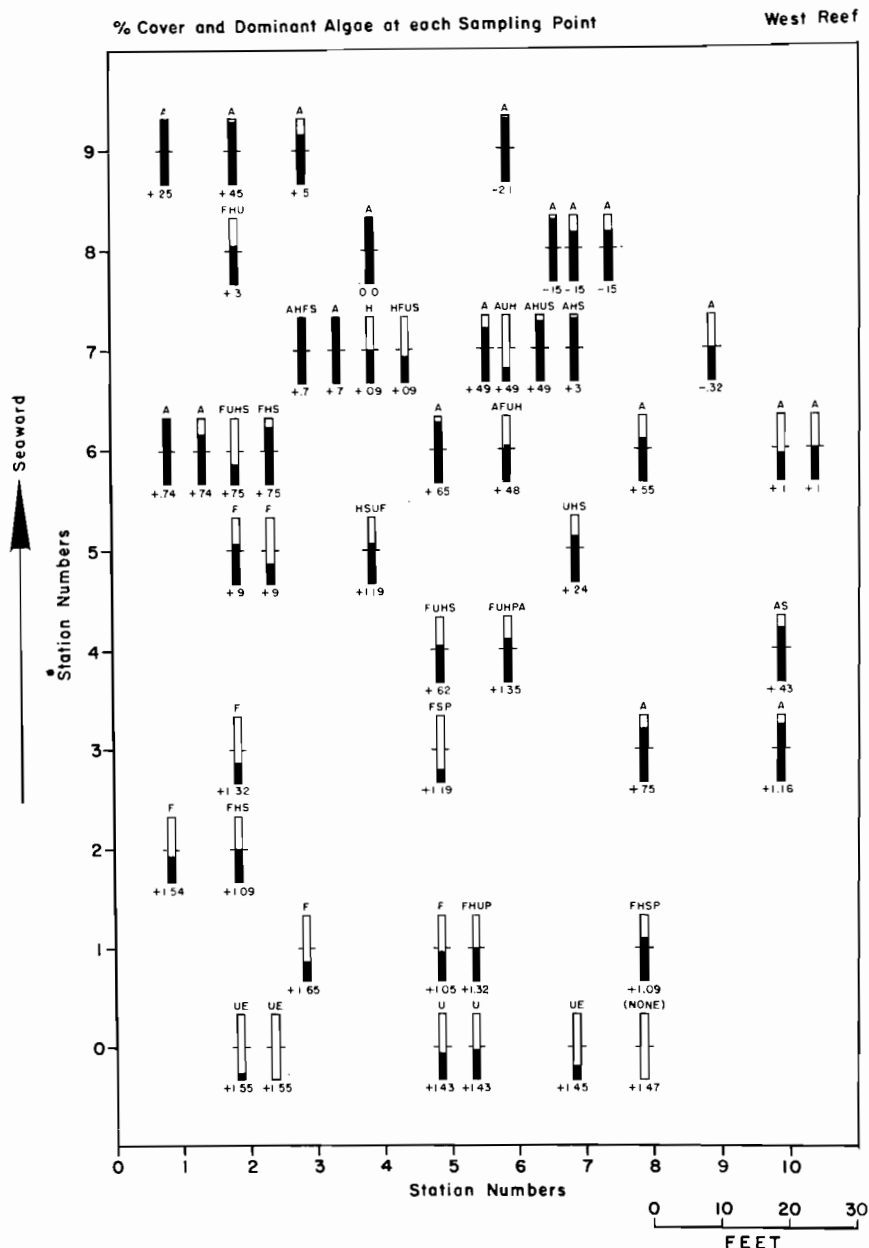
Figure 41. Per cent cover and dominant algae at each sampling point, West Reef. Each bar represents a sampling point. Amount of blackening of the bar indicates the per cent cover. Numbers below bar indicate tide level of the sampling point. Letters indicate the dominant algae at the sampling point: A = *Alaria pylaii*; F = *Fucus distichus*; H = *Halosaccion glandiforme*; S = *Spongomorpha*; U = *Ulva*; E = *Enteromorpha*; P = *Porphyra*.

PRESENCE OF FAUNA ON FIVE SAMPLING AREAS

SPECIES	BEACH TRANSECTS	VERTICAL TRANSECTS	EAST REEF	WEST REEF	TIDAL POOL
Balanus cariosus					
Balanus glandula					
Chthamalus dalli					
Cancer oregonensis					
Telmessus cheiragonus					
Pugettia gracilis					
Pagurus hirsutiusculus					
Idothea wosnesenskii					
Mesodotea					
Exosphaeroma oregonensis					
Strongylocentrotus drobachiensis					
Pinnixa ? echinoides					
Dermasterias imbricata					
Evasterias troschelii					
Henricia leviuscula					
Leptasterias					
Ophiopholis aculeata					
Cucumaria curata					
Stichopus californicus					
Nereis vexillosa					
Nephthys caeca					
Glycera					
Nerine foliosa					
Cirratulus cirratus					
Phyllodoce groenlandica					
Abarenicola pacifica					
Thelepus crispus					
Arctonoe pulchra					
Pectinaria					
Echiurus echiurus					
Cerebratulus					
Tonicella lineata					
Mopalia ciliata					
Katharina tunicata					
Acmaea scutum					
Acmaea pelta					
Acmaea digitalis					
Acmaea mitra					
Littorina sitkana					
Littorina scutulata					
Thais lamellosa					
Thais lima					
Buccinum baeri					
Margarites pupillus					
Searlesia dira					
Fusitriton oregonensis					
Natica clausa					
Mytilus edulis					
Clinocardium nuttallii					
Venerupis staminea					
Macoma balthica					
Macoma nasuta					
Saxidomus giganteus					
Saxicava					
Mya arenaria					
Pododesmus macroschisma					
Pandalus ?					

■■■ Present in number, more than one   - - - - - Very rare, occasional, only one occurrence

Figure 42.   Presence of fauna on five sampling areas.

very low number of species that occurred there. Conversely, the West Reef, where many fewer quadrats were taken, had the highest number of species occurring more than once. It should also be remembered that the West Reef was characterized by but a single zone whereas the other areas were differentiated into three distinct zones.

It is also of interest to note the number of species in common among the various sample areas. This summary is elaborated in Figure 42 which lists each of the 57 species of invertebrates encountered during sampling at each of the five study areas such that it is easy to see which species were common among the various shore types. The exact allocation of each individual species to sample area may be easily accomplished using

Figure 42. Presence of fauna on five sampling areas.
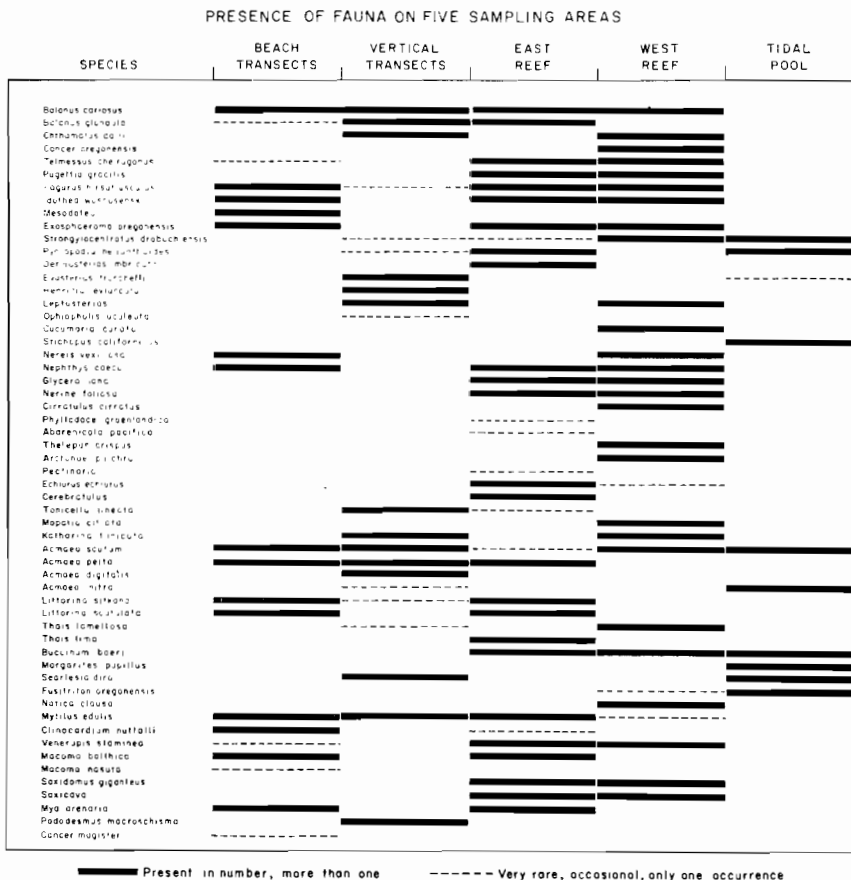
TABLE 9. SUMMARY OF SPECIES NUMBERS, TIDAL RANGE, TOTAL QUADRATS, AND TOTAL AREA SAMPLED FOR FOUR SAMPLE AREAS

Area	Species present		Total no. species in common with			Extreme of tidal range worked	Total no. of quadrats	Total area sampled in m^2
	Total no. occurring	No. occurring more than once	Beach Transects	Vertical Transects	East Reef			
Beach Transects	20	15		7	14	—1.5 to 9.2	286	71.5
Vertical Transects	21*	17	7		10	—2.3 to 11.2	47	11.75
East Reef	33	26	14	10		—1.4 to 4.88	55	13.75
West Reef	32**	28	11	9	19	—.32 to 1.65	50	12.5

* Excluding bryozoans and tunicates, at least one species of each was very common on the verticals and not found elsewhere.
** Excluding the green-yellow encrusting sponge which was not found elsewhere.

PRESENCE OF ALGAE ON FOUR SAMPLE AREAS

SPECIES	BEACH TRANSECTS	VERTICAL TRANSECTS	EAST REEF	WEST REEF
Ulva				
Enteromorpha intestinalis				
Spongomorpha				
Ectocarpus				
Chordaria flagelliformes				
Syctosiphon lomentaria				
Colpomenia sinuosa				
Dictyosiphon foeniculacens				
Laminaria persanata				
Laminaria platymeris				
Alaria pylaii				
Fucus distichus				
Cytoseira germinata				
Porphyra				
Cryptosiphonia woodii				
Halosaccion glandiforme				
Rhodymenia palmata				
Rhodomela larix				
Odonthalia floccosa				
Zostera marina				

Figure 43.   Presence of flora on four sampling areas.

this figure. The final figure, 43, provides the same comparisons of floral presence among the study areas. In both of these latter figures the main point to be noted is the high number of species of invertebrates and algae which occurred on the East and West Reefs as opposed to the other areas.

GENERAL DISCUSSION AND COMPARISONS

General Discussion of Results

The results have shown that of the four tidal sample areas, the Beach Transects, Vertical Transects, East Reef, and West Reef, representing four different shore types (the tidal pool has been removed from consideration), three, the Beach Transects, Vertical Transects, and East Reef, have shown a pattern of obvious horizontal banding of the algae, invertebrates, or both. It has been further demonstrated that within these three areas, many species did show strong concentration within one or another part of the tidal zone. The fourth area, West Reef, did not show zonation due to its reduced vertical extent in the tidal zone and must therefore be considered to represent a single low zone.

The results have further brought into focus a number of problems of distribution of species and zones which it is necessary to consider in some detail at this time.

Belt transects—beach: An examination of the figures of the distribution and abundance of each species with tide level and per cent cover (Figs. 14 to 22) suggests certain trends. In Figure 22 it is seen that there was a high extension of *Ectocarpus* in the first two transects and a diminished extent in transects #3 to #5, that *Zostera marina* was not found in the first two transects, and that the lower margin of the *Fucus* cover showed a tendency to move downward from transects #1 to #5. Since other environmental factors in the transect appeared to vary only slightly, it is suggested that the influence of the freshwater outflow adjacent to transect #1 best explains the presence of these distributional patterns. The freshwater outflow can be expected to have a profound effect on osmotic balance in most marine organisms. The effect of this inflowing fresh water should diminish as one moves away from its source, hence a diminishing effect can be expected with each succeeding transect.

Similar patterns of micro-distribution were demonstrated by the graphs of individual species density, particularly *Nereis vexillosa*, *Exosphaeroma oregonensis*, *Acmaea pelta*, *Idothea wosnosenskii*, and *Mytilus edulis* (Figs. 16, 18, 19, and 20). A separate plot was made of the median individual in each transect for each of these species (Fig. 27); the results indicated a definite trend toward lowering of zonal boundaries moving from transect #1 to #5. The effect of the outflow of the freshwater stream is again suggested as the explanation for these trends.

Although this one explanation of the downward warping of zones has been offered, it is also possible that the actual distribution in the invertebrate species may have been determined by lack of cover, especially of

Fucus cover (Fig. 22). That this alternative explanation should be considered is warranted by the observation (Fig. 22) that there was almost no *Fucus* cover until +2.0 ft in transect #1, just the point which has been stated as the lower level of most organisms in that transect. Similarly most of the organisms showed a sudden reduction in numbers to 0 at the upper border of *Fucus*, which occurred at the 4.4–5.0 ft level.

The grouped data demonstrate very effectively the bimodal distribution patterns which existed in *Acmaea pelta* (Fig. 25) and *Littorina sitkana* (Fig. 24). The high peak at +.6 in *Acmaea pelta* corresponds to the small peak seen in *Mytilus edulis* at the same level (Fig. 25). This small peak in *Mytilus* represents the *Mytilus* reef area which existed in transect #5 whereas the high numbers of *Acmaea* were provided by those which have been recorded from these *Mytilus* shells. The bimodal peaks in the number of *Littorina sitkana* correspond well with the peaks in the per cent cover (Fig. 24); since *Littorina sitkana* was most abundant on the fronds of *Fucus*, the reduction in *Fucus* as estimated by cover could result in the observed reduction in *L. sitkana*. *Pagurus hirsutiusculus* also showed a similar reduction in numbers with reduction in *Fucus* cover (Fig. 26).

The graphs of *Littorina sitkana* and *Littorina scutulata* demonstrate effectively some exclusion of one in the areas of abundance of the other (Fig. 24). Interspecific competition is tentatively suggested to explain the distribution. A somewhat similar situation is found with the two isopods *Idothea wosnosenskii* and *Exosphaeroma oregonensis* (Fig. 26), but the exclusion is neither as dramatic nor as complete.

Codistribution of *Nereis vexillosa* and *Mytilus edulis* (Fig. 25) quantifies the observation that *N. vexillosa* was most abundant among the byssal threads of *M. edulis*.

Belt transects—vertical: Examination of the figures for the distribution and abundance of the nine major invertebrate species indicates some interesting distributional features. The three species of barnacle show a mutual vertical displacement in their centers of abundance which, further, have an interesting apparent correlation with the adult size of the three species (Fig. 34). The largest barnacle species, *Balanus cariosus*, was found lowest; *Balanus glandula*, of intermediate size, overlies that species while *Chthamalus dalli*, the smallest, was found at highest levels. Both *B. glandula* and *C. dalli* had narrow vertical ranges compared to *B. cariosus* (Figs. 34 and 39), but within these narrow belts, the two species existed in very large numbers (Fig. 34).

Certain trends among the centers of presence of several species of invertebrates may be noted. For the organisms of the high levels (*Acmaea*

digitalis, Chthamalus dalli, and *Balanus glandula*), center of presence was reduced to a minimum on transects #4 and #7 (Fig. 38). Transect #7 further showed the lowest center of presence of *Katharina tunicata* and *Acmaea scutum* (Fig. 38). Since these transects were highly protected it may be suggested that this lowering of the effective species distribution or of the region of maximum density was characteristic of protected faces and most strongly affected those organisms dwelling highest in the intertidal zone. This trend was much less obvious in mid-tide organisms such as *Balanus cariosus* (Fig. 38). Per cent cover on these two transects was lower at all levels also (Fig. 37). It may also be observed that there was a compression of tidal range of *Mytilus edulis* in transect #4. This may also be a function of the protection or perhaps the lack of suitable cracks in the rocks.

Transect #7 was unique in several additional ways. It was the only transect without *Acmaea digitalis; Acmaea pelta* was absent; it was the only one with *Searlesia dira; Fucus* descended to 0.0 tide level whereas it normally had its lower limit at +1.5 to +2.0 ft; there were no laminarians in the lowest zone (Figs. 29, 30, 31, and 32).

Both protected transects (#4 and #7) were situated at right angles to the incoming line of swell. Thus the swell passed these faces without breaking against them whereas in the other transects the vertical surfaces almost directly faced the advancing wave front. Here, the swell broke against these faces and sent splash water high up the rocky surfaces, keeping the higher zones wet and allowing the existence at these high levels of filter feeding organisms.

Transect #2, the only one facing north to the closed end of the bay and hence not facing the sea swell, showed no pronounced trend in the reduction of distributed levels relative to those transects facing the sea swell (Fig. 38). Such changes might have been expected if the breaking swell against these faces with concomitant splash were the principal determinant of the level of zones and organisms. However, this face is strongly subject to the influence of wind-formed waves which may have an equal splash height.

Belt transects—comparisons of beach and vertical: In comparing the vertical transects with those on the beaches several important differences can be noted. Twelve species of algae were recorded from the vertical rock surfaces, while but seven were noted from the beaches. Of the latter species, only *Ectocarpus* was unique to the beach environment. Twenty-one species of macro-invertebrates were recorded from the verticals as compared with 20 on the beaches. While not greatly different in total number, the species composition was very different. Only one pelecypod

was found on the verticals whereas five were recorded on the beaches (Fig. 28). Of these five only *Mytilus edulis* was common to both areas. No echinoderms were found on the beaches whereas six species were taken on the vertical rock surfaces. Isopods were absent from the vertical transects while three species were found on the beaches. Similarly, large polychaetes were absent from the verticals and two species were found on the beaches. No chitons were recorded from the beaches, but two species were found on the verticals. All four species of *Acmaea* were found on the vertical transects. *Balanus cariosus*, *Acmaea scutum*, *Acmaea pelta*, and *Mytilus edulis* were common to both areas. Some of these differences are easily explained. The absence of pelecypods on the vertical faces was due to the absence of the soft substrate for these burrowing forms. A similar explanation can be offered for the absence of polychaetes (except *Nereis vexillosa*). Isopods were probably absent because a suitable under rock habitat was missing. It is less easy to explain other stated differences, but they may be attributable to (1) the increased wave action on the vertical faces, (2) the slope of the faces, (3) the granitic substrate or (4) some combination of these.

A feature common to both areas was the lack of algal cover at higher levels. However, a continuous cover existed on the vertical transects from the water level up to the end of the *Fucus* at +7.5 ft. On the beaches, cover was often not continuous up from low water and gaps occurred (compare Figs. 22 and 37).

One of the more striking comparisons between the beaches and the vertical rock faces was the shifting upward on the latter of the upper limit of *Fucus*. On the beaches the *Fucus* line ran near mid-tide level (4.4 ft) whereas on the vertical transects it was near +7.5 ft or very near MHW (+7.67 ft). The lower limit had likewise shifted up on the verticals and was at +1.5 to +2.0 ft whereas the lower level on the beaches was +.5 to +1.0 ft. In addition the *Fucus* zone had broadened by approximately one foot on the verticals compared to the beaches. This shift upward and broadening of the zone appears attributable to the more exposed situation of the vertical areas with consequent wetting.

Random sampling—comparison of East Reef and West Reef: The observed and described differences between the East and West Reefs have been quantified in the result section in Tables 2 and 4. It is pertinent here to discuss some of these differences. Aside from the apparent dominance on both reefs of the ubiquitous *Balanus cariosus*, the fauna of the two reefs was quite different either in species composition or in relative abundance of equivalent species.

Major organisms present on the East Reef and absent on the West

Reef included *Littorina sitkana*, *Littorina scutulata*, and *Balanus glandula*. Since these species were higher tidal forms this absence is not surprising. Since *Chthamalus dalli* was not recognized until sampling was nearly completed on the East Reef it cannot be considered in this comparison. It was thus found on the East Reef, but the extent of its distribution there is unknown. Unfortunately limited field time prevented a re-sampling of the higher levels of the East Reef to rectify this oversight.

Mytilus edulis was virtually absent (two individuals) from the West Reef whereas it was one of the dominants on the East Reef.

Pycnopodia helianthoides and *Dermasterias imbricata* were also absent from the West Reef. Both species are characteristically to be found in eelgrass (*Zostera marina*) beds which were absent from the West Reef.

Species present on the West Reef but absent on the East Reef were *Katharina tunicata*, *Cucumaria curata*, *Leptasterias* sp., *Nereis vexillosa*, *Mopalia ciliata*, and *Cirratulus cirratus*. This finding is particularly strange in the case of *Nereis vexillosa* which data from the beach suggested to favor *Mytilus* areas; on the reefs its distribution was rather the reverse of that shown by *Mytilus*. Reasons for the absence of *Katharina tunicata*, *Mopalia ciliata*, and *Leptasterias* sp. are not apparent. All were found on the large rocks the size range of which existed also on the East Reef. *Cucumaria curata* and *Cirratulus cirratus* are probably limited to low tide rocky areas, whereas, on the East Reef the lower tidal zone was an eelgrass (*Zostera*) bed anchored in soft substrate.

Strongylocentrotus drobachiensis was common on the West Reef and virtually absent (one individual) on the East Reef. This distribution appeared to follow that of the *Alaria* kelps under which S. *drobachiensis* was most commonly found.

Exceptional distributions which appeared in the data include the replacement of species of the same genus on the two reefs. Thus, *Thais lima* and *Acmaea scutum* were found on the East Reef while *Thais lamellosa* and *Acmaea pelta* were present on the West Reef, although at different tidal levels.

Certain species were found on both reefs but in differing numbers. *Glycera nana*, *Nephthys caeca*, *Nerine foliosa*, *Saxidomus giganteus* and *Pugettia gracilis* were represented in more quadrats and by more individuals on the West Reef than the East Reef. Statistical comparison of these differences, however, demonstrated only the abundance of *N. caeca* to be significantly differently between the two reefs (Table 6).

Some species were quite similarly abundant on both reefs. Thus, *Exosphaeroma oregonensis* had an abundance of 25.93 on the East Reef and 21.40 on the West Reef. *Idothea wosnosenskii* was similar with

abundance values of 4.5 and 4.68 respectively. Statistical tests of significance also demonstrated no significant difference between the respective values on each reef (Table 6).

Finally, some species showed considerable differences in abundance although present on both reefs in a comparable number of quadrats. Hence *Pagurus hirsutiusculus* had an abundance of 4.93 on the West Reef but 14.85 on the East Reef, and *Balanus cariosus* had an abundance of 89.63 on the West Reef and 198.00 on the East Reef. Both of these differences were tested statistically and found to be highly significant (Table 6). In part, these figures on *B. cariosus* resulted from the larger size of individuals on the West Reef than on the East Reef.

Random sampling—comparison of tide pool and West Reef: As was noted in the results, the two most abundant organisms in the tide pool were *Strongylocentrotus drobachiensis* and *Acmaea scutum*. Since these two species were also found on the West Reef in numbers, it is profitable to compare the abundance figures for the species between the two areas. *Strongylocentrotus drobachiensis* was considerably more abundant in the pool than on the reef (30.46 as opposed to 3.89). This difference is shown statistically to be highly significant ($t = 4.02$ for 49 degrees of freedom). Similarly *Acmaea scutum* was also more abundant in the pool than on the reef (17.46 as opposed to 8.07). This difference is shown to be significant statistically ($t = 2.04$ for 62 degrees of freedom). It would appear on this evidence and on the observation that these two species were found only occasionally elsewhere, that the optimum areas for them were subtidal, not tidal. Perhaps this is also true for *Acmaea mitra* which also had the greatest number of individuals in this pool.

Finally, it was only in this pool, of all the sample areas, that *Stichopus californicus* and *Margarites pupillus* occurred. It would seem they must be considered essentially subtidal forms.

Zonal Boundaries

Zones as observed on the shore were not always sharply delimited one from the other. Whereas in some cases zonal interfaces appeared to be very sharp, especially when viewed from a distance, closer analysis with quantitative sampling showed that a transition area of greater or lesser extent was almost always present. The distribution of certain species (i.e. *Mytilus edulis* on the beach transects) reflected the existence and extent of the transitional areas. In general, for Three Saints Bay, the transitional sections were greater in vertical extent between lower and middle zones and were lesser between middle and upper zones.

Tidal limits for the defined zones have been presented for each sample
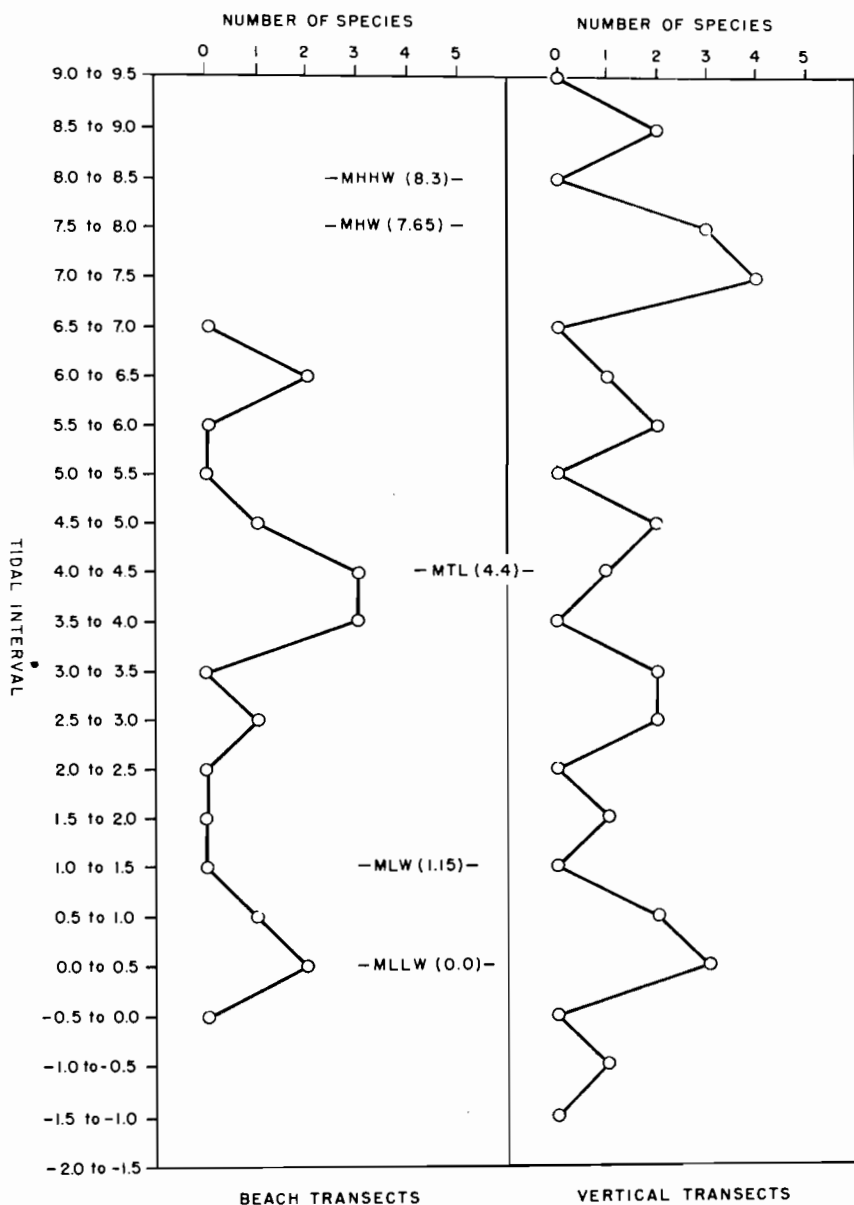
Figure 44.   Upper limits of range of organisms on the Beach Transects and Vertical Transects for each .5 ft tide interval.

COMPOSITE DIAGRAMMATIC
REPRESENTATION OF THE
PATTERN OF ZONATION OF
THE WEST REEF.

Edge of the reef

KEY

Balanus cariosus

Halosoccion glandiforme

Ulva

Fucus distichus

Encrusting sponge

Alaria
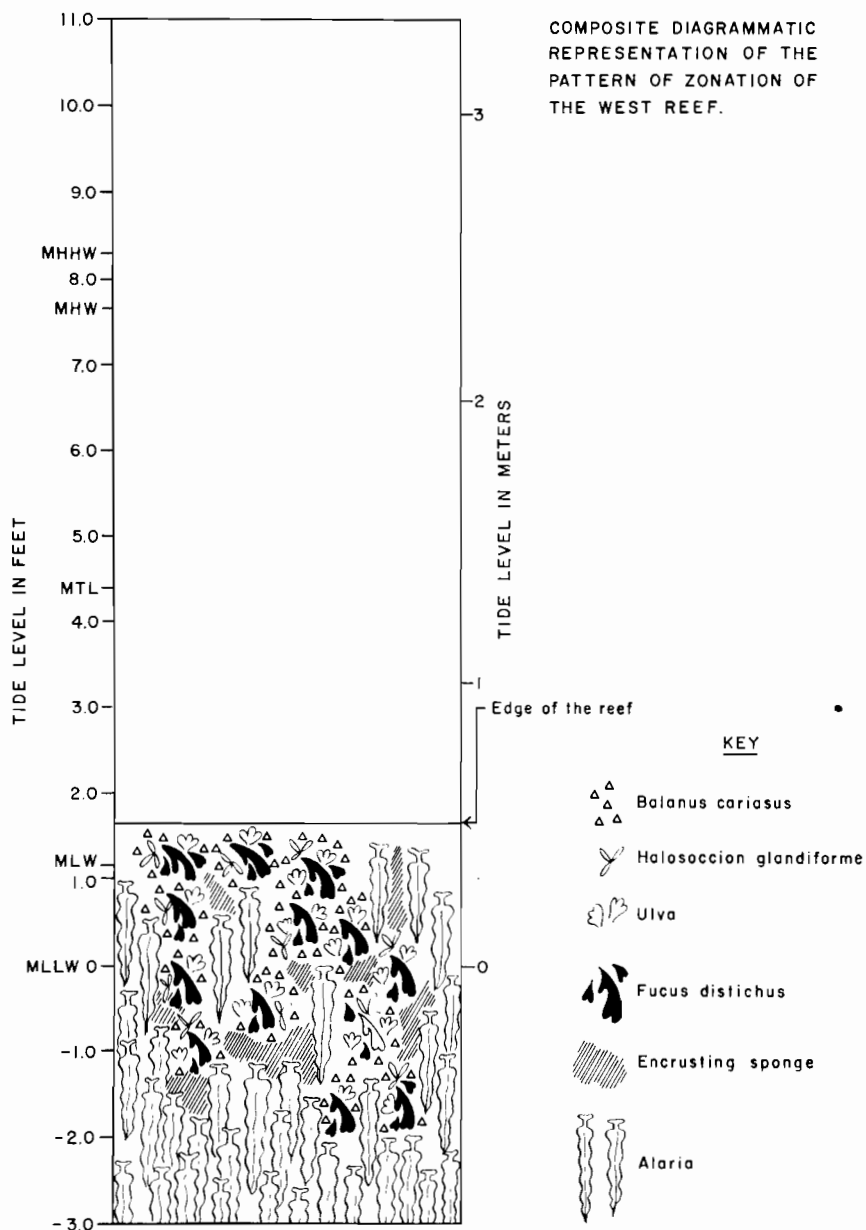
Figure 45.   Composite diagrammatic representation of the pattern of zonation of
the West Reef (Sample Area #1).
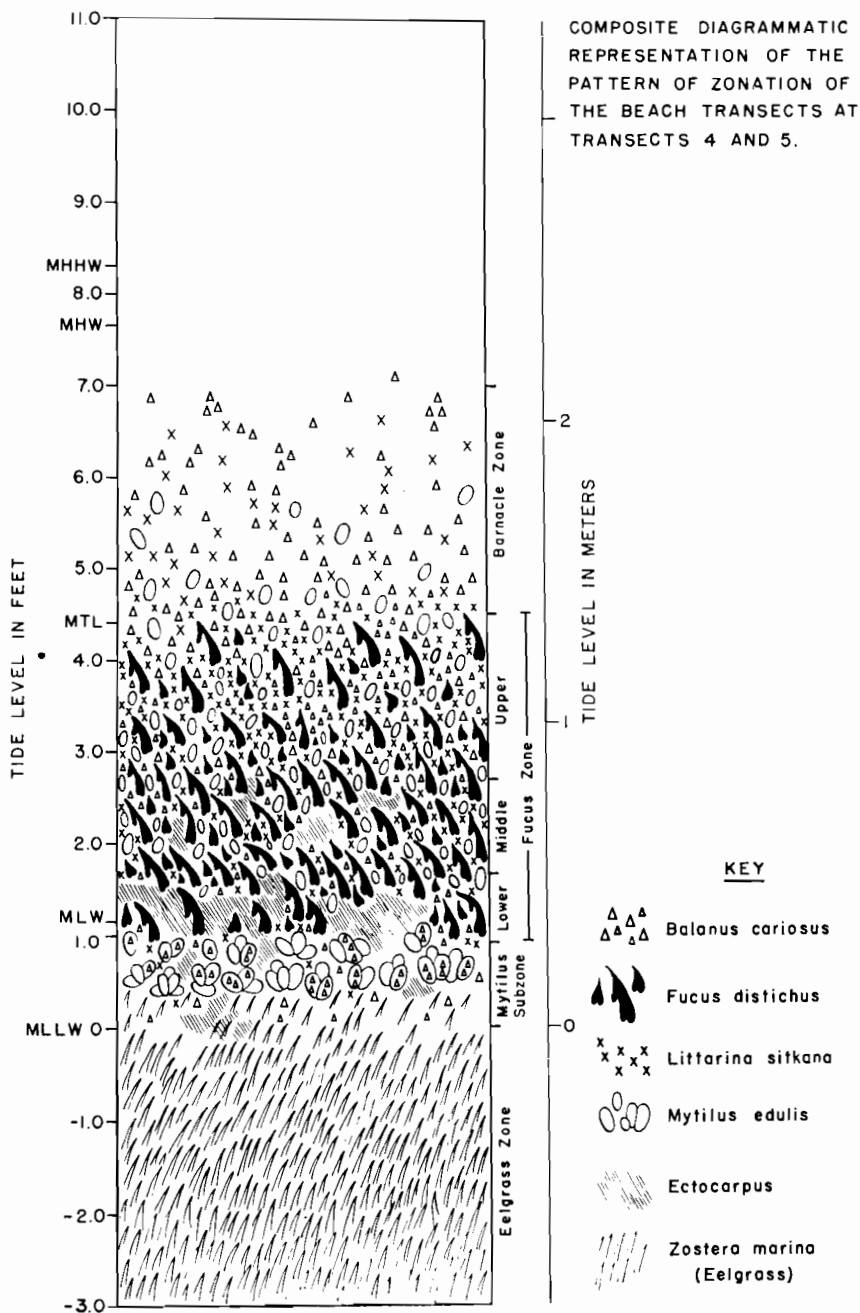
Figure 46. Composite diagrammatic representation of the pattern of zonation of the Beach Transects (Sample Area #2).

area. It would be assumed that, if these physiognomically distinct zones are truly integral units of interdependent organisms, limited by tide level or other physical factors, the invertebrates which characterize each would also be limited to the same tidal levels as the zones themselves. This has been effectively demonstrated in the results for many species; but in order to test further this assumption, the number of species reaching upper limits at each .5 ft tide interval was plotted for the vertical and beach transects, where the sampling method allowed this precision. The results (Fig. 44) suggest the hypothesis to be true. On the beach the upper limit of the eelgrass (*Zostera*) zone occurred between 0.0 and .5 exactly where the peak in species limits occurs. Similarly the *Fucus* zone terminated above between 4.4 and 5.0; here again a peak occurs. On the vertical transects the data are not conclusive for all levels. The upper *Fucus* line was noted to lie between 7.0 and 7.5, which range also represents a peak in the species limit graph. The results are less confident for the lower limit of *Fucus* or the upper edge of the laminarian zone where the species limits showed a peak again at 0.0 while the zonal boundary lay between 1.0 and 1.5. Perhaps this may be explained by loss of *Alaria* and *Laminaria* before the actual beginning of the *Fucus* zone. Absence of the very large protecting algae with extensive holdfasts may well have restricted the distribution of organisms to lower levels. One of the major dominants of the laminarian zone, *Odonthalia floccosa*, extended considerably into the lower part of the *Fucus* zone. Hence there was a broad transition zone within which one could not expect sharp upper limits of organisms.

The validity of these zones, and aggregation of characteristic species within them, has been demonstrated. Hence the shoreline of Three Saints Bay may be verified as including three horizontal intertidal zones which succeed each other vertically.

Zonation

In order to characterize visually the zonation which has been described and compared among the four sampling areas, diagrammatic representations of the patterns of zonation in each of these sampling areas have been constructed and are presented in Figures 45, 46, 47, and 48. Certain liberties have been taken in the construction of these diagrams, the major one of which was to limit the representation to the conspicuous major components of each zone. In addition little attempt was made to consider substrate although it strongly influenced the pattern of organisms on the West Reef and the barnacle zone of the East Reef where many of the species were confined to the very large rocks. The pattern was more

COMPOSITE DIAGRAMMATIC REPRESENTATION OF THE PATTERN OF ZONATION OF THE VERTICAL TRANSECTS

(Only conspicuous major components shown.)

KEY

Acmaea digitalis

Chthamalus dalli

Enteromorpha intestinalis

Balanus glandula

Balanus cariosus

Fucus distichus

Halosaccion glandiforme

Ulva

Odonthalia floccosa

Alaria

Laminaria
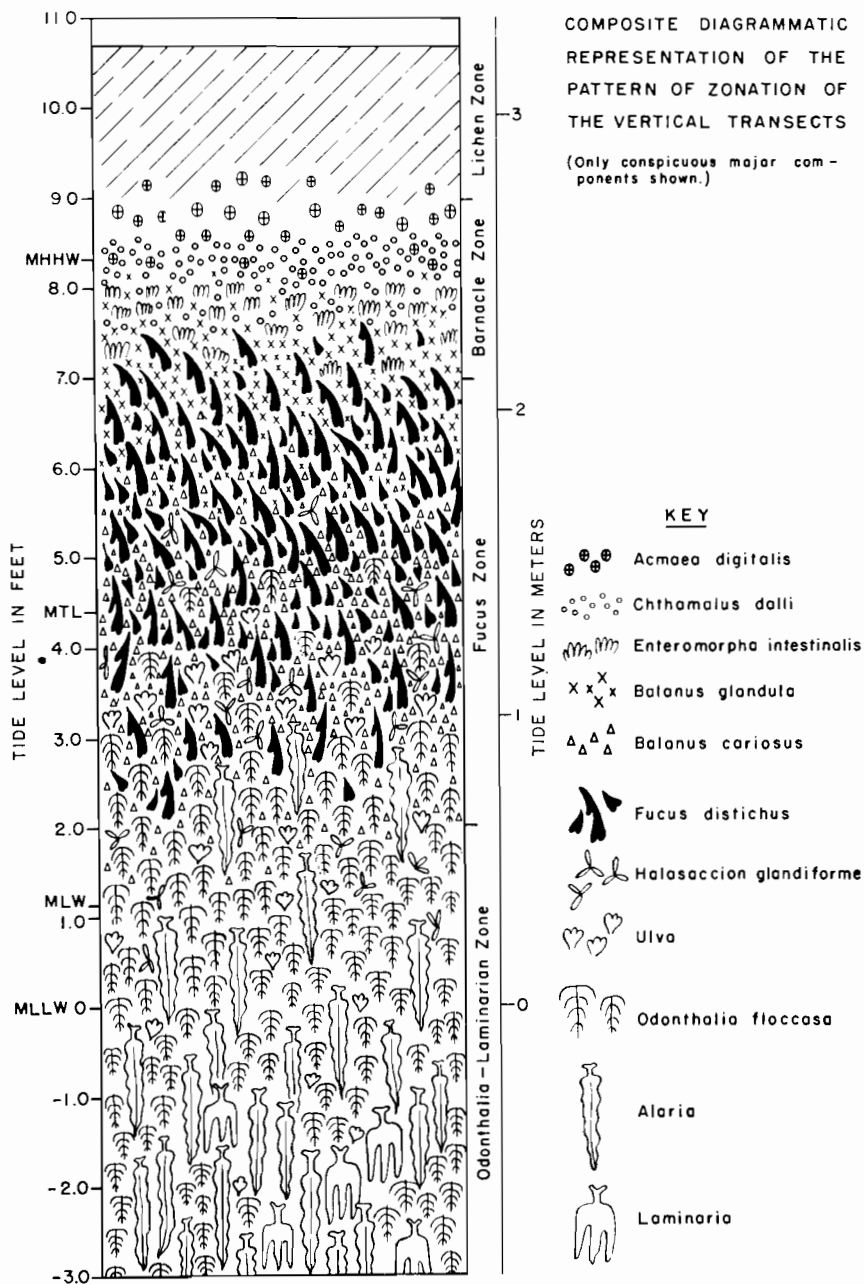
Figure 47. Composite diagrammatic representation of the pattern of zonation of the Vertical Transects (Sample Area #3 and #4).
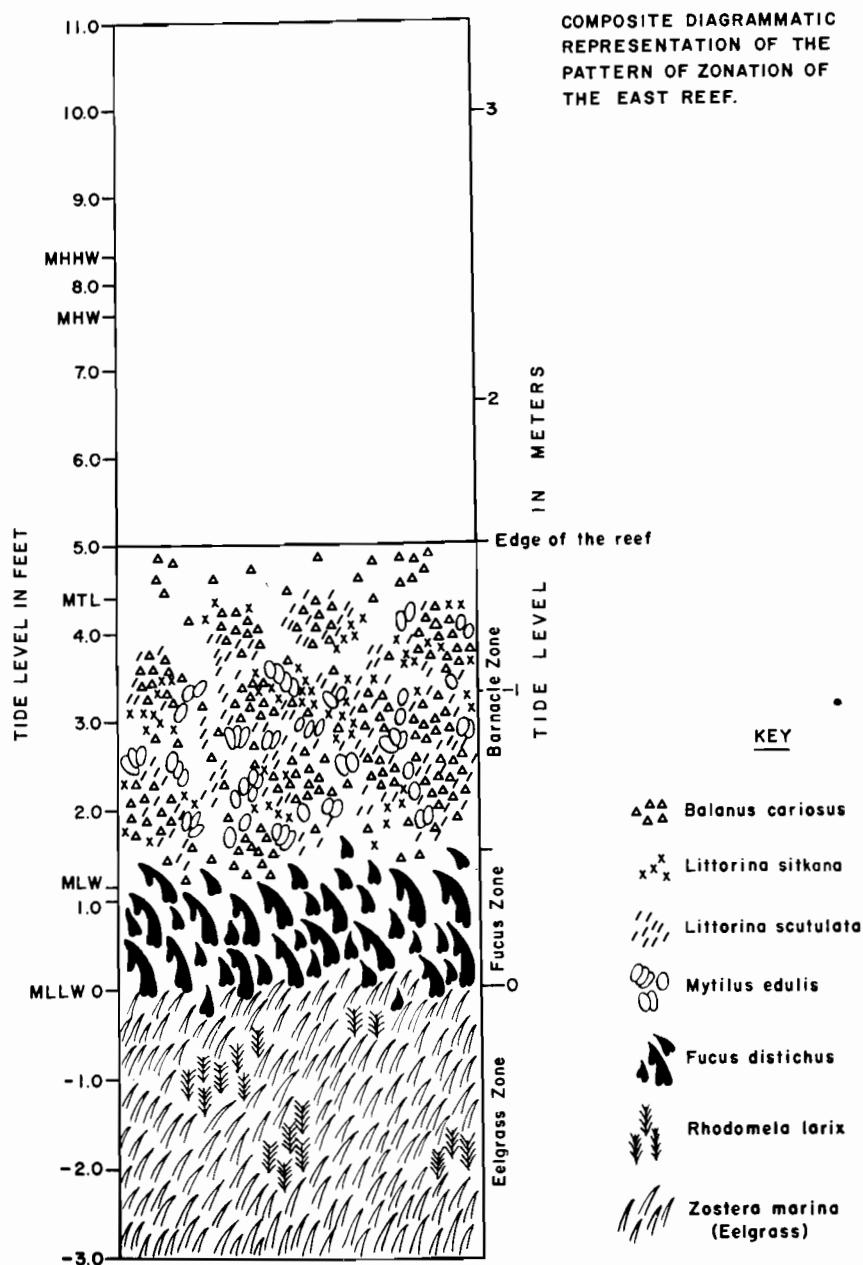
Figure 48. Composite diagrammatic representation of the pattern of zonation of the East Reef (Sample Area #6).

DIAGRAMMATIC REPRESENTATION OF A CROSS-SECTION OF THE WEST REEF
TO SHOW THE NICHES OF SOME OF THE MAJOR ORGANISMS

KEY

Fucus distichus	Leptosterias	Strongylocentrotus drobachiensis	Saxidomus giganteus
Halosaccion glandiforme	Cucumaria curata	Nephthys caeca	Natica clausa
Alaria	Balanus cariosus	Nerine foliosa	Buccinum baeri
Spongomorpha	Exosphaeroma oregonensis	Mopalia ciliata	Thais lamellosa
Ulva	Idothea wosnoseriskii	Katharina tunicata	Nereis vexillosa
Encrusting sponge	Cirratulus cirratus	Venerupis staminea	Burrowing anemone
	Acmaea scutum	Glycera nana	

Figure 49.   Diagrammatic cross-section of the West Reef.

uniform on the vertical and beach transects. The diagram of the beach transects omits consideration of transects #1, #2, and #3 since these were more or less strongly influenced by the freshwater stream outflow; transects #4 and #5 are more representative of the larger cobble beach area which the diagram is meant to represent. Finally, in all the representations there is no concerted attempt to show absolute numerical differences in organism density among the sampling areas.

These diagrams illustrate some points not previously emphasized. On the West Reef (Fig. 45) it will be noticed that a conspicuous component is a species termed encrusting sponge (probably a species of *Haliclona*). This sponge may also be seen in Figure 49 in more natural representation. This sponge was very common on this reef and covered very extensive areas in a continuous mat. It was never observed in the other sampling areas and thus aided in giving a unique appearance to this reef. It is probable that some of the invertebrate species (e.g. polychaetes) found on this reef may have been dependent on the existence of this sponge.

Another previously unemphasized point was the existence on the vertical transects (Fig. 47) of the alga *Enteromorpha intestinalis*. This alga formed a very prominent bright green belt in the barnacle zone on nearly all the vertical transects.

PACIFIC COAST ZONATION
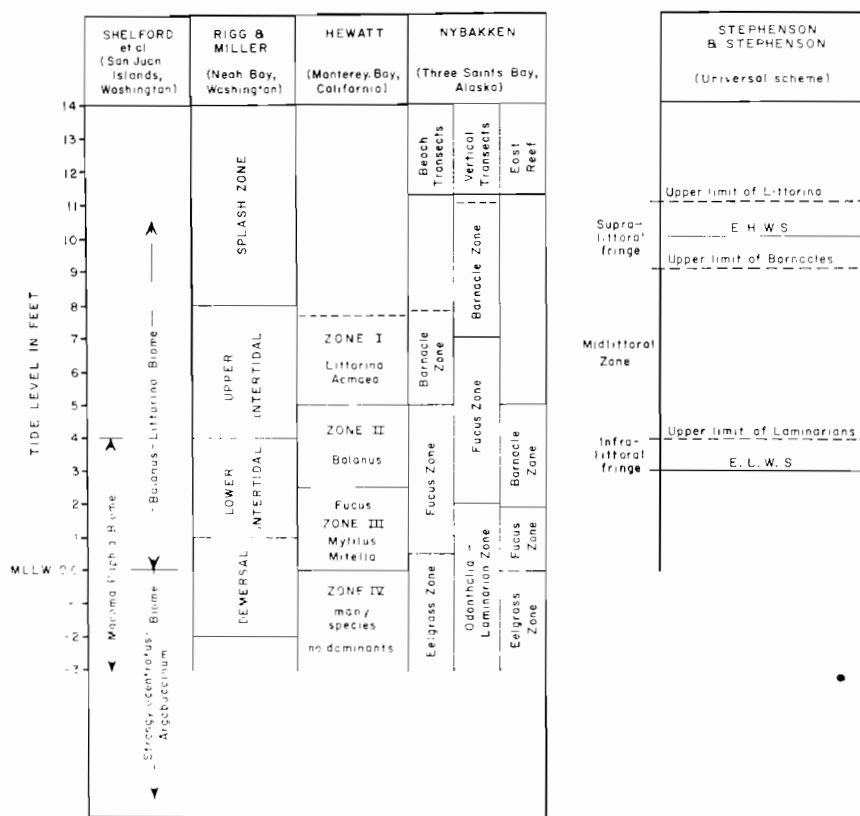
Figure 50. Zonation in the Pacific coast of North America as observed by several authors, including a representation of the universal scheme of Stephenson and Stephenson, 1949.

A comparison between the eelgrass (*Zostera*) zones of the East Reef and the beach transects shows the presence of *Rhodemela larix* on the East Reef and its absence from the beach transects. This alga formed a prominent brown area in the otherwise prevalent green of the eelgrass wherever there was a rock for it to attach.

On the beach transects an attempt was made to subdivide the *Fucus* zone into three subzones, a lower one with a high number of *Ectocarpus*, a middle zone where *Fucus* was most dense, and an upper zone where *Fucus* was thin. This was not considered in the results because this division proved very subjective and species densities did not warrant its consideration.
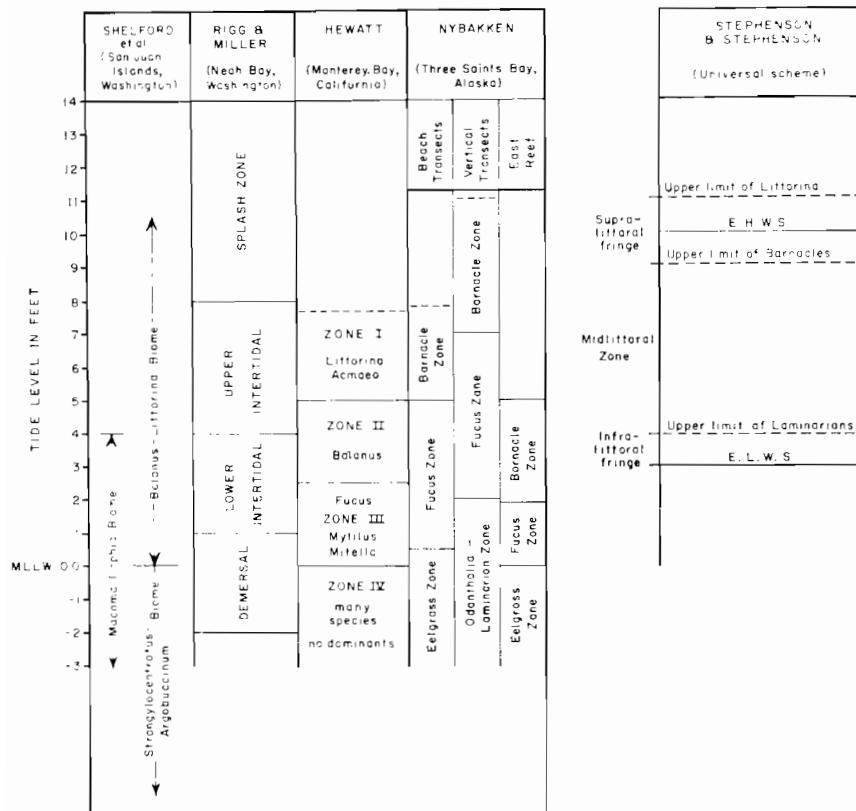
Figure 50. Zonation in the Pacific coast of North America as observed by several authors, including a representation of the universal scheme of Stephenson and Stephenson, 1949.

The *Mytilus* reef area has been designated as a separate zone on the representation of the beach transects. By its conspicuous appearance particularly in transect #5 it perhaps warranted this distinction, but overall more rightly belongs as a part of the *Fucus* zone since it was not found consistently on this shore.

The final figure of this series, Figure 49, illustrates the spatial relationships among some of the more conspicuous organisms of the West Reef, whereon was found the greatest number of species of any situation studied in Three Saints Bay.

Comparison With Previous West Coast Studies

In order that the results of this study may be tied to and compared with those from other regions, it is pertinent to consider schemes of zonal description which have been proposed heretofore. Perhaps most useful is the universal scheme proposed for rocky shores by Stephenson and Stephenson (1949) wherein three principal zones are also described (Fig. 50). The main intertidal area extending from the upper limit of laminarian algae to the upper limit of barnacles forms what they have termed the "midlittoral zone." The zone from the upper limit of barnacles to the upper limit of *Littorina* forms their "supralittoral fringe," and the area between extreme low water of spring tides (ELWS) and the upper limit of laminarian algae forms their "infralittoral fringe." In this three-part division of the intertidal area correspondence is most easily seen between the established *Alaria* or *Odonthalia-Laminaria* zone of Three Saints Bay and their infralittoral fringe. Since no levels are set for the upper limit of this zone save as it is the upper limit of laminarians, similar if not exact correspondence is made between the lower levels of the verticals and the entire West Reef. Since the Stephenson scheme does not include soft bottom shores, the eelgrass (*Zostera*) zones of the beaches and East Reef cannot readily be compared with this classification. Their existence, however, only at the lowest levels would seem to qualify them also as part of the infralittoral fringe.

Complications arise when consideration is given to the midlittoral zone of Stephenson and Stephenson. This zone is bounded at its upper edge by the "upper limit of barnacles." It is not difficult to consider the upper limit of barnacles as the end of a zone; however, on the shores investigated the upper limit of barnacles marked the upper limit of the highest, not the middle, zone. Only on the vertical faces was appreciable fauna found above the upper limit of barnacles. To fit the present zones into this scheme it then becomes necessary to consider the *Fucus* zone and the barnacle zone as observed and characterized as two major subzones of

the midlittoral of Stephenson and Stephenson. If this be done, correspondence is maintained. Indeed, Stephenson and Stephenson state that there is a strong tendency for this zone to be subdivided into two sections, of which the upper is dominated by barnacles.

The uppermost zone or "supralittoral fringe" of Stephenson and Stephenson extends upward to the upper limits of *Littorina*. The lower part of this zone is also characterized by the black lichens (*Verrucaria* sp.). If one considers the upper limit of barnacles as the midlittoral limit, that leaves only the verticals with any extent above barnacles to compare here. The verticals did have the black lichens (*Verrucaria* sp.) and by that token fit into the scheme. However, the two species of *Littorina* on the shores were always found either in the barnacle zone (East Reef) or the *Fucus* zone (beaches) in greatest densities and never extended higher than the barnacles. At least in Three Saints Bay *Littorina* cannot be used to characterize the supralittoral fringe zone. A better biological indicator here would be *Acmaea digitalis* which with the black lichens extended above the limits of barnacles.

Once the distributions determined for Three Saints Bay have been related to the Stephenson and Stephenson scheme it is very easy to compare the results obtained in Three Saints Bay with those reported by Stephenson and Stephenson (1961) for Vancouver Island, the most northerly point on the Pacific Coast for which systematic ecologic studies presently exist. In this study the Stephensons characterized the supralittoral fringe by *Littorina sitkana* and *Littorina scutulata*. These two species were at all times in Three Saints Bay associated with the barnacles. They were never observed higher on any shore. The Stephensons do, however, report these species as commonly extending into the midlittoral where, in fact, we found them most abundant.

The midlittoral around Vancouver Island was found by the Stephensons to be well marked and usually subdivided into one, two, or three subzones. At Horswell Bluff they found a division into an upper barnacle subzone and lower *Fucus* subzone, similar to the major zonation we have set forth for Three Saints Bay. The barnacle subzone at Horswell Bluff consisted primarily of *Chthamalus dalli* and *Balanus glandula* whereas the *Fucus* subzone had considerable numbers of *Balanus cariosus*. Additionally, some shores showed an abundance of *Mytilus edulis* in the lower *Fucus* zone. These results are especially comparable to ours for the vertical faces, where all three barnacle species appeared.

Results from the infralittoral fringe showed commonly a typical laminarian community with *Alaria*, *Laminaria* and related algae. Results from Three Saints Bay are similar except that in the "infralittoral" zone of the

vertical transects dominance was shared between *Odonthalia floccosa* and the two major laminarians, *Alaria pylaii* and *Laminaria platymeris*. The Stephensons also reported a bare area from the infralittoral zone as well as an area dominated by large anemones. Neither of these subzonal types was observed in Three Saints Bay.

Hewatt (1937) worked a belt transect on an outer semi-exposed coast in Monterey Bay, California, but his results are difficult to relate to the present work done in a protected bay due primarily to differences in species making up the sampled communities. For example, he discusses 90 species; only six of these were found in Three Saints Bay while another nine are in the same genus but were represented by different species in Three Saints Bay. Of the more prominent organisms of Three Saints Bay, only *Balanus glandula*, *A. pelta*, *A. scutum*, and *L. scutulata* were common to both areas. *B. cariosus*, *Mytilus edulis*, and *Chthamalus dalli* were absent from Hewatt's area.

Hewatt found four zones on his shores separated by the three pronounced peaks in his graph plotting the numbers of species reaching upper or lower limits of range against tide level (Fig. 50). Hewatt's most pronounced peak in this plot occurred at MLLW (0.0 ft). The other peaks occurred at +2.5 to +3.0 (MTL) and +5.0 (near MHW). He stated that his lowest zone (below 0.0 ft), the zone comparable to our eelgrass (*Zostera*) or laminarian zone, was not characterized by any single dominant on his transect (Fig. 50). This was not found to be true in Three Saints Bay where *Zostera marina* dominated sand-silt shores at the lower level, *Alaria pylaii*, *Laminaria platymeris*, and *Odonthalia floccosa* dominated this zone on the vertical faces, and *Alaria pylaii* dominated on the West Reef.

The +2.5 to +3.0 ft (MTL) peak corresponded to the upper limit of *Fucus* and *Pelvetia* just as we have noted a similar break at the upper limit of *Fucus* (also near MTL) in Three Saints Bay. He notes, as have I, that this is a very striking line in the intertidal zone. He postulates that the prominent faunal break occurring here is due to the lack of cover above this line, a suggestion which partially concurs with our observations. Since this break occurs at MTL he suggests it as the reason for the boundary, a postulate we have made for this break on the beaches. *Balanus cariosus* was a dominant member of the *Fucus* zone on the beaches and vertical faces in Three Saints Bay and probably determined the presence and absence of other organisms, whereas there was notable lack of barnacles in the *Fucus* zone at Monterey.

The third zone, limited above by the peak at the +5.0 level, was dominated by *Balanus glandula* according to Hewatt and corresponds

well with our barnacle zone, particularly on the vertical faces where *B. glandula* was also a dominant. Hewatt's final zone, extending above the +5.0 peak, corresponds to the Stephensons' "supralittoral fringe." It compares to the area dominated by black lichens (*Verrucaria*) and *Acmaea digitalis* above the barnacles on the vertical faces in Three Saints Bay. In this zone Hewatt listed but one species—an isopod (*Ligyda occidentalis*).

Thus it can be seen that a physiognomically similar set of zones was found on the exposed coast of Monterey Bay as in the more protected shores of Three Saints Bay, but that the zones were quite different in species composition.

With the zones firmly in mind, the distribution of the six species previously noted as common to both areas may be compared. Among the six species, good correspondence is found for *Balanus glandula* which existed above the *Fucus* in both areas. *Acmaea digitalis* was also reported from the lower part of the *B. glandula* zone. Here we must note a discrepancy since *A. digitalis* in Three Saints Bay was found above the *B. glandula*, at least never below them. *Acmaea pelta* and *Acmaea scutum* were both reported as characterizing the *Fucus* zone. However, in Three Saints Bay these were species of wide vertical range and *A. pelta* was found in both *Fucus* and barnacle zones. *A. scutum* on the other hand appeared to be a low level organism which occasionally ranged up into the *Fucus* zone. It was certainly most abundant in Three Saints Bay in the tide pool. *Acmaea mitra* was also reported from the *Fucus* zone in California, but in our work it was definitely a lower zone constituent and was most abundant subtidally. *Littorina scutulata* was found by Hewatt to be a characteristic inhabitant of the *Balanus glandula* zone. Our results place it there for the East Reef but in the *Fucus* zone for the beach transects.

It is more difficult to compare the shore zones of Three Saints Bay with the communities found in protected waters of the San Juan Islands by Shelford and associates (1935). They have divided all intertidal and shallow water areas into a series of four large biomes some of which do include parts of the intertidal and others of which do not.

Shelford et al. first consider the *Zostera* community a faciation of their "*Macomia-Paphia*" biome (Fig. 50), but the discussion is brief due to their own limited investigation of the zone. They, however, do not list any starfish to be as common in that area as we found *Pycnopodia* and *Dermasterias* in Three Saints Bay. The dominants listed for the biome, and presumably thus for the faciation, include *Macoma balthica* which we found as the most abundant species of this zone on the beaches and

Cardium corbis (= *Clinocardium nuttalli*). Other dominants reported included *Venerupis staminea* and *Saxidomus giganteus*, which we encountered only sporadically in *Zostera* and more commonly on rocky-cobbly shores (East Reef and West Reef). But certainly they did not characterize the zone in Three Saints Bay.

The laminarian zone as we have characterized it is considered by Shelford et al. as a faciation, appearing between MLLW and 15 or 20 m in depth, of their "*Strongylocentrotus-Argobuccinum*" biome (Fig. 50) We found it to extend higher than MLLW on the two areas where it occurred in Three Saints Bay (West Reef to +1.65 ft and vertical transects to +3.0 ft). As dominant species in this faciation they list *Nereocystis leutkeana* and species of *Alaria* and *Laminaria*. *Nereocystis* was not found in the tidal parts of the laminarian zone in the bay but *Alaria* and *Laminaria* have already been noted as the dominants. Invertebrate dominants were *Strongylocentrotus drobachiensis* and *Argobuccinum* (*Fusitriton*) *oregonensis*. *Strongylocentrotus* was a prominent member of the West Reef where it had an abundance of 3.89/.25 m² whereas Shelford gives 40–200/10 m² as the abundance. *Fusitriton* was not observed on reefs in the bay save for one immature individual on the West Reef and a few individuals found subtidally in the pool sampled.

The rest of the intertidal zone which we have characterized in two zones, *Fucus* and barnacle, is classed together in what Shelford has termed the "*Balanus-Littorina*" biome (Fig. 50). It is here that he states that his "*Macoma-Paphia*" biome often overlaps the lower half of this biome, a point we noted in stating that many of the dominants of his "*Macoma-Paphia*" biome are clams whose presence is more dependent upon substrate conditions in our experience than on surface zonation. We certainly found them common in *Fucus* zone of East Reef and below the *Alaria* in the laminarian zone of the West Reef.

Within this biome our groups of speices correspond to Shelford's "*Balanus-edulis*" association. This association is dominated by *Balanus cariosus* and *Mytilus edulis* and exists in bays in the Puget Sound area. This fits well with our results from the beach transects, vertical transects, and East Reef where *Balanus cariosus* and *Mytilus edulis* were dominant species. Other dominants listed for this association by Shelford included *Littorina scutulata*, *Acmaea digitalis*, and *Acmaea* sp. *L. scutulata* was a dominant only on our East Reef and *A. digitalis* only on the vertical faces. If by "*Acmaea* sp." Shelford means either *A. pelta* or *A. scutum* then it is possible to consider these as dominants on our beach transects and East Reef.

As one of the subdominants of this formation or biome Shelford has

listed *Littorina sitkana* which in Three Saints Bay was more of a domi-
nant or characteristic organism than was *L. scutulata*. He also listed
Thais lamellosa and *Thais canaliculata*. *Thais lamellosa* was the only
one found in our sampling areas and was most commonly a dweller of
the lowest tidal levels, thus falling outside of Shelford's "*Balanus-Littorina*"
biome and perhaps within his "*Strongylocentrotus-Argobuccinum*" biome.

Rigg and Miller's (1949) work was done in Washington at Neah Bay,
which is more open to the effects of open sea than was Three Saints Bay.
It is an area, however, with similar tidal constants (Neah Bay has
diurnal range of 8.2 as compared with 8.3 for Three Saints Bay and MTL
is the same for both at 4.4) as well as such other environmental factors
as high rainfall, foggy days, presence of vertical faces, and boulder
beaches. It is thus profitable to attempt comparisons with that study
even though they considered the algae and invertebrates separately and
arbitrarily divided the shore into four zones before beginning work.
Fortunately they characterized these zones with approximate vertical
limits in reference to the tide so comparisons between levels of inverte-
brates can profitably be made. There was no attempt at quantification.

The four zones they established were: splash zone, +8.0 to +14.0 ft;
upper intertidal, +4 to +8 ft; lower intertidal, +1.0 to +4.0 ft; and
demersal, +1.0 to –2.0 ft (Fig. 50). The splash zone extended up from
MHW and encompassed a part of our barnacle zone (vertical transects)
and all above it, the Stephensons' supralittoral fringe, and part of Hewatt's
upper zone. The upper intertidal is referable to part of our barnacle
zone (East Reef, beach transects) and part of the *Fucus* zone (vertical
transects), part of Stephensons' midlittoral (upper subzone), and Hewatt's
Balanus zone. The lower intertidal is referable to our *Fucus* zone (East
Reef, beaches) part of the *Odonthalia-Laminaria* zone, the lower part of
the Stephensons' midlittoral and part of Hewatt's *Fucus-Pelvetia* zone.
The demersal zone is referable to our *Zostera* and laminarian zones (East
Reef, Beach Transects, West Reef), the Stephensons' infralittoral fringe
and the lower half of Hewatt's *Fucus-Pelvetia* zone and all of his lowest
zone (Fig. 50).

On one gently sloping, shelving shore Rigg and Miller found the
greatest number of invertebrate species of their study area. This is the
only shore with specific relation to our sample areas and so will be the
only one considered. Here the splash zone was characterized by *B.
cariosus, B. glandula, C. dalli, L. sitkana,* and *A. digitalis*. With the
exception of *A. digitalis* this is the same grouping which dominated the
barnacle zone on the East Reef, but at considerably lower tide levels (+1.9
to +5.0). With the exception of *L. sitkana* and *B. cariosus* this was also

the species group prominent in the highest zone on the vertical surfaces where tide levels more nearly correspond (+7.5 to 11.0). The upper intertidal at Neah Bay was similar to the splash zone and was characterized by *B. cariosus, B. glandula, L. scutulata,* and *Mytilus californianus.* With the exception of *M. californianus* (here replaced by *M. edulis*), this was again similar to our barnacle zone on the East Reef. The lower intertidal of Rigg and Miller's shelving shore was not characterized by any of the organisms of our *Fucus* zone except as *B. cariosus* was found down into it in small numbers. The demersal zone of Neah Bay was very rich in species and included many species which were found on our East Reef eelgrass (*Zostera*) zone, West Reef, or vertical *Odonthalia-Laminaria* zone, to which it is comparable. Included were *Dermasterias imbricata, A. scutum, A. pelta, C. oregonensis, Evasterias troschelli, Henricia leviuscula, Katharina tunicata, Lepasterias, Venerupis staminea, Pugettia gracilis, S. drobachiensis,* and *T. lamellosa.*

Of this group of species several were found in other zones in Three Saints Bay in addition to the three low zones mentioned. *A. scutum, Katharina tunicata,* and *Leptasterias* were taken from the *Fucus* zone of the vertical surfaces, and *Venerupis staminea* from the *Fucus* and barnacle zones (East Reef). These species had a greater vertical range on Kodiak Island than the same species reported in Neah Bay.

In addition to the above discussed dominant invertebrates, a considerable number of other species were found in common with Three Saints Bay. To facilitate comparisons, Table 10 has been drawn up which compares the tidal levels of the species common to the two areas.

It may be observed from the table that the species distributions in Neah Bay match quite well our distributions for Three Saints Bay for about half of the species. Large discrepancies occur particularly in major organisms such as *Littorina,* the barnacles, and *Acmaea.* Particularly for the two *Littorina* species are the results different. This is due to the fact that these organisms were characteristic of the middle *Fucus* zone (beaches) in Three Saints Bay and were absent from the vertical faces. The lower levels for barnacles probably reflects reduced wave action and splash in Three Saints Bay in contrast to Neah Bay since they characterize physiognomically similar zones in both areas. *Acmaea pelta* presents an interesting case in that it occurred at higher levels in Three Saints Bay than in Neah Bay. The explanation for this is not known. Similar higher levels of occurrence for the two *Thais* species and *Katharina tunicata* in Three Saints Bay are not explained.

In summary, the defined and characterized zones of Three Saints Bay have been contrasted to zonations established by other investigators

TABLE 10.   COMPARISONS OF THE TIDE LEVELS OF OCCURRENCE OF
SPECIES COMMON TO NEAH BAY AND THREE SAINTS BAY

Species	Tidal range	
	Neah Bay	Three Saints Bay
*Balanus cariosus**	—2.0 to +14.0	— .7 to +7.3
*Balanus glandula***	+1.0 to +14.0	+ .35 to +8.7
Chthamalus dalli	+8.0 to +14.0	+1.43 to +8.9
Acmaea pelta	—2.0 to + 1.0	+ .1 to +8.3
Acmaea scutum	—2.0 to + 8.0	— .32 to +7.5
Littorina sitkana	+8.0 to +14.0	— .2 to +6.85
Littorina scutulata	+4.0 to + 8.0	— .2 to +3.81
Thais lima	—2.0 to + 1.0	+1.15 to +2.99
Thais lamellosa	—2.0 to + 1.0	—1.15 to +3.1
Katharina tunicata	—2.0 to + 1.0	— .32 to +6.2
Margarites pupillus	—2.0 to + 1.0	Subtidal in pool
Searlesia dira	—2.0 to + 1.0	—1.3 to +2.8
Cancer oregonensis	—2.0 to + 1.0	+ .3 to + .55
Evasterias troschelli	—2.0 to + 1.0	— .9 to +1.5
Dermasterias imbricata	—2.0 to + 1.0	—1.32, —.88
Strongylocentrotus drobachiensis	—2.0 to + 1.0	—2.3 to +1.45
Venerupis staminea	—2.0 to + 4.0	— .9 to +2.99
Pugettia gracilis	—2.0 to + 1.0	—1.4 to +1.79

*   Common only between +1.0 to +8.0

** Common only between +4 to +14.0

at other points on the Pacific coast of North America and have been found
to reaffirm the general scheme of subdivision of the intertidal zone into
zones or communities which can be characterized by the same assem-
blages of algae, invertebrate types, growth form or some combination of
these. In many cases it has been shown similar genera and species occur
in widely separated areas along the Pacific coast.

SUMMARY

An account, both qualitative and quantitative, is given of the fauna, flora, and zonation of four intertidal shores of differing aspect, slope, wave exposure, and substrate along with one tide pool in Three Saints Bay, Kodiak Island, Alaska as studied during June, July, and August of 1963.

The methods used in obtaining data for this study included the belt transect and random sampling from a surveyed grid. Belt transects were used to sample a cobble beach and a series of vertical granite faces whereas two rock and boulder beaches and the tide pool were sampled at randomly selected stations.

It was determined that there were three physiognomically distinct zones on all shores in which the substrate was stable in the presence of wave action. These zones succeeded each other vertically. The lowest zone was defined to be one of eelgrass (*Zostera marina*) where the substrate was soft mud or sand or to be a mixture of large laminarian algae where a rocky substrate occurred. This zone was continuous subtidally and extended up to between 0.0 and +1.5 ft.

The middle zone on all shores of occurrence was dominated by the alga *Fucus distichus*. The tidal limits of this zone were shown to vary among the sample areas depending on aspect and wave action. On protected shores the upper limit was near mean tide level whereas on exposed rock faces it approached mean high water.

The highest zone on all shores was devoid of large algae and dominated by one or more of the barnacles *Balanus cariosus*, *Balanus glandula*, and *Chthamalus dalli*, of which one species, *Balanus cariosus*, was also a common dominant of the *Fucus* zone. This barnacle zone extended up to as high as 11.0 ft on the vertical faces.

The distributions and abundances of the fifty-seven species of invertebrates which were considered in this study in part reflected the described zones. Some species were found to be entirely restricted to a single zone whereas others demonstrated high concentration of numbers in one zone while extending in lesser numbers to other zones.

APPENDIX: SPECIES ACCOUNTS

These individual accounts of the 57 species of invertebrates, encountered during the course of intertidal sampling, summarize information for each concerning (1) tide levels at which the species was found; (2) observed aspects of ecology in Three Saints Bay; (3) distribution and abundance in Three Saints Bay; and (4) comparisons of the ecology of the species as observed in Three Saints Bay with published data on the ecology in other parts of its range where such data exist.

The tide levels as reported here were the extremes within which the species was found and do not give an indication as to the levels at which the most individuals were found, nor the preferred levels of occurrence. In the case of those species recorded once, the tide level is the level of the quadrat of occurrence.

The organization of this section follows that of the annotated systematic index of Ricketts and Calvin (1962). Molluscan species names follow LaRocque (1953); Annelid species names, Berkeley and Berkeley (1948, 1952); and other groups, various authors.

Several species discussed in this account have not been identified to species and hence bear only generic names. These species are unidentified because of an absence of comparative material or because the author was unable to verify the species identification.

<div align="center">

Phylum Nemertea

Order Heteronemertea

</div>

Cerebratulus sp. Tide level: East Reef: −.90, −.88

Three large, bright red nemerteans attributable to this genus were taken on two occasions from under rocks in mud-sand in the *Zostera* zone on the East Reef. Although the species was not determined with certainty, the large size and bright red color and physical characteristics would seem to place it as *C. montgomeryi*, a species found abundantly in such a habitat along the Alaskan coast according to Coe (1910). Coe (1940) gives the habitat of this species as under rocks and in mud near the low tide level.

The absence of suitable reference materials precluded the identification of this species.

<div align="center">

Phylum Annelida

Class Polychaeta

Sub Class Errantia

</div>

Arctönoe pulchra (Johnson, 1897) Tide level: West Reef: −.32

This polychaete is a commensal on echinoderms and gastropods and

two individuals are recorded for a single quadrat of the West Reef. It seems probable that these fell off one or two of the 25 *Strongylocentrotus drobachiensis* which were recorded from this same quadrat. Since the *S. drobachiensis* were rarely saved after counting, or examined in counting for commensals, this polychaete is probably considerably more abundant than these figures would indicate.

Phyllodoce groenlandica Oersted, 1843   Tide level: East Reef: +1.15

A single specimen of this polychaete was taken in one quadrat of the East Reef in an area of no algae cover. No notes on the ecology were recorded from Three Saints Bay. Berkeley and Berkeley (1948) do not record anything except that it is dredged and also taken on the littoral zone.

Glycera nana Johnson, 1901   Tide level: West Reef: −.32 to +1.05
East Reef: −.9 to +1.15

This polychaete was common on the West Reef where it was taken in 20 quadrats with an abundance of 1.4 and with single quadrat ranges of one to three. It occurred in only four quadrats with an abundance of 1.25 on the East Reef. In both localities this species was found burrowing in the substrate usually within the first 2 cm of the surface and often just beneath the larger rocks.

Nephthys caeca (Fabricius, 1780)   Tide level: Beach Transects: −1.4 to +.45
East Reef: +.70 to +2.08
West Reef: −.32 to +1.43

One of the more widely distributed species of polychaetes in Three Saints Bay, *Nephthys caeca*, was found on the Beach Transects, and East and West Reefs. On the Beach Transects it was an infrequent subsurface inhabitant of the lower levels (Fig. 21) with greatest density of four per quadrat. On the East Reef this species occurred in but five quadrats with an abundance of 1.0. On the West Reef, however, individuals were more frequent, occurring in 22 quadrats with an abundance of 1.91 and a single quadrat range of one to four. *Nephthys* was here found burrowing in the substrate or directly beneath large surface rocks (Fig. 49). Although Berkeley and Berkeley (1948) recorded this species from clean sand, in all cases where found in Three Saints Bay, it occurred in muddy sands or silt.

Nereis vexillosa Grube, 1851 Tide level: Beach Transects: −.5 to +3.7
(Clam worm)   West Reef: −.21 to +1.32

This polychaete was found in the Beach Transects and the West Reef as one of the most conspicuous inhabitants of the intertidal zone in Three Saints Bay. It was present in each of the Beach Transects but reached its greatest densities in #5 (Fig. 20), where, at the +.4 tide level, one quadrat yielded 24 individuals. This quadrat was dominated by *Mytilus edulis* but was algae free. This "*Mytilus* reef" did not occur in transects #1 to #3. *Nereis vexillosa* was very sparse in transects #1 and #2 (Fig. 20). This may be attributed to the effect of the outflow of the fresh-water stream, to the low *Fucus* cover, or the low densities of *Mytilus edulis*. The exact determinant of abundance is unknown.

On the West Reef *Nereis vexillosa* occurred in 17 quadrats with an abundance of 3.65; greatest density was 18 individuals per quadrat. Here the species was found burrowing in the mud-sand substrate at a depth of 10 cm. This contrasts markedly with its beach habitat where it was always found among the byssal threads of *Mytilus edulis*. That this latter is its more common habitat is indicated by Ricketts and Calvin (1962) but MacGinitie (1935), while reporting it common in *Mytilus* beds also states it to be found under rocks. Spawning behavior and egg development have been described by Johnson (1943).

Sub Class Sedentaria

Nerine foliosa (Audouin and Milne Edwards, 1833)   •

<div align="right">

Tide level: East Reef: +.70 to +2.99

West Reef: +.49 to +1.54

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This species was found most commonly on the West Reef where it occurred in 19 quadrats with an abundance of 2.42 and with single quadrat range of one to five. On the East Reef, the only other area where it was observed, specimens were found in eight quadrats with an abundance of 2.0.

Nerine was found in the mud-sand substrate at a depth of 2 to 10 cm inhabiting a very extensive burrow. The latter was lined with a bright yellow-brown parchment-like substance which was presumably a secretion of the worm.

Until the present study, this polychaete was known from the Northeast Pacific by a single partial specimen (Berkeley, personal communication). It is therefore one of the more important zoogeographic records of this study. In addition, Berkeley reports that the size of the Kodiak specimens exceeded the maximum recorded size for this species which was about 16 cm (Berkeley and Berkeley, 1952). The maximum size of specimens taken at Three Saints Bay was near 30 cm.

The species *foliosa* has variously been allocated to the genera *Nerine*

and *Scolecolepis*. Berkeley (personal communication) prefers the use of *Nerine* on the basis of priority.

Cirratulus cirratus (Müller, 1776)   Tide level: West Reef: −.21 to +1.16

This common and conspicuous polychaete on the West Reef was found in 20 of the 50 quadrats investigated and had an abundance of 3.45 (Table 4), but was not observed elsewhere in the region. This worm was almost always found at the boulder—substrate interface with its tentacular filaments reaching out over the rock and the surface pavement of cobble. Little of the ecology of this species on the Pacific Coast seems to have been recorded outside of Berkeley and Berkeley (1952) who record it from among barnacles on pilings around the low tide mark.

Thelepus crispus Johnson, 1901   Tide level: West Reef: +.09, −.15

Two individuals of this species were recorded from two quadrats on the West Reef. Both occurrences were in quadrats with heavy cover of *Alaria*. They were found under large rocks which is the habitat recorded for them by Ricketts and Calvin (1962).

Abarenicola pacifica Healy and Wells, 1959
(Lugworm)   Tide level: East Reef: +2.08

This species was represented in the sampling by a single individual from a single quadrat on the East Reef. The substrate in the quadrat was mud-sand which is similar to that recorded by Healy and Wells (1959) in the Puget Sound area. However, there was not a noticeable presence of organic debris in this quadrat such as they have described as one of the requirements of the habitat.

Pectinaria sp.   Tide level: East Reef: −.90

A single unidentified species of this genus occurred in one quadrat from the *Zostera* zone of the East Reef in a mud-sand substrate. Although no more were seen in the sampling areas, exploratory dredging turned up more of this same species from the floor of the lagoon in 55 ft of water and also from the head of the bay in subtidal eelgrass beds.

This species remains unidentified due to the fact that the specimen was not saved after keying it to the genus in the field. Therefore it proved impossible to have it identified when the rest of the polychaetes were done by C. Berkeley.

Phylum Echiurida
Echiurus echiurus (Pallas, 1766)   Tide level: West Reef: −.15
                                                   East Reef: +.7 to +2.99

This echiuroid worm was found fairly commonly in its characteristic U-shaped tube beneath a surface layer of cobble at the mid-tidal levels of the East Reef. A single individual was recorded from the West Reef. The actual substrate in which it was found was mud-sand which is similar to what Gislen (1940) records for its substrate preference in Sweden. Gislen (1940) points out that this circumboreal species has also been recorded from substrates ranging from sand to soft black mud. The species was mid-tide in distribution in Three Saints Bay whereas Gislen (1940) records that on the European coasts it is usually found at the low tide level or subtidally.

Gislen (1940) reports a single figure for maximal density of 20 specimens in a square foot of bottom, but does not indicate whether this was a single sample occurrence or based on several samples. The highest single quadrat density in Three Saints Bay was seven, considerably below the density recorded by Gislen.

A complete discussion of the biology of the European subspecies of this worm is found in Gislen (1940).

The specimens of *Echiurus echiurus* taken in Three Saints Bay belong to the subspecies *alaskanus* described by Fisher (1946). Fisher (1946) records them from Alitak Bay on Kodiak Island in gravelly sand.

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Phylum Arthropoda

Class Crustacea

Sub Class Cirripedia

Order Thoracica

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Balanus cariosus (Pallas, 1788) Tide level: Beach Transects: −.7 to +7.3
East Reef: +.48 to +3.81
West Reef: +.32 to +1.65
Vertical Transects: +.4 to +6.1

This barnacle was another of the most ubiquitous animals found on the shore of Three Saints Bay and existed over the greatest tidal range. The only sampling area where it was not present was the tidal pool which was essentially a subtidal environment. Not only was this barnacle common on all shores, but it dominated middle levels of the Beach Transect and Vertical Transect areas as well as the middle and high levels of the East Reef and the entire West Reef (Figs. 14, 24, and 34).

As might be anticipated from such a widespread species, *B. cariosus* varied in general form in each of the sampling areas. On the beaches individuals were quite small (⅜ inch diameter) and very much reduced

in height (⅜ inch high). Were it not for its unique lack of a calcareous base plate, it would have been difficult to distinguish from the smaller *B. glandula* which was essentially absent from that area. The individuals were also of small size on the East Reef (⅜ × ⅜ inch). The largest individuals of this species were found on the West Reef (1½ to 2 inches high and 1 to 1½ inches diameter) where they exceeded by several times the size of individuals found elsewhere except those on the Vertical Transects. These approached the size of those on the West Reef (1 to 1¾ inches high and 1 to 1¼ inches diameter).

Variation in individual size was coincident with variation in abundance or density per quadrat of occurrence. On the East Reef the abundance was 198.0 (single quadrat density range nine to over 500) while on the West Reef with larger individuals it was only 89.63 (single quadrat density range 10 to 315). On the Beach Transects, where the smallest *B. cariosus* occurred, at the optimum levels densities exceeding 300 individuals per quadrat were common. In transect #5 densities of over 400/.25 m² were recorded several times. In no case, however, did individuals of *B. cariosus* cover more than 50% of the substrate of the quadrat. Hence higher densities were possible.

Densities exceeding 500/.25 m² were recorded from the Vertical Transects which, also, had individuals of large size. However, it was also here that the extreme of crowding occurred. In these areas of high density on the vertical surfaces individuals of *B. cariosus* completely covered the surface. Nowhere else was this condition even approached and hence the high density coincident with large individual size. On the West Reef almost no young *B. cariosus* were observed, whereas in the other sample areas abundant spat were observed.

This species was typically the lowest dwelling of the three barnacles found in Three Saints Bay when they occurred together (Fig. 34). However, for unknown reasons it dominated the entire barnacle zone of the East Reef even though *B. glandula* was present on this reef.

B. cariosus was commonly associated with *Fucus* to form a prominent band or zone in the intertidal region of Three Saints Bay. The barnacle was not, however, limited to *Fucus* (compare Figs. 14 and 22) or to existence of algal cover. Indeed, on the vertical faces *Fucus* was found attached to *B. cariosus*. An anomaly occurred on the East Reef where *B. cariosus* was either absent from the *Fucus* zone or present in low numbers compared to its abundance on the algae-free rocks from higher up in the intertidal. The reason for this is not understood.

With *B. glandula, B. cariosus* is one of the two most common barnacles of the Pacific coast (Ricketts and Calvin, 1962). Shelford (1930)

designates *B. cariosus* as one of the chief dominants of the intertidal of rocky coasts of all Pacific North America from Alaska to San Diego. Results of this study would tend to confirm that dominance for the Three Saints Bay area as well. A suggestion that this dominance may be transitory is given by Rice (1930) who points out that where *B. cariosus* and *B. glandula* occur together, an alternation of abundance is possible due to the fact that the life cycle of barnacles is only two years. The conditions occurring at spawning and at settling time may determine which species temporarily dominates.

Balanus glandula Darwin, 1854   Tide level: Vertical Transects: +5.1
to +8.7
East Reef: +.35 to +3.08
Beach Transects: +.3

This barnacle was common only on the Vertical Transects although it was also found in small numbers on the East Reef and as one isolated occurrence on the Beach Transects. On the vertical surfaces this species reached densities exceeding 500 individuals /.25 m² while on the East Reef it occurred in 17 quadrats with an abundance of 16.18 with a quadrat density varying from 2 to 34. The latter is a very low number per unit area when numbers of 141/dm² have been reported elsewhere for this species (Worley, 1930). Indeed, the whole barnacle zone of the East Reef was dominated by large numbers of *B. cariosus* such that the occurrence of *B. glandula* was sporadic.

On the Vertical Transects this barnacle occupied an area between *B. cariosus* and *C. dalli* and showed overlap with both (Fig. 39). It was a dominant in the range of +6.0 to +7.5 ft on these vertical faces.

Rice (1930) reports the highest densities of this species to occur in the first meter below average high tide while our results show close agreement in demonstrating greatest abundance only about a foot below MHW.

Chthamalus dalli Pilsbry, 1916   Tide level: Vertical Transects: +6.7 to
+8.9
West Reef: +1.43 to +1.55

The smallest of the barnacles encountered in Three Saints Bay, *Chthamalus dalli* existed in vast numbers within its tidal range. Therefore numbers were only estimated. The highest densities were on the vertical surfaces. Ricketts and Calvin (1962) state that a sample count of this barnacle in the San Juan Islands showed 72,000/m², and Worley (1930) reports densities of 714/dm². It is fully possible that densities approaching

half these figures, or more, existed on the Vertical Transects. On the West Reef, where it was found only in four quadrats immediately next to the shoreward edge of the reef, actual counts were made and the abundance was 263.25.

Chthamalus dalli also occurred on the East Reef, but failure to recognize it until it was too late to take samples precluded its inclusion in the study.

C. dalli occurred highest in the intertidal of the three barnacles found in Three Saints Bay. Its center of abundance on the verticals was usually above MHW (Fig. 39). It was often found associated with *B. glandula* in the lower half of its tidal range on the vertical faces, usually between 7.0 and 7.5 ft. Contrary to Ricketts and Calvin (1962) it was found associated with *B. cariosus* but only on the East Reef, for which no quantitative data were taken. It was never associated with *B. cariosus* on the vertical surfaces. Rice (1930) found *C. dalli* to reach highest densities about 1 m below average high tide whereas in Three Saints Bay the highest densites were found to be above MHW, at least on the exposed verticals.

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Sub Class Malacostraca

Order Isopoda

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Exosphaeroma oregonensis (Dana, 1852)
(Pill bug)   Tide level: Beach Transects: +.1 to +4.4
                                        East Reef: +.55 to +3.81
                                        West Reef: +.74 to +1.55

This isopod was a common inhabitant of the undersurface of stones, both large and small, on the Beach Transects, the East Reef, and the West Reef. On the Beach Transects this species marked the highest density in transect #1 where 30 individuals were recorded from a single quadrat (Fig. 19). In levels where it was common, however, the usual density was near 10. The species was most often found in quadrats with dense *Fucus cover* (compare Figs. 19 and 22).

On the East Reef this isopod was found most often under the large boulders in the upper part of the reef above the *Fucus* band. Menzies (1954) records a similar habitat for the species. On this reef *Exosphaeroma* was found the most abundantly of the three sampling places and was found in 27 quadrats with an abundance of 25.93 with a density range of 1 to 72 individuals per quadrat.

The species did not occur as frequently on the West Reef but was found in the same habitat as on the East Reef. It was recorded from 15 quadrats

on this reef with an abundance figure of 21.4. A high single quadrat density of 88 individuals was recorded once and one of 82. Six quadrats had six or less per quadrat.

It has been decided to retain the older name on advice of Barrett (personal communication) despite a revision of the genus *Exosphaeroma* by Menzies (1954) which places this species in the genus *Gnorimosphaeroma*. In addition, Menzies divided this species into two subspecies, one of which is found in fresh or brackish water and the other an inhabitant of marine areas. Riegal (1959) has suggested the elevation of the two subspecies to full species based on the lack of intergradation between the two groups. While the systematic position of their populations is not yet resolved, it appears that the form occurring in Three Saints Bay is the typically marine one.

Idothea wosnosenskii (Brandt, 1851)

Tide level: Beach Transects: +.4 to +4.3
West Reef: –.15 to +1.65
East Reef: +1.86 to +3.38

Although not usually found in aggregated numbers, this large isopod was a common constituent of the intertidal zone of Three Saints Bay. It was also observed in the subtidal waters of rocky reef channels and was brought up with detrital plant material from the bottom.

On the beach, *Idothea* was found in all five transects, but only in #4 did the density exceed 10 per quadrat and there only once (Fig. 20). *Idothea* was far less common on the East Reef where it occurred in only six quadrats with an abundance of 4.5 and with single quadrat range of 1 to 11. On the West Reef it was more numerous and was found in 31 quadrats with an abundance of 4.68 with single quadrat densities varying from 1 to 39.

Idothea was commonly found on the beach among *Fucus* fronds, whereas on the reefs it was found most frequently under the larger rocks. It was also commonly associated with *Mytilus* clumps. Menzies (1950) reports this isopod as most frequent on the alga *Ulva*, but it was not so observed in Three Saints Bay. Further, he records this species from the middle and upper intertidal zones. This agrees with our vertical distribution in the beaches and on the East Reef where many occurred from +1.0 to +4.0. On the West Reef, however, the species was recorded from low tide levels near MLLW.

On the West Reef, the highest densities (39) occurred in those quadrats immediately adjacent to the shoreward edge of the reef where it met the more unconsolidated gravel of the upper beach.

Mesodotea sp.   Tide level: Beach Transects: +.5 to +2.3

This uncommon isopod was represented in the sampling areas by six individuals from five quadrats all collected on the Beach Transects usually associated with the more common *Idothea wosnosenskii* or *Exosphaeroma oregonensis*. No species of this genus are mentioned by Ricketts and Calvin (1962) in their discussion of the Pacific Coast intertidal invertebrates.

This species remains unidentified because Barrett (personal communication) could not give a positive identification of it.

Order Decapoda

Pagurus hirsutiusculus (Dana, 1851)
(Hermit crab)   Tide level: Beach Transects: −.3 to +4.3
                                      West Reef: −.32 to +1.65
                                      East Reef: −.76 to +3.38
                                      Vertical Transects: −1.3 to +.2

This ubiquitous hermit crab was found in all sampling areas except from within the tidal pool. However, it is recorded by but a single individual on the Vertical Transects.

On the Beach Transects this species reached its highest density between +1.0 and +2.0 ft in transects #3, #4 and #5 (Fig. 17). The highest single quadrat densities were 57 and 56, both from quadrats in transect #5. The species was most commonly observed under *Fucus* fronds and the high densities of *Pagurus* in the transects coincide with the high *Fucus* density (Fig. 26). On this beach area, and indeed wherever observed in the bay, this hermit crab was found inhabiting shells of *Littorina sitkana*. Since these mollusks do not grow larger than 1 cm, no large *P. hirsutiusculus* were ever seen; it is not known whether or not maturity was reached at the small sizes observed or whether the intertidal zone was populated from other areas or deeper water.

On the West Reef *P. hirsutiusculus* was found in 29 quadrats with an abundance of 4.93; the highest quadrat density recorded was 27. This hermit crab was considerably more prevalent where sampled on the East Reef where it occurred in 33 quadrats with an abundance of 14.85 with a single quadrat density range from 1 to 53. On both reefs the species was found underneath loose surface rocks, the habitat recorded for this species by Makarov (1938). However, it was also commonly recorded in Three Saints Bay from sandy areas.

Cancer oregonensis (Dana, 1852)   Tide level: West Reef: +.3 to +.55

This small, rounded member of a genus which includes the edible crab (*C. magister*) was found only on the West Reef where it occurred in five quadrats with an abundance of 1.4. Ricketts and Calvin (1962) state that it is restricted almost totally to an under-rock type of habitat. It was in just such a habitat we found it on the West Reef.

Cancer magister (Dana, 1852)   Tide level: Beach Transects: +1.0
(Dungeness crab)

Although this is a common species in Alaskan waters and is caught commercially, its only appearance in the sampling areas was one individual obtained in Beach Transect #3. The species is a subtidal inhabitant and only occasionally strays into the intertidal area. It frequented eelgrass beds in Three Saints Bay where it was commonly caught in less than 6 ft of water in nets and traps set for fish.

Pugettia gracilis Dana, 1851   Tide level: East Reef: –1.4 to +1.79
(Graceful kelp crab)   West Reef: –.32 to +1.16

This spider crab, found on the West and East Reefs, was particularly abundant on the former where it occurred in 27 quadrats with an abundance of 3.27 with quadrat densities ranging from 1 to 10; on the East Reef it occurred in seven quadrats with an abundance of 1.43 and with quadrat densities of one to four. On the West Reef a white color phase was particularly prevalent. Its more normal color is some variation of red which adapts it well to a habitat in coralline algae, a habitat where it was also observed. The species was found under rocks or on the large kelp on the East and West Reefs. It also occurred in deeper water and was often brought up in traps set for fish in 20–30 ft of water. The deeper individuals were usually larger than the intertidal forms and of a darker red color.

Telmessus cheiragonus (Tilesius, 1815)
(Kelp crab)   Tide level: Beach Transects: +2.0
                                                West Reef: –.32 to +1.35
                                                East Reef: –.88, +.06

This cancroid crab was not uncommon in Three Saints Bay having been observed commonly in most environments with a dense kelp cover. However, it did not turn up frequently in the sampling areas. Only one individual was recorded from Beach Transect #1 where it was found in *Fucus* cover. On the East Reef two individuals were recorded one each from the *Zostera* zone and the *Fucus* zone. Neither of these quadrats had any other surface fauna present. The greatest number of *Telmessus* was

found on the West Reef where they occurred in five quadrats with an abundance of 1.4. On this reef the crabs were usually found under the protective cover of *Alaria*. It was also taken from under rocks and in dredge hauls from 13 ft on sand-mud bottoms.

Phylum Mollusca
Class Amiphineura
Order Polyplacophora

Katharina tunicata (Wood, 1815)
(Black chiton)   Tide level: Vertical Transects: −.1 to +6.2
West Reef: −.32 to +1.32

This large black chiton was the most common chiton in Three Saints Bay, appearing in the sampling areas on the West Reef and on the vertical surfaces. In the latter, abundance was low, usually 10 or less, but on transect #3 one quadrat had 40 individuals (Fig. 36). *Katharina* was very common on the West Reef where it was found in 36 of the quadrats with an abundance of 4.06; highest single quadrat density was 14.

The habitat of *Katharina* on the vertical faces was in the crevices between individuals of *Balanus cariosus* and inside the dead shells. On the West Reef the species was always found up on the larger rocks, usually on the tops or sides and often in the crevices among *Balanus cariosus*. However, it was also often found on the open rock surface (Fig. 49) whereas most chitons tend to avoid light. This phenomenon of remaining exposed on the top of rocks has been reported for *Katharina* by Giese, Tucker, and Boolootian (1959) who also report on the reproductive cycle of this species in Monterey Bay, California.

Mopalia ciliata (Sowerby, 1840)   Tide level: West Reef: −.21 to +1.65
(Hairy mopalia)

This species was common on the West Reef (Table 4) where it occurred in 19 of the 50 quadrats with an abundance of 2.37 and with a quadrat range of one to five individuals. Here it occurred with the more abundant *Katharina*, invariably on the sides of very large rocks, usually partly hidden by algae or in the crevices between barnacles. The species was further recorded from the boulder bottoms of reef channels.

Tonicella lineata (Wood, 1815)   Tide level: Vertical Transects: −2.3 to
(Lined chiton)   −1.3
East Reef: −.88

The lined chiton was recorded from four of the seven Vertical Transects

(five individuals) and a single time on the East Reef from the *Zostera* zone where the single individual was found on a rock surrounded by soft substrate. It was also found at the upper ends of well washed tidal channels and on the outer edge of open rocky reefs. Ricketts and Calvin (1962) state this species to be the most abundant shore chiton in Southeast Alaska, but this was certainly not true in Three Saints Bay where *Katharina tunicata* was by far the most abundant.

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Class Gastropoda
Order Archaeogastropoda

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Acmaea pelta Eschscholtz, 1833
(Shield limpet)   Tide level: Beach Transects: +.1 to +5.3
                                              Vertical Transects: +3.8 to +8.3
                                              East Reef: +.55 to +3.81

In areas of maximum abundance on the Beach Transects and East Reef this common limpet showed a complementary distribution to that of *A. scutum* which was restricted to the West Reef and tidal pool. *A. pelta* was also found on the Vertical Transects, where it occurred in a single quadrat in each of three transects (Fig. 35). The highest number of individuals per quadrat was six.

A. pelta was present in all five Beach Transects in varying abundance (Fig. 18). The highest single quadrat densities (420, 170) occurred in transects #4 and #5 in a unique subarea of these two transects which was devoid of algae and dominated by large numbers of *Mytilus edulis* forming a reef.

On the East Reef *A. pelta* was very abundant; the species was found in 30 quadrats with an abundance of 160.17 and a quadrat density range of 42 to 562.

The preferred habitat of this species on the Beach Transects was either on the shells of *Mytilus edulis* or the fronds of *Fucus distichus*. However, on the East Reef this limpet was found primarily on the lower sides of the large rocks of the reef and was not often found associated with *Fucus distichus*.

Test (1945) states that this species is the most eurytopic of all the ones which she investigated in California and is found in all major intertidal zones from high to low tide. Shotwell (1950) records the upper limit of this species as +6.0 ft (near MHW) in Oregon, somewhat less than the upper limit in Three Saints Bay on the Vertical Transects (8.3 ft) (MHHW). Ricketts and Calvin (1962) state that north of Northern California this species occurs high up with *A. digitalis*. This relationship

was not found in the seven vertical transects in Three Saints Bay, although both species did occur in contiguous quadrats (Fig. 35).

Acmaea scutum Eschscholtz, 1833
(Pacific plate limpet)   Tide level: Beach Transects: −.1, +.1, +.7
                                                                 to .8
                                             Vertical Transects: +1.2 to
                                                                     +7.5
                                             East Reef: +3.38
                                             West Reef: −.32 to +1.65
                                             Tide Pool

Another of the more ubiquitous of the shore invertebrates, this limpet was the only invertebrate which was found in all five sampling areas. It was taken once on the East Reef and only three individuals were found on the Beach Transects.

The greatest numbers of this species were recorded in the tide pool where it was present in every quadrat and had an abundance of 17.46 with quadrat densities ranging from 4 to 38. On the West Reef this limpet was taken in 40 quadrats with an abundance of 8.07. The highest single quadrat density on the West Reef was 30. Whereas very small *Acmaea* were abundant on the verticals and may have been the young of *A. scutum*, large adult or subadult forms were not as common as in the tide pool or on the West Reef. The distribution on the vertical surfaces was also patchy with the species being absent from one transect and present in only one quadrat in two other transects (Fig. 35). Where present on the Vertical Transects, *A. scutum* usually had a density of around 10 individuals per quadrat of occurrence; greatest density recorded from these transects was 18.

The habitat of this species on the West Reef included principally the sides of the large rocks where it was commonly found in or near clumps of *Fucus, Halosaccion, Spongomorpha,* or *Ulva.* In the tide pool it occurred in the open on the tops of small cobbles which formed the floor of the pool. On the vertical faces it was common among *Balanus cariosus* and also in any rock crevices. The species was observed outside the sample areas on many boulder and bedrock reefs.

Shotwell (1950) states that the tidal range for this species on the Oregon coast is from below MLLW up to +6.0 or near MHW. This is in good accord with our data from Three Saints Bay. Test (1945) also records it from both high and low intertidal zones and states it is most characteristic of the intermediate zone; accurate tidal levels are not in-

cluded, however. She further concurs with our observations that the species is restricted to rocky substrates.

Acmaea digitalis Eschscholtz, 1833   Tide level: Vertical Transects:
(Fingered limpet)   +6.6 to +10.2

In Three Saints Bay, this species was found only on the vertical surfaces, where it was consistently present in six of the seven transects. Among transects, numbers of individuals varied quite widely (Fig. 35), correlated with the variable presence of rock crevices in each transect. Test (1945) states that on the California coast, this species seeks shelter in crevices and is scarce where such crevices are absent or infrequent. In the Kodiak area, this species occurred the highest in the intertidal zone of any of the invertebrates investigated. Its abundance centered around MHW and extended up into the black lichen band above 10.0 ft (Fig. 39). This intertidal distribution is appreciably higher than that for this same species on the Oregon Coast (Shotwell, 1950). Shotwell reports the lower limit at +3.5 ft (near MTL) and the upper limit at +6.0 ft or lowest higher high water. In Three Saints Bay the species was never found as low as MTL.

Acmaea mitra Eschscholtz, 1833
(Miter limpet)   Tide level: Vertical Transects: –1.4 to +.4

This species was represented by a single individual in Vertical Transect #2 and by six individuals in five quadrats in the tide pool. We also observed it in low, open channels and on rocky reefs in pools which were almost never exposed. The upper limit is lower than that given for *A. mitra* by Shotwell (1950) who places the upper limit at +2.0 ft on the Oregon coast where tide levels are less than 1 ft different than levels in Three Saints Bay. Most individuals of the species occurred in the tide pool or were observed submerged in water indicating a subtidal habitat or at best low intertidal. This low level habitat is supported by Test (1945) who also indicated that the presence of the species is determined, on California shores, by the presence of *Microcladia* sp. or other microscopic algae for food.

Order Mesogastropoda

Littorina sitkana Philippi, 1846   Tide level: Vertical Transects: +4.5 to
(Sitka periwinkle)   +6.2
                                Beach Transects: –.2 to
                                     +6.85
                        East Reef: +1.15 to +3.81

This was the more common of the two species of *Littorina* and was a conspicuous inhabitant of all rock and cobble beaches which were observed in the Three Saints Bay area. It was not found on the West Reef probably because the reef did not extend high enough into the intertidal.

L. sitkana was most abundant on the Beach Transects, particularly in transects #3, #4, and #5. In these three transects single quadrat densities exceeding 200 were common and in transect #5 several quadrats had densities of over 500 (Fig. 15). The highest single quadrat density was 650 recorded also from transect #5. Transects #3, #4, and #5 also showed a peculiar bimodal distribution of high densities. *L. sitkana* had very high densities just below +2.0 and again at +4.0–4.5. The high density at +2.0 occurred near the center of the *Fucus* cover (Fig. 22) while the high density at 4.0–4.5 coincided with the upper edge of the *Fucus* zone.

On the East Reef *L. sitkana* was not found in the *Fucus* zone but was limited to the upper algae-free area of the reef. Within this area this snail occurred in 25 quadrats with an abundance of 106.44; greatest quadrat density was 303 and lowest was 12.

The habitat of this mollusk on the Beach Transects was most commonly on the fronds of *Fucus distichus* or, where that alga was absent, at the base of or underneath the cobble pieces making up the substrate. On the East Reef this species was found on the larger rocks, but more commonly at the base of the larger rocks.

Littorina scutulata Gould, 1849   Tide level: Beach Transects: −.2 to
(Checkered periwinkle)   +6.9
East Reef: +.9 to +3.81

Littorina scutulata is the smaller of the two species of the genus found in Three Saints Bay, but occurred in the same localities as *L. sitkana*. Whereas *L. sitkana* reached its highest abundance on the beaches, *L. scutulata* was most abundant on the East Reef.

On the East Reef this species occurred in 27 quadrats with an abundance of 104.51 or very nearly the same as that recorded for *L. sitkana* (106.44); the greatest quadrat density was 344. Numbers of individuals per quadrat on the beach transects were far less, averaging less than 10, with highest single quadrat density at 30. These zones of highest density occurred quite sharply between +.5 and 1.0 tide levels and just below the areas with high densities of *L. sitkana*.

This species was found at the base of rocks and cobbles of all sizes on both the Beach Transects and the East Reef. On the East Reef it was also living among the barnacles on the larger rocks.

North (1954) states that this species prefers a zone 2 or 3 ft on either side of high water, but our results showed that 2 or 3 ft below MHW was the upper limit for this mollusk in Three Saints Bay. MacGinitie (1935) also records it as inhabiting areas well above low tide. North (1954), MacGinitie (1935), and Ricketts and Calvin (1962) all concur in our observations that the species is confined to a rocky substrate.

Margarites pupulla Gould, 1849   Tide level: subtidal in pool
(Puppet margarite)

This gastropod was found in the tidal pool, where it occurred quite commonly with an abundance of 2.42 with a density range of one to five (Table 7). The species was also observed in well agitated rocky reef channels and in other tide pools. It thus appears to be another example of a normally subtidal animal which penetrates the intertidal only where permanent tide pools appear.

Natica clausa Broderip and Sowerby, 1829
(Arctic natica)   Tide level: West Reef: +.5, +.3, +.1, +.4

This species was a rare constituent on the West Reef where four individuals were found in four quadrats. In all cases the animal was discovered about two-thirds buried in the mud-sand substrate below the surface pavement of cobble. This is an arctic species but has been recorded as far south as California (Abbott, 1954) where it occurs in deep water.

Order Neogastropoda

Fusitriton oregonensis (Redfield, 1848)   Tide level: subtidal, in pool
(Oregon triton)

This was the largest intertidal gastropod observed. The six individuals found in the tidal pool were aggregated near or on the very largest rocks in the pool. Their occurrence in the tide pool and absence from any other observed or sampled intertidal area on Kodiak, indicates the species to be primarily a subtidal inhabitant. Indeed, Philpott (1925) reports the species to be very common in Puget Sound, but usually in dredgings to a depth of 110 m.

Searlesia dira (Reeve, 1846)   Tide level: Vertical Transects: −1.3 to
(Dire whelk)   +2.8
                subtidal in pool

A few individuals of this species were found in Vertical Transect #7

(six individuals) and in the tide pool (seven individuals) and it was observed in small numbers on rocky surfaces of channels in rocky reefs. While this species is said to be the commonest littoral snail northward from British Columbia, according to Ricketts and Calvin (1962), on Kodiak it occurred as a low intertidal to subtidal animal in much lesser abundance.

Thais lima Martyn, 1784   Tide level: East Reef: +1.15 to +2.99
(File dogwinkle)

This gastropod was found only on the East Reef where it was found in 15 quadrats with an abundance of 5.73 (Table 2); and a single quadrat range of 1 to 30. On the East Reef the species was found in the upper barnacle zone where they were observed feeding on *Balanus cariosus*. The species was also observed on the boulder reef adjacent to the East Reef sampling area where it was found on the gravel and cobble substrate; here the gastropod was observed feeding on *Mytilus edulis*.

Thais lamellosa (Gmelin, 1792)   Tide level: Vertical Transects: +1.0 to
(Frilled dogwinkle)   3.1
                                                West Reef: –.15 to +1.65

This predatory gastropod was found once in Vertical Transect #6, but was a fairly common species on the West Reef where it was found in 18 quadrats and had an abundance of 1.78 (Table 2). There the snail was usually found on the side or top of the largest boulders near or among the *Balanus cariosus* upon which it was observed to be feeding. Ricketts and Calvin (1962) consider this species an animal of quiet waters, yet in Three Saints Bay it was only found in the more exposed areas.

Buccinum baeri Middendorf, 1848   Tide level: East Reef: +1.93, +2.08
(Baer's buccinum)   West Reef: +.09 to 1.35
                                                 Tide Pool

This gastropod was quite uncommon on the East Reef (four individuals) and in the tidal pool (two individuals) but was more common on the West Reef where it occurred in nine quadrats with an abundance of 2.11 and with a quadrat range of one to six. In both reef localities the animal was always found underneath large rocks which were about half buried in the underlying mud-sand substrate. In the tidal pool the species existed on the open cobble. Observations from other beaches in the Three Saints Bay area indicate that the species was often to be found aggregated under rocks in the lower intertidal zone.

A number of species of *Buccinum* are reported in the literature for the

North Pacific based on variations in shell color, size, and sculpture, but Talmadge (personal communication) suggests that these are merely local and geographical variations of a single species the earliest name for which is *baeri*.

<div align="center">

Class Pelecypoda
Sub Class Lamellibranchia
Order Filibranchia

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Mytilus edulis Linné, 1758   Tide level: Beach Transects: −.1 to +4.9
(Edible mussel)   Vertical Transects: +2.1 to +7.7
                                           East Reef: +.7 to +3. 81
                                           West Reef: +.10

This pelecypod was one of the most characteristic invertebrates of the intertidal rocky and cobble areas in Three Saints Bay; the black band formed by the clusters of individuals was a conspicuous feature of the tidal zone. *Mytilus* was absent from the subtidal environment of the tidal pool, but, as has been noted, surrounded the pool. This species was virtually absent from the West Reef (two individuals) which was too low for its optimal development.

The greatest abundance of *Mytilus* occurred on the Vertical Transects where more than 500 individuals were found in several quadrats (Fig. 36). However, in all cases the size of the individuals was smaller than those on the Beach Transects. This contrasts markedly with Mossop (1921) who reports the largest individuals from rocky edges and reefs. On the beaches the greatest abundance occurred in transects #3, #4, and #5 (Fig. 16); the highest density recorded was 395, but single quadrat densities exceeding 300 occurred several times (Fig. 16). The level of greatest abundance on the beaches was centered around +2.0 in the area of heavy *Fucus* cover (compare Figs. 16 and 22). A secondary center of abundance in transect #5 occurred near +0.5 which corresponded to the unique area in this transect where *Mytilus* was found clustered in a reef devoid of algae. This beach was of cobble and gravel as noted previously and thus it is interesting to note that Mossop (1921) states that no *Mytilus* were found on sloping gravel shores in her area.

Although on the Beach Transects *Mytilus* reached its greatest abundance under heavy *Fucus* cover, on the East Reef the species was very uncommon in the *Fucus* zone and reached its highest abundance above that zone in the *Balanus*-boulder area. On this reef *Mytilus* occurred in 30 quadrats with an abundance of 60.33 with a quadrat range of 1 to 222.

The habitat of this species varied on the different sampling areas. On

the beach transects the *Mytilus* were found in small clumps half buried in the cobble or gravel substrate and with their byssal threads anchored to each other and to the larger cobble pieces. On the vertical faces the species was found crowded into cracks and crevices in the rocks and in the dead shells of *Balanus cariosus*. The habitat on the East Reef was similar to that encountered on the Beach Transects except that they usually occurred as individuals in the substrate attached to the larger pieces of rock.

Mossop (1921) records the range of this species in the intertidal as from low water up to +4.0 ft on sloping shores; distribution in Three Saints Bay agrees. Yocum and Edge (1929), however, record the tidal range from mid-tide level to above the high tide mark. This range coincides well with our results from the Vertical Transects (Fig. 39) but not with the distribution on rocky or cobbly sloping shores.

Pododesmus macroschisma (Deshayes, 1839)
(Rock oyster)   Tide level: Vertical Transects: −1.0 to +.6

Two individuals of this rock oyster were taken, one each from Vertical Transects #3 and #4. This low level species was not observed elsewhere. It is considered a low-tide species by Ricketts and Calvin (1962) and by Abbott (1954) who also considers it to be a very common form on the Pacific coast. It was not common in Three Saints Bay.

Order Eulamellibranchia

Clinocardium nuttalli (Conrad, 1837)   Tide level: Beach Transects:
(Nuttall's cockle)   −1.4 to +.45
                                                                          East Reef: +1.79

This cockle, except for the single occurrence on the East Reef, was found only at the low tide level in the eelgrass (*Zostera*) beds on the Beach Transects. Even here it was not abundant (Fig. 21); the highest density was four individuals per ⅟₁₆ m² quadrat. The single occurrence on the East Reef is of interest because it is from considerably higher in the intertidal than the specimens found on the Beach Transects. Secondly, the specimen was not taken in the *Zostera* beds of the reef, while on the beach area this was the common habitat of the species. The absence of this cockle from the *Zostera* zone of the East Reef is noteworthy in demonstrating the differences between two seemingly uniform areas. *Pycnopodia helianthoides* shows a similar distribution.

Clinocardium nuttalli is an active animal and only a very shallow burrower so that the animal lies near the surface. On very low tides in Three

Saints Bay these cockles were commonly found resting on top of the *Zostera* entirely exposed. According to MacGinitie (1935) this exposure results when the animal migrating over the flats is caught by the receding tide.

Clinocardium was taken in a mud-silt or mud-sand substrate. Fraser (1931) reports the substrate preference as uniform sand which is not very coarse. He further states that where the cockles occur in beaches of coarse gravel they are confined to small patches of uniform sand or gravel. Smith and Gordon (1948) report *Clinocardium* from mud in Elkhorn Slough in California.

Macoma nasuta (Conrad, 1837)   Tide level: Beach Transects: –.8
(Bent-nose macoma)

This clam was recorded a single time in Beach Transect #5 where it was found 5 cm down in the mud-sand substrate. Abbott (1954) records this species as one of the most common species of pelecypod on the Pacific coast in mud areas.

Macoma balthica Linné, 1758   Tide level: Beach Transects: –.6 to +.8
(Balthic macoma)   East Reef: +.7 to +2.08

This pelecypod was a frequent inhabitant of the mud-sand substrate of the Beach Transects where it was found in the low intertidal in the *Zostera* zone and reached densities of 12 per 1/16 m². On the East Reef it was found at mid-tide levels, not in the *Zostera* zone. Although occurring in but three quadrats on the East Reef, it had an abundance of 4.67. It is a shallow burrower in soft substrates and was never found exposed.

Mya arenaria Linné, 1758   Tide level: Beach Transects: –.7 to +.5
(Soft shell clam)   East Reef: –.9 to +2.08

This clam is not native, but was imported from Europe and is now well established on the Pacific Coast. The species was recorded from low levels of Beach Transects #1 and #3 where six individuals were found buried in the soft mud-silt substrate (Fig. 28). It was also recorded on the East Reef from four quadrats representing all three major bands of zonation (*Zostera, Fucus,* barnacle). Although the precise habitat cannot be assessed from these few occurrences, the species appears to be more broadly distributed ecologically in the north. Ricketts and Calvin (1962) report it as a common inhabitant of mud flats, often in estuaries. It has a remarkable capacity to survive under anaerobic conditions.

Venerupis (Protothaca) staminea (Conrad, 1837)
(Pacific littleneck clam)   Tide level: Beach Transects: –.8
                                              East Reef: –.9 to +2.99
                                              West Reef: –.32 to +1.54

This small edible clam was abundant on both the West and East Reefs, but was represented by only a single individual on the Beach Transects. On the East Reef this species was found in 15 quadrats with an abundance of 16.6 and with a density range per quadrat of 1 to 61. On the West Reef it occurred in 43 quadrats with an abundance of 11.56 with a density range per quadrat of 1 to 51 individuals.

This clam was usually found within 5 cm of the cobble surface embedded in mud-sand or gravel immediately adjacent to large rocks or cobble pieces (Fig. 49). It was not encountered in areas free from surface rocks and the subsurface substrate was often mixed with shell debris.

MacGinitie (1935) reports it from among rocks in Elkhorn Slough but Fraser and Smith (1928b) report the best beaches to be of coarse sand or fine gravel while Ricketts and Calvin (1962) state the species to prefer clayey gravel or gravel mixed with sand or mud. Smith and Gordon (1948) state it is found in sand and gravel down as far as 25 cm and in borer holes in Monterey Bay.

Saxicava sp.   Tide level: West Reef: –.15 to +1.32
(Boring clam)   East Reef: +1.79 and +2.08

This genus of boring clams was found occasionally on both the West and East Reefs. It was, however, more abundant than present figures would indicate. Due to its small size and boring habit, many were overlooked. The only other recorded data concerning this pelecypod is that in the West Reef it was found in the encrusting sponge and boring into rock.

There are two species of *Saxicava* on the Pacific Coast according to LaRocque (1953), *S. arctica* and *S. pholadis*. The specimens which we found remain unidentified because on the basis of material available at the time of this study it was not possible to distinguish between the two.

Saxidomus giganteus Deshayes, 1839
(Smooth Washington clam)   Tide level: West Reef: –.32 to +1.32
                                            East Reef: –1.40 to +2.56

Specimens of this clam were taken on the West and East Reefs. The species occurred in eight quadrats on the East Reef with an abundance

of 2.0 and maximum density of 10 per quadrat. On the West Reef it was more common and occurred in 27 quadrats with an abundance of 5.07 and up to 20 individuals per quadrat. This species was strongly associated with *Venerupis staminea* on both reefs and density measures for both species were closely correlated. This close correlation of these two clams corroborates the work of Fraser and Smith (1928a) in British Columbia. Specimens of *S. giganteus* from the east reef were all small (less than 2 inches) whereas the West Reef sampling produced some very large individuals (in excess of 3 inches).

Saxidomus was always found deeper in the substrate than *V. staminae* and was not restricted to the area around the bases of rocks. The deeper substrate from which they came often had a higher shell fraction. Smith and Gordon (1948) report the close relative *S. nuttalli* from sand and small rocks in Monterey Bay.

Although live *S. giganteus* were not observed elsewhere in the Three Saints Bay area, the dead shells were very common on most beaches of the area.

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Phylum Echinodermata
Class Asteroidea
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Dermasterias imbricata (Grube, 1857)   Tide level: East Reef: −1.32, −.88 (Leather star)

This species of large starfish, second only to *Pycnopodia helianthoides* in size, was rare, two specimens being taken on the East Reef. This species appears to be another dweller of the *Zostera* beds as both specimens from the East Reef were taken at the low levels in *Zostera*. Verrill (1914) records its habitat as at or just below low tide and states it to have been recorded only from shallow water areas.

Evasterias troschelli (Stimpson, 1862)   Tide level: Subtidal in pool
Vertical Transects:
−.9 to +1.5

Although a fairly common starfish over most of its range this asteroid occurred only once in the tidal pool sampled and once each in Vertical Transects #3, #4, and #6. On the Vertical Transects the three individuals which occurred were all found near the MLLW mark. Additional observations outside the sampling areas indicated that the species was common on the rocks in the *Alaria-Laminaria* levels of the vertical faces-talus slope area and was even more abundant on the rocks just below the reaches of the lowest tides. The species was not observed on gravel or soft bottomed shores.

Henricia leviuscula (Stimpson, 1857)   Tide level: Vertical Transects:
(Blood star)   −1.9 to +2.8

The blood red color of this starfish makes it difficult to miss in the inter-
tidal zone. This species was encountered only on Vertical Transects #5
and #6 with a total of five individuals. They were usually found under
algae in these transects. This species was also observed occasionally on
the rocky reefs at Cape Liakik.

Leptasterias sp.   Tide level: Vertical Transects: +3.9 to +.70
                                                    West Reef: −.21 to +1.65

An unidentified species of this genus was common in the *Fucus* area
of the Vertical Transects. The species was also found on the West Reef
where it occurred in 37 quadrats with an abundance of 3.41 and a single
quadrat density range from 1 to 11.

On the West Reef the species was found on the sides of the large rocks
and also underneath the large rocks.

This genus includes 11 species in the North Pacific according to Verrill
(1914) all of which are quite variable and difficult to distinguish. This
variability coupled with the lack of comparative material made allocation
to species impossible by the author.

Pycnopodia helianthoides (Brandt, 1835) Tide level: East Reef: −1.4 to
(Sunflower star)   −.56
                                                                Vertical Transects:
                                                                −2.4 to −.4

Individuals of this species are among the largest starfish in the world
(Verrill 1914), but only small individuals were found in the intertidal
sampling areas. Although a single individual of this species was recorded
from a Vertical Transect, the animal was primarily an inhabitant of the
eelgrass areas of Three Saints Bay. On the East Reef individuals were
found only in the *Zostera* bed at the seaward edge of the sample grid
where the species was taken in 10 quadrats and had an abundance of 2.0.

The species was also very abundant in the subtidal parts of the *Zostera*
beds seaward of the sample area on the East Reef and the larger individ-
uals were found there. Although rather extensive *Zostera* beds occurred
below the Beach Transects in the protected lagoon, no *Pycnopodia* were
ever observed there. Ricketts and Calvin (1962) record this species from
low tide horizons on rocky surfaces. Although found there in Three Saints
Bay, it was far more common in the *Zostera* beds, particularly those on
the East side of the bay. *Pycnopodia* was also found under rocks and in

cracks in large boulders on the beach adjoining the East Reef sampling area.

Class Ophiuroidea

Ophiopholis aculeata (Lyman, 1860)   Tide level: Vertical Transects:
+.7 to +1.9

This brittlestar occurred only once in all the sampling in Vertical Transect #6 where a single individual was collected at the +1.0 tide level. The same species was observed to be common under rocks on boulder beaches facing Sitkalidak Straits south of the camp. This is a species with an exceptionally wide geographic range (Ricketts and Calvin, 1962) in the north temperate zone.

Class Echinoidea

Strongylocentrotus drobachiensis (Müller, 1776)
(Green sea urchin)   Tide level: Vertical Transects: –2.3 to –.5
East Reef: –.90
West Reef: –.32 to +1.45
Tide pool

This was the only sea urchin which occurred in the sampling areas of Three Saints Bay. Although the prevalence of numerous tests in *the high tide drift line along the cobble beaches all around the bay indicated this animal was of common occurrence, it was sampled in numbers only on the West Reef and in the tidal pool. One individual was recorded from the East Reef and one from the vertical face. Additional observations of the presence of this organism are confined to subtidal situations. It was observed covering the bottom of small, shallow algae free tide pools at Cape Liakik and was abundant on the subtidal cobble reef next to the West Reef. The animal appears to be essentially a subtidal form.

The greatest numbers of *S. drobachiensis* were encountered in the tidal pool where it occurred in every quadrat and had an abundance of 30.46 (Table 7) with single quadrat densities varying from 1 to 143. On the West Reef the species was taken in 27 quadrats with an abundance of 3.89; highest single quadrat density was 25.

On the West Reef this urchin was always found under the protective cover of *Alaria* kelp or else in crevices between or next to the larger rocks (Fig. 49). In addition it often was found slightly buried in the mud-sand substrate. The specimens taken on the West Reef were generally of a larger size than those taken in the tide pool, averaging 1.5–2.0 inches in diameter in the pool and 2.0–2.5 inches on the West Reef.

Class Holothuroidea

Cucumaria curata Cowles, 1907   Tide level: West Reef: −.21 to +1.65

A common inhabitant of the West Reef, this holothurian was not found in any of the other sampling areas. On the West Reef this species occurred in 33 of the 50 quadrats with 149 individuals for an abundance of 4.51 (Table 4). The single quadrat density varied from 1 to 17. On the West Reef the species was found primarily at the interface between the large boulders and the reef base substrate often partially buried in the mud-sand substrate below the rocks (Fig. 49). Filice (1950) has reported them from the seaward edge of *Mytilus californianus* beds in California while Ricketts and Calvin (1962) report that they are found among foliose coralline algae in Monterey Bay. Occurrence of this species in Alaska seems not to have been reported previously. In fact, Ricketts and Calvin (1962) report that it is not known outside of Monterey Bay.

Stichopus californicus (Stimpson, 1857)   Tide level: Subtidal in pool (California sea slug)

This large holothurian was found only in the tide pool among the areas sampled, where it was found in six quadrats with an abundance of 1.33 We found the species also to be quite common in a restricted area just offshore of the tide pool sampled. Here they occurred commonly in about 10 to 15 feet of water. The substrate in this case was sand, despite Ricketts and Calvin (1962) and Courtney (1927), who report that this is a rock dwelling species. Those occurring in the tide pool were the only ones encountered living on rocky substrate. These were also much smaller than individuals collected by dredge from the subtidal sand areas. Courtney (1927) reports that the species is found from the shoreline to depths of about 80 m and that it spawns in shallow water along rocky shores.

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