SOME ASPECTS OF THE INTERTIDAL ECOLOGY OF MARINE ORGANISMS ON VANCOUVER ISLAND BETWEEN VICTORIA AND PORT RENFREW

by

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ABSTRACT

The intertidal ecology of approximately seventy miles of coast, along the southwest shores of Vancouver Island from Port Renfrew to Victoria, was studied during the period from May 1957 until July 1958. This coast is a transition area between the open ocean at Port Renfrew and more sheltered waters east of Victoria, which are much freshened by the influx of the Fraser River.

Attention was concentrated on the more conspicuous forms, mostly on those algae of the order Laminariales which do not occur in the more sheltered localities. Observations were made at twenty-six stations spaced along this coast. In collecting specimens, particular attention was given to those algae where identification is difficult or doubtful. These collections were made to complement the direct observations on those entities which could readily be identified in the field. The presence or absence of the entities studied was noted at each station. The distribution of some of the very conspicuous forms was determined along most of the coast between the stations. Any distinct upper or lower limits in the intertidal organisms at a station were recorded. Limited observations were made at fourteen other points, where these were needed to elucidate questions raised by the earlier data. Conditions of the physical environment, particularly of salinity, sea temperature, and tidal rhythms, were monitored at each

of the stations wherever possible.

Most of the twenty-six stations were occupied at least once each summer. Some of the more centrally located ones were visited at various times throughout the year in order to observe seasonal changes in the organisms and environmental conditions studied. When two or more measurements of the same upper or lower limit of an organism were made at different times, these replicates were used to calculate error in the technique used in finding the levels of these limits.

The open coast forms penetrate varying distances along the coast into Juan de Fuca Strait in an easterly direction. Evidence is presented that different factors in the physical environment may be limiting for the geographical distribution of different organisms.

Thirty-six vertical limits of the organisms studied are discussed. These are all the limits which were measured at nine or more stations throughout the area studied. The heights of each limit were plotted against the headland to headland distance between stations. Each limit was approximated by a line of least squares. The validity of this approach is discussed.

The limits studied were grouped as follows:

1. Limits which are very variable throughout the area studied.

2. Limits which are more variable on the coast west of Sooke, than east of it.

3. Only slightly variable limits which have a definite slope downward from Port Renfrew to Victoria.

4. Only slightly variable limits which have no definite slope between Port Renfrew and Victoria.

Various combinations of factors are suggested as explanations for these various types of limits. These factors include surf, light, desiccation, and nutrients, together with adult size and longevity of the organism. The theory of critical tidal factors is criticised.

Species of the order Laminariales in this area which are as yet of questionable taxonomic status, are found in the following genera: *Hedophyllum*, *Alaria*, *Costaria*, *Cymathere*, and *Laminaria*. Of these, *Hedophyllum* and *Alaria* were studied in some detail. *Hedophyllum* was cultured from zoospores obtained from the sporophyte, through gametophyte stages, to what was presumably a young sporophyte of the same entity. The young sporophytes were not grown to stage where positive identification of secondary morphological characteristics was possible. The alternation of generations observed conformed to the pattern known for the other members of the Laminariales. *Hedophyllum subsessile* (Areschoug) Setchell, one of the two species of *Hedophyllum* reported from British Columbia, is reduced to synonomy under the other, *H. sessile* (C. Agardh) Setchell. A transitory stage in the development of *H. sessile* in its second season corresponds closely to the herbarium material on which Setchell appears to have based his description of *H. subsessile*. Variations in the bullation of the lamina of *H. sessile* are largely the result of environment, probably of exposure to, or shelter from, sunshine.

Although the species of Alaria (A. marginata Postels and Ruprecht, A. nana Schrader, A. tenuifolia Setchell, and A. valida Kjellman and Setchell) reported from British Columbia are very variable, they may usually be distinguished by the morphological characters of those sporophylls which are in a mature and fertile condition. These four species are therefore regarded as taxonomically valid in this study.

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INTRODUCTION

Outline of Problem.

In many parts of the world, including British Columbia, intertidal organisms are more abundant on coasts facing the open ocean than they are in more sheltered areas. This abundance is evident not only by the greater standing crop, but also by the number of species which to varying degrees are restricted to exposed coasts. In the problem treated here, the marine intertidal ecology of the southwest coast of Vancouver Island was chosen for study. This coast offers a relatively uncomplicated and accessible shoreline, where a gradual transition from an open coastal environment (at Port Renfrew) to a sheltered one (at Victoria) can be observed. The vertical and general geographical distributions of some of the intertidal organisms in this area were determined. The fine detail of the horizontal distributions was not fully studied. Analyses were made of some of the various environmental factors which were thought likely to account for the distributions observed. The greatest emphasis was placed on the determination of salinity distribution and tidal rhythms. Some attention, however, was given to substrate, sea and air temperature, dissolved oxygen, pH, wind, surf, rainfall and humidity. The study was restricted chiefly to the more conspicuous forms of the intertidal zone: the algae of the order Laminariales, the more common sessile invertebrate animals, and the marine seed plants.

Materials and methods.

The investigation was carried out almost entirely by hiking along the beach.

Living material was collected in polyethylene bags, which were then placed inside waxed cardboard cartons to prevent crushing of the specimens. The collections were carried to a central cache where they were preserved in a mixture of 7% formalin and 93% sea water. Later the preserved material was brought to the University of British Columbia, where it was identified and subsequently prepared as herbarium material.

Salinity samples were drawn from about one foot below the water surface in 80 ml. bottles. After the sample was taken, the bottles were corked and the corks and tops of the bottles sealed with wax. The samples were stored in a cache until such time as they were taken to the University in Vancouver for analysis. Salinity determinations were made by titration of a sample aliquot with silver nitrate solution standardized against Eau de mer normale prepared for the purpose by the laboratory at Charlottenlund, Denmark. The indicator used was potassium chromate. Salinity was calculated using the tables prepared by Pickard (1957) and based upon the work of Knudsen (1901) and Tully (1950). The method is described in detail by Strickland (1957, No. 2, pp. 1-8). Strickland calculates its accuracy as $\pm$ .06 ‰. The salinity values presented in Figure 3 are possibly subject to an additional, systematic error noted in Data Report No. 11, Institute of Oceanography, University of British Columbia (Anon., 1957b, p. [35a]). This error would mean that the true values are not more than 0.25 ‰ greater than those shown.

Temperatures were determined with an ordinary laboratory thermometer, measuring to the nearest 0.1 C^{o}.

The limited pH measurements made were taken using pH papers (pHydrion paper) manufactured by the Micro Essential Laboratory, Brooklyn 10, New York, N.Y.

Tidal heights were measured first on a pole marked off in six-inch units. During periods of heavy surf, it was difficult to estimate these heights precisely. In such cases, the precise time was noted when one of these marks was under water for about fifty per cent of a brief period of observation (usually about one minute). Since the poles were frequently carried away by wave action, observations were made later from marks painted at six-inch intervals on prominent boulders. Interpolated heights were noted on the hour. The relative heights obtained were plotted on a curve, and compared with the corresponding curves drawn from the data obtained at Victoria and Tofino by tide gauge and provided by the Canadian Hydrographic Service. The observed heights were related to the datum used for the tidal levels predicted by the Canadian Hydrographic Service. The series of observations was incomplete, since readings were not taken at night. Thus, only qualitative observations can be drawn from these data.

The vertical distribution of organisms in the intertidal zone is usually determined by a levelling technique. A vertical pole is set up, with a measured scale clearly marked off on it. A horizontal line is projected with the help of a spirit level from the point being studied to the equivalent level on the pole. The corresponding point on this scale is then noted. The level obtained is related to a known datum, either by reference to a surveyed bench mark or by noting the level of low water and assuming that the predicted and the actual tide heights are the same.

Some modifications of the above method were made, with a view to making possible precise work by a single investigator. A pole was set up with a single, very obvious mark situated about six feet above low water level. A line was sighted from the horizon to the mark, and a plumb at the end of a measuring tape was dropped to the object to be levelled. The levels were noted from the tape as positive or negative values to be added to the height of the mark, which is related to the level of the sea at low water. This modified method is more convenient than the conventional one in a number of ways. The pole does not have to be held upright in the surf, but may be wedged between rocks even in an oblique position. Obstructions which interrupt a direct line of sight between the object to be levelled and the horizon do not prevent levelling, if they do not rise to the height of the mark on the pole. If this mark is replaced by a light, levelling may be performed at night. The levels of points which are some distance away from the pole may be determined, since only a mark and not a figure must be distinguished. On the other hand, objects situated above the mark or light on the pole are difficult to determine. Successful use of the method requires that one can distinguish the horizon clearly.

There are many sources of error in levelling. There is often much uncertainty in determining upper and lower limits of intertidal organisms. While a clearly defined upper boundary is usually to be found in the distribution of an entity, there are often stragglers above it. These stragglers are common in anamolous conditions, such as tide pools and overhangs. Lower limits are often indistinct. They may be spurious, with the entity occurring unnoticed in the subtidal zone. This study is largely restricted to average upper limits, and lower limits were noted only when they seemed distinct. The upper limits were average in the sense that they were taken as the highest point of common occurrence of the organism on relatively uniform rock, facing directly towards the sea. Individuals which appeared to be stragglers were noted separately. At certain locations levels were determined three times in the summer of 1957, and once more in the summer of 1958. In these cases, when different values were obtained at different times, these were averaged.

In addition to errors involved in estimating the average level, there were errors derived from rounding off the figures obtained, and from variation between the predicted and the actual level of low water. The values obtained when the same limit was determined at different times for the same location were used to estimate the total error in the levelling technique. Using the values for 30 limits, each determined at three different times in the summer of 1957, the standard deviation was found to be 0.7 feet. When using the values for 30 limits, each determined both in 1957 and 1958, it was found to be 0.4 feet. The validity of these figures is difficult to evaluate. While an attempt was made to make the chosen limits representative, they were heavily biassed in favour of upper limits and the limits of larger, more conspicuous forms. Limits belonging in both of these categories (upper limits of more conspicuous forms) constitute the bulk of the values available for use in the calculations. As will be discussed later, the limits of some smaller forms are much more variable from place to place than are those of the larger forms. Thus, the error calculated is probably too great for the larger forms, and too small for the smaller ones. Finally, any actual change in the height of a limit which occurs between the dates of the replicate observations used would appear as an error. The figures given above seem to be good indications of the order of magnitude of the true value, which is also confirmed on page 126. This makes the levels obtained in this research significant to the nearest foot.

There is one possible error in levelling which may be systematic, and not appear in the above calculations. The levels obtained at Stations 1 to 5 inclusive (Port Renfrew area) were related to the level of the lower low water on the day when the observations were made. This lower low water was assumed to be the same level as that predicted for Clayoquot for the relevant day. All the other stations, except Station 36 (Camp Bay, South Pender Island), were related to the low tide predicted for Victoria. Station 36 was related to Sidney, Vancouver Island. While it is customary to use Port Townsend tide tables (with a large correction) to find the time of low water in the San Juan Islands, the Victoria tables were used in calculating the levels at Stations 33 and 34. This was done to avoid the necessity of introducing another datum into the calculations. At the time of this study, predicted levels for Port Renfrew and Sooke were not issued. The levels of the lower low water predicted for the same day at Victoria and Clayoquot are generally different. Usually the Clayoquot value is lower than the Victoria one. This difference averaged about 0.4 feet during the summer of 1957, but it sometimes amounted to more than one foot. It was not possible to arrive at a correction for use in calculating levels at stations intermediate between Victoria and Clayoquot. However, no consistent anomaly appears in the levels between Stations 5 and 7.

The field program was supplemented by culturing Hedophyllum sessile (C. Agardh) Setchell from zoospores through the gametophyte stages to the young sporophyte. All species of the order Laminariales studied to date appear to be virtually identical in morphology during this portion of their life cycle. Thus the entities observed in this work were not positively identified. If any species of the order, other than H. sessile, had been introduced into the cultures, it would not have been detected. It would require a very precise technique to remove all doubt from the results of such work. First, the original sporophyte plant should be identified, and later preserved as a herbarium specimen. A sporangium would be removed from the plant by microdissection, and single spores isolated. The resultant gametophytes would then be raised separately. When they are mature, the female plants should be fertilized by the male. The resulting sporophyte should be raised until it is positively identified from secondary morphological characters. This entire procedure does not appear to have been successfully completed. A portion of it, from the isolation of the spores to the sexually mature gametophyte and early sporophyte, was done by Schreiber (1930).

Routine methods in culturing Hedophyllum were used in this research. A fertile piece of the sporophyte was wiped free of excess moisture, and stored for a few hours in the dark in a cool, moist situation. A plastic dish was lined with glass microscope slides, and filled with filtered sea-water. The fertile material was placed in this dish and exposed to light for a few hours. Random selections of twenty slides each were then put into six trays, and each of the latter was placed in a transparent plastic container. These containers were then filled with the culture solutions, until the top edges of the slides were just covered. The amount of solution in each container was about 300 ml.

These cultures were also planned as an experiment dealing with the effect of salinity, water origin, and inorganic nutrients on the growth of Hedophyllum. Hedophyllum occurs naturally on the open coast where the surface salinity is about 32‰, and extends into Juan de Fuca Strait to places where the salinity does not often fall below 30‰ (Fig. 25). The water used for the cultures was taken from the Sooke area (which is representative of the more sheltered area in the Hedophyllum distribution) and from the Vancouver area (which is well away from the nearest occurrence of Hedophyllum). These had salinities of about 30‰ and 27‰ respectively. The inorganic nutrients used were nitrate and phosphate. The instructions for making the stock are given in Papenfuss (1942). It was felt undesirable to dilute the cultures by adding too large a quantity of the stock, which is made up with fresh water. Therefore, the stock was made up to ten times the concentration used by Papenfuss. The quantity added was reduced to give the same concentration of nutrients in the culture solutions. The sea salt was obtained by gradually boiling down sea water. The culture solutions used were as follows:

(1) water from Sooke.
(2) water from Sooke with nutrients added.
(3) water from Sooke with nutrients and 3 gms./L. sea salt added.
(4) water from Vancouver.
(5) water from Vancouver with nutrients added.
(6) water from Vancouver with nutrients and 3 gms./L. sea salt added.

The water was always filtered, usually by a Type AA Millipore filter, and aged at least a week.

About once a week the cultures were agitated, rinsed, and the solution changed. The cultures were kept at a temperature of about 13° C., under fluorescent light. The lights were 6 feet long, 660 watts power, and at a distance of 7 inches from the cultures.

Growth was estimated by a ranking based upon a microscopic examination of several slides from each culture. When this tint became appreciable, the cultures were also ranked on a basis of the depth of the brown tint apparent on the slides. Estimates of growth were discontinued when quantities of diatoms began to appear in the cultures.

There was no reason for thinking that these cultures were contaminated by other species of the order Laminariales. However, this has been known to happen before with similar methods

(Scagel, personal communication). Since the zoospores remain motile for only a few hours (Papenfuss, 1951), it seems impossible that they could have been introduced into water which was aged at least a week, even if they evaded the filter. It seems more probable that alien zoospores could be adhering to the fertile sporophyte material used. However, in this particular case, this material was kept for about 36 hours after collection before it was used. It is unlikely that zoospores which had already been released before the material had been collected, could endure this period of emergence well enough to be able to detach themselves from the material, attach to a slide, and survive as gametophytes. Even if such were the case, it would seem probable that the great majority of the plants grown in the culture were Hedophyllum. Unlike the diatoms, which eventually overran the cultures, alien species of the Laminariales would have no means of multiplying themselves once they were introduced into the cultures.

The area investigated. (Fig. 1)

Oceanographically, Juan de Fuca Strait may be interpreted as comprising three parts (Herlinveaux, personal communication). The outer, or most seaward part can be bounded by a parallelogram formed by lines connecting Tatoosh I., Carmanah Point, Port Angeles, and Race Rocks. This outer portion is about 100 kilometers long, 20 kilometers wide, and 200 meters deep. It is in communication with the Pacific Ocean at all depths through a trough running southwest from Tatoosh I. The middle part is a basin roughly bounded by a semicircle having a radius of 30 kilometers with New Dungeness as its centre. This basin has a somewhat irregular sill, with a maximum depth of about 70 meters, running in a southerly direction from Victoria. The inner part of the Strait consists of the multitude of channels which form a network among the various Gulf Islands and San Juan Islands. The deepest of these is about 200 meters.

More precise locations for the shore stations are given in Appendix I.

Field program.

Attention was concentrated on the north shore of the outer section of Juan de Fuca Strait, particularly between River Jordan and Sooke. Bases of operation were established near Sandstone Creek and Muir Creek (Stns. 9 and 13).

Once a month, in June, July, and August 1957, collections and observations of vertical distributions of intertidal organisms were made at Sandstone Creek (Stn. 9), Glacier Point (Stn. 10), Sheringham Point (Stn. 12), Muir Creek (Stn. 13), and Otter Point (Stn. 14). These triplicate observations were made in order to determine whether any changes had occurred in the vertical limits of intertidal organisms in the time which elapsed between observations. They also permitted a calculation of error in the levelling data.

Also, during the summer of 1957, levelling data and collections were obtained at Observatory Point (Stn. 1), Magdalena Point (Stn. 5), Black Creek (Stn. 8), Flea Beach (Stn. 11), Muir Point (Stn. 15), West of Cooper Cove (Stn. 16), Seventeen-Mile Point (Stn. 17), Smythe Head (Stn. 22), Race Rocks (Stn. 23), and Ogden Point Breakwater (Stn. 29). More cursory observations were made at Sombrio River (Stn. 3), San Simon Point (Stn. 6), and Clover Point (Stn. 30).

The sea temperature was measured and salinity samples were taken whenever a location was visited. Most of the other field data were collected at Sandstone Creek and Muir Creek.

During the winter of 1957-8, a few spot checks were made in the area to observe winter conditions. These checks were made at Sandstone Creek on November 22, Otter Point on December 17, Muir Point on January 31, Sandstone Creek and Muir Creek on March 10 and 11 respectively, and Otter Point and Sheringham Point on April 8 and 9 respectively. Material was obtained for cultures of *Hedophyllum* during the first three of the above trips, on November 22, December 17, and January 31. Only the last of these collections resulted in cultures which were successful to any great degree. The procedure used for this set of cultures is described on pages 8-11.

The positions of some plants of *Hedophyllum sessile* which had survived from the previous summer were mapped at Muir Creek on March 11. Their development was noted on subsequent visits, during the early summer of 1958.

During the summer of 1958 observations were repeated at the situations visited during the previous summer and some other places were observed. Collections and levelling data were obtained at Observatory Point (Stn. 1), Minute Creek (Stn. 2), Sombrio River (Stn. 3), Sombrio Point (Stn. 4), Magdalena Point (Stn. 5), Pete Wolf Creek (Stn. 7), Black Creek (Stn. 8), Sandstone Creek (Stn. 9), Glacier Point (Stn. 10), Flea Beach (Stn. 11), Sheringham Point (Stn. 12), Muir Creek (Stn. 13), Otter Point (Stn. 14), Muir Point (Stn. 15), West of Iron Mine Bay (Stn. 18), Donaldson Island

(Stn. 19), East of Iron Mine Bay (Stn. 20), Smythe Head (Stn. 22), Great Race Rock (Stn. 23), William Head (Stn. 24), Albert Head (Stn. 25), Clover Point (Stn. 30), Cadboro Point (Stn. 31), and Gordon Head (Stn. 32). More cursory observations were made at a number of other points, a few of them being in western Washington and in the San Juan Islands, U.S.A. These additional points were at Mukkaw Bay (Stn. 1b), Waadah I. (Stn. 1a), Donaldson I. (Stn. 19), Dyke Point (Stn. 26), Saxe Point (Stn. 27), Portage Inlet (Stn. 28), Near Deadman Bay (Stn. 33), Goose I. (Stn. 34), Brown I. (Stn. 35), Camp Bay (Stn. 36), and Admiralty Head, Whidbey I. (Stn. 37). The principal 1957 observations were repeated in 1958 in order to see if there were noticeable changes in populations from year to year. The additional 1958 observations were made mainly to elucidate certain questions raised by the interpretation of the earlier data. Observations were made on the open coast at localities other than Port Renfrew to see if the latter is typical of the open coast. In the same way, some observations were made east of Victoria to support the findings there. Some field experiments concerning the growth of Hedophyllum (Fig. 28) were performed on San Juan Island (Stn. 33).

REVIEW OF LITERATURE.

The literature in marine ecology is so extensive, that only the main authorities referred to continuously below, and a few representative studies, are discussed here. There are many important contributions to marine ecology which are not directly pertinent to the present study. They deal with organisms or conditions which are different from those encountered in this research. Reference to most of these contributions may be found in one of the recent review articles on the subject, such as Feldmann (1938), Gislén (1943), Chapman (1946, 1957), and Hedgpeth (1957). All of these papers have extensive bibliographies which cover the field of marine ecology, and algal ecology in particular, even if they are not ostensibly review articles. Contributions of less general scope are quoted where they are pertinent.

The physical oceanography of Juan de Fuca Strait has been studied in part by Waldichuk (1957). Tidal currents in the Strait have been studied by Herlinveaux (1954). More recently, Herlinveaux (1957, personal communication) has made a complete study of the physical oceanography of the Strait. A data record, covering cruises made in the Strait during the year 1951-52, issued by the Pacific Oceanographic Group, Fisheries Research Board of Canada (Anon., 1955) was used extensively in this investigation.

Consideration of the algae in this study was restricted to certain members of the Chlorophyta, Phaeophyta, and Rhodophyta. A key to genera of these phyla has been published by Scagel (1957). In the same work, he also covers the relevant literature, local records, and herbarium material available. There is no comprehensive modern taxonomic study on the algae of this area. However, the work of Smith (1944) on the Monterey Peninsula, and of Doty (1947a, 1947b) in Oregon, have some applicability to British Columbia. The work of Setchell and Gardner (1920, 1925) and of Kylin (1925) are in most cases the most recent comprehensive studies of the local intertidal flora.

Ricketts and Calvin (1952), Johnson and Snook (1927), and Cornwall (1955) were the references for the limited animal identifications made. Descriptions of the marine tracheophytes are found in Jepson (1951) and Morong (1893) gives an illustrated monographic treatment.

Studies on intertidal ecology in areas close to the one studied here are those of Muenscher (1915b, 1916), Rigg and Miller (1949), and Scagel (personal communication). Muenscher (1915b, 1916) studied and compared the algal ecology of San Juan Island and Shaw Island, in the San Juan Islands. He noted that some open coast forms, such as Egregia and Hedophyllum, may only be found, in the area of his study, on the southwesterly shores of San Juan I. He described the vertical distributions of various algal communities.

Rigg and Miller (1949) described the vertical distribution of organisms in the area around Waadah I. They compared several localities exposed in varying degrees to the direct action of surf.

Scagel (personal communication) covered the intertidal ecology of Queen Charlotte Strait along the northeast coast of Vancouver I., and noted both the geographical and the vertical distributions of organisms in a transition area between the open coast at Hope I. and more enclosed shores in the vicinity of Alert Bay. An early and limited stage of this study, dealing with the larger algae, has been described by the same author (Scagel, 1958).

The fact that intertidal organisms occur in various ways other than random is almost self-evident. Study of the various sorts of order in their occurrence has a long history. The first major synthesis of accumulated observations on such distributions is that by Forbes and Godwin-Austen (1859). The first serious attempt to relate these distributions to conditions of the physical environment is that of Lorenz (1863), which was in many ways before its times. Good general discussions of the history of marine ecology in its various aspects may be found in the relevant contributions in Hedgpeth (1957), particularly those by Hedgpeth (Chaps. 1, 2, and 13) and Doty (Chap. 18).

Studies of the distributions of organisms associated with the intertidal zone usually deal with only one or two aspects of such distributions. For the purposes of this discussion these aspects are classified as follows:

1. Gross geographical distribution. Studies of this cover different continents, or different latitudes of the same continent.

2. Geographical distribution. Studies of this cover areas of about the same latitude on the same continent. Usually these studies are comparisons of exposed and sheltered coasts.

3. Horizontal distribution. Studies of this cover areas extending for distances within a few orders of magnitude of the tidal amplitude.

4. Vertical distribution. Studies of this cover the intertidal and the upper subtidal zones.

5. Secular distribution. Studies of this cover changes in the same population over periods of time.

Two approaches have been adopted in the literature concerning these various distributions. An organism may be considered as one of a variety of organisms which are to be found in a characteristic environment (synecology), or it may be considered individually in relation to its physical environment, and any proven interrelationship with other organisms considered as an aspect of its biological environment (autecology). Furthermore, an investigation proceeds through various stages. First, the distribution must be described. Then it should be explained tentatively by correlations with conditions in the environment. Finally, these explanations should be confirmed by experimental work on the organism itself.

Gross geographical distribution is not of immediate concern in this investigation. Setchell's theory (1893, 1917, 1920a, 1920b, 1935) suggesting that this type of distribution is mainly governed by sea temperature and distributional boundaries such as oceans, is well supported. More recent and sophisticated versions may be found in Ekman (1935) and Hutchins (1947). The geographical distribution of algae in the northern Pacific has been described by Okamura (1932).

Geographical distribution on a smaller scale has been the subject of much work. The great bulk of it is descriptive. It is not difficult on _a priori_ grounds to deduce that gross variations in salinity (Setchell, 1893; Rigg, 1913) and substrate play an important role in such distributions. If an organism could grow in fresh water, it would presumably not be marine, but would penetrate into rivers. Organisms which require a firm substrate are virtually restricted to rocky shores. Beyond this, however, most suggestions are frankly speculative. Thus Chapman (1942) suggested sea temperature and Lami (1934) suggested cloud cover as possible factors.

So many different factors may interact in so complex a fashion that it is virtually impossible to determine the role of any one without extensive experimental work or reference to other simplified situations. A good example of this sort of investigation is that of Osterhout (1906a, 1906b). Osterhout (1906a) studied the algae which grew close to the water line on ships which plied between San Francisco and up-river ports. When the ship arrived loaded at San Francisco these plants were in water of 27‰ salinity. As the ship was unloaded, they were exposed for about six hours, and dried down with salt crystals over them. The ship was then loaded, and they were submerged again. The ship then proceeded up-river through water of steadily decreasing salinity, and spent a day in completely fresh water. Then the ship returned to San Francisco. Osterhout then (1906b) experimented with growing representatives of the green, red, and brown algae in different salinities, including distilled water and saturated brine. These plants included such open coast forms as species of Plocamium and Ptilota. He found that they survived several months in all of the salinities used. From this he concluded that the role of salinity in the distribution of marine algae has been exaggerated. Hurd (1919) found that Nereocystis can survive extensive dilution of sea water, if this dilution is done gradually. Brown (1915) investigated the survival of various of the larger algae in diluted sea water. She found that resistance was variable, but that many of the forms can survive several days of immersion in fresh water.

Horizontal distributions of organisms have been the object of only a few studies. Many of them are comparisons of the populations of positions with varying degrees of exposure to direct wave action. Since the hydrographic conditions, such as high salinity, generally associated with exposed coasts should be relatively constant over the areas studied, these investigations are not necessarily scaled down versions of what are called studies of geographical distributions above. These contributions include Hedgpeth's (1953) comparison of various pilings in the Port Aransas area, Evan's (1947) study of 37 stations along about ten miles of coast in the Plymouth area, and Southward and Orton's (1954) comparison of the outer and inner faces of the Plymouth breakwater. Some papers which consider other aspects of the fine detail of distributions are those by Colman (1933), Zanefeld (1937), Kitching (1935), Grubb (1936), Morton (1954), and Womersley (1956). Colman (1933) did an excellent survey of an area of rocky shore, Church Reef, near Wembury, by means of traverses related to a bench mark. Zanefeld (1937) compared the various parts of a breakwater, which is a situation as physiographically constant as any which may be found in the field. Kitching (1935) performed a detailed survey of several almost vertical areas of cliff in Argyll. Grubb (1936) compared two reefs which are the two sides of a syncline. These therefore virtually mirror images, one having a south and the other a north exposure. Morton's (1954) is virtually the only paper concerning crevice faunas, which were considered in relation to air temperature and illumination. Womersley (1956) studied the populations of a sheltered inlet. His paper is also notable for the thoroughness with which the physical environment is discussed. A fairly uniform conclusion which is drawn in most of these papers is that zones of organisms become narrower in a vertical plane and draw closer to mean sea level in situations which are more sheltered from wave action. The diagram presented by Stephenson (1942, p. 226) cannot be interpreted in this connection, as it is not related to mean sea level, and does not indicate whether the abscissa is in a large or small scale. Doty (1957, p. 564) explains this convergence by the fact that persistent wave action increases the effective amplitude of the tide in terms of submergence in the upper and emergence in the lower intertidal zones. However, some of these studies mention a number of exceptions to the generalization. Laminaria digitata (Linnaeus) Lamouroux has a virtually constant upper limit, in spite of differences in wave action (Evans, 1947), or in general illumination and slope of the substrate (Southward and Orton, 1954). On the other hand, Zanefeld (1937, Map II) observed variations in the zonation of certain of the Fucaceae when most of the conditions of the physical environment appeared to be constant. Southward and Orton (1954) noted some contradictions to the generalization. For example, in the upper part of the intertidal zone, Fucus spiralis Linnaeus has a wider and higher zone on the more sheltered side of Plymouth Breakwater.

Tide pools, which have been reviewed by Doty (1957) are special studies in their own right, and are not treated in this investigation.

It seems unquestionable on *a priori* grounds that the zonation of the intertidal zone is a result of some aspect of the pattern of emergences and submergences induced by tidal rhythms (Doty, 1957, p. 555). A zone is used here in the sense of a horizontal band of some kind, usually with a characteristic population. The intertidal zone is used in an indefinite sense to describe the vertical range of shore which may be exposed to air or wetted with sea water.

The rejection of this *a priori* assumption by Stephenson and Stephenson (1949, p. 303) is somewhat shallow. While, as they say, zonation of a sort does appear around non-tidal bodies of water, it is incomparably better developed around tidal bodies.

It is generally agreed (Doty, 1957, p. 536) that most intertidal organisms are disseminated in a relatively wide vertical range, and are killed off by adverse factors at a later stage in development, except in the relatively narrow zone where they are to be found in the adult stage. However, certain invertebrates are known to show preferences for certain kinds of substrate (Pomerat et al., 1942, 1946). The release of motile reproductive bodies of certain algae is closely associated with features of the tide, usually on a rising tide. In addition, Smith (1947) found that the gametophytes of *Ulva* fruit only at the beginning of a series of spring tides, while the sporophytes sporulate later in the same series. Since the reproductive bodies of most algae settle in a relatively short time after release, the highest level to which the sea rises during that period may enforce an upper limit in the distribution of the alga.

The death of a higher portion of the intertidal population of a species, apparently through drying, sunburn, or heat death has often been observed (Rigg, 1917, p. 317). Other possible factors in the lethal effect of exposure are freezing in winter, excessive salinity caused by the drying down of sea water on the plant, or reduction of salinity by rain. The work of Kanwisher (1957) and Osterhout (1906a) seems to have thrown doubt on these three latter as important factors in most cases. However, this work concerns only vegetative survival and growth. Delf (1942) does not assemble much concrete evidence in favour of her suggestion that salinity increases are an important factor. Doty and Archer (1950) favour temperature effects rather than salinity, but note indications that there is no universal factor involved, which works in the same way for most algae. However, it has been found that species from higher in the intertidal zone can survive desiccation for a longer period than can those from lower areas (Muenscher, 1915a).

Sessile intertidal filter feeding animals must be submerged for a portion of time sufficient for them to gain enough food to live. A similar factor may be effective with algae, since they obtain their nutrients from sea water. It is perhaps significant that *Prasiola meridionalis* Setchell and Gardner, the highest intertidal marine macroscopic alga in this area, is commonly associated with sea-bird droppings (Scagel, 1957).

Moore (1935) is unable to account for the formation of the lower limit in Balanus, as spat settles at levels below the lower limit of the adult distribution. With algae, Baker (1910) suggests that lower limits are formed by the higher species suffering from competition by less specialized, larger, and faster growing lower species. This has been confirmed in part by Burrows and Lodge (1951), who cropped Ascophyllum nodosum (Linnaeus) LeJolis to 10 cm. height. After this, Fucus vesiculosus Linnaeus plants grew in the area. The competition would presumably be for light.

Both the intensity and the spectral quality of sunlight is changed by passage through sea water. The diminution of light certainly is responsible for enforcing some lower limits of subtidal algae through reduction of photosynthesis. It is possible that light may have a similar effect in the intertidal zone (Chapman, 1942). Gail (1918) found that Fucus sporelings were killed when held continuously at a depth of more than one meter, apparently by diminution of light. Similar work by Gail (1922) and Klugh and Martin (1927) showed similar results, but the optimum depth for some of the intertidal forms seems to be too great for lack of light to be limiting in the intertidal zone. For instance, Ectocarpus confervoides was found to have an optimum at a depth of between two to three meters in New Brunswick. Trevarthen (Chapman, 1957, fig. 1) worked on the effect of desiccation and submergence on the rate of photosynthesis and respiration in Hormosira banksii (Turner) Decaisne. She found that desiccation reduces both photosynthesis and respiration greatly. Deep submergence at high tide reduces photosynthesis somewhat, but does not reduce respiration. Thus the periods just after emergence, just after submergence, and just before emergence, seem to be the most favourable for the plant. Her results indicate that the plant might be approaching its compensation point at the lower limit of its distribution.

The effect of wave action on the vertical limits of intertidal organisms has been noted above (p. 21). Burrows et al. (1954) state that the raising of upper limits by wave action occurs only when persistent cloud cover and fog also obtains. The increments of up to 12 feet they mention in these circumstances is much greater than the 2 foot increase in height allowed by Johnson and Skutch (1928) and Colman (1933). The latter figure presumably applies to comparisons of situations with the same climate.

Organisms of the same species in different situations can show differing degrees of adaptation or resistance to adverse conditions. Zanefeld (1937) showed that species of the Fucaceae from higher levels reach their dry weight after a longer period of drying than do those from lower levels. This seems to be the effect of modifications in the cell walls. Carnahan (1952) likewise found that the water loss was slower from the higher individuals of <u>Hormosira banksii</u> (Turner) Decaisne. It is well known (Scholander et al., 1952) that arctic marine invertebrates may show active adaptation in their respiration rates. There is some evidence (Segal et al., 1953) that molluscs of the lower intertidal zone may be cold adapted relative to higher members of the same species. Algae can become adapted to light of a lower intensity or a different spectral quality by changes in the quantity and proportion of their different pigments (Blackman, 1905; Lubimenko, 1925). Sometimes an adaptation to one adverse factor appears to be related to resistance to another. Delf (1942) mentions that resistance to extremes of temperature and salinity seem to be correlated. This differential in adaptation between various parts of a population should be considered in experimental work concerning the effects of adverse factors.

The sharpness of the limits of some intertidal organisms, and the tendency of these limits to be grouped at certain levels, or breaks, is not easy to explain (Colman, 1942). The explanation which is the most favoured at the present time is the theory of critical levels or critical tidal factors. A beginning of the theory and the use of the term "critical level" (p. 466) referring to certain features of the tidal curve was made by Colman (1933).

The apparently somewhat involved origins of the theory are discussed by Doty (1957, p. 558). Doty (1946) developed the idea for the mixed semi-diurnal tides of the Pacific coast of Oregon and California. Mixed semi-diurnal tides are characterized by two high and two low tides during each 25 hour period, these pairs of tides being usually of different heights. If in this situaion the duration of maximum submergence or emergence is plotted against height in the intertidal zone, the resulting curve is stepped. This means that an organism at a certain height can experience an emergence about twice as long as that which can be experienced by another organism immediately below it. Thus an organism just above lowest lower high water (LLHW) will be submerged at least once a day and can experience an emergence of the order of 20 hours' duration. An organism a little lower is always submerged twice a day and can experience a maximum emergence of the order of 10 hours (Doty, 1957, Fig. 11). A similar situation obtains for duration of maximum submergence at such levels as HHLW. Doty (1946) relates certain of such features of the tidal curve as LLHW to these steps in the curve of maximum exposure or submergence against height. He found that the breaks, or groups of limits of organisms, tended to occur at one or other of these related levels. Thus, there are three kinds of level; the feature of the tidal curve, such as LLHW; the step on the plotted curve, such as the increase of maximum emergence from 10 to 20 hours; and the breaks. The theory proposes to relate all three. However some papers dealing with the general subject of tidal levels in relation to distributional limits do not do this. The terminology is confused in consequence. Colman (1933, p. 466), Chapman (1942, p. 241), Doty (1946, p. 321), and Womersley (1956, p. 76) use the term "critical level" in the sense of feature of the tidal curve related to a break without reference to the steps. However, Beveridge and Chapman (1950, p. 40) and Carnahan (1952, p. 40) appear to use critical level as a synonym for break. Doty (1946, pp. 319-320) reserves the term "critical tidal factor" for a feature of the tidal rhythm which has been related to a step. Presumably a tidal factor is the feature itself, which may or may not be related to a step. The writer follows Doty's use of the terms tidal factor and critical tidal factor. The term critical level is avoided below, since the limits of individual organisms, rather than breaks, are considered in this investigation.

If the theory of critical tidal factors is to be used to suggest a cause of breaks or individual limits of distribution, care should be taken to make the correlations significant. Thus Beveridge and Chapman (1952) use 11 tidal factors (in the sense defined above) where the tidal amplitude is about 10 feet. It appears probable that some of the correlations found may be purely coincidental. Nevertheless, such an approach can be of value in a purely descriptive way, providing a means by which the zonation of two areas with different tidal amplitudes can be compared.

Doty and some of his students have pursued experimental work to confirm the theory of critical tidal factors. Doty and Archer (1950) proved experimentally that a two or three-fold increase of an unfavourable factor in the environment may mean the difference between the satisfactory growth and the death of an alga. However, the work indicates that no single factor was responsible for the limiting of all the algae used. Doty and Fahey (Doty, 1957, pp. 559-560) found that tidal factors in nature do actually cause an abrupt increase in unfavourable factors at the levels where breaks are found.

Secular changes in intertidal populations are closely connected with the life cycles of the various organisms involved. Johnson and Skutch (1928) found great variability in zonation from year to year, both in heights and the composition of the populations. Evans (1947), on the other hand, found that the zonation on Church Reef was almost the same as that determined by Colman (1933). Doty (1957, p. 551) notes that the zonation of the larger and usually perennial organisms is more constant with season than is the zonation of the smaller, presumably shorter-lived forms. The reason for this is probably the fact that the distributions of large, perennial organisms are governed by environmental conditions over a greater extent of time and space. These conditions should usually be more constant in their effect. Larger organisms also probably have a greater resistance to temporary unfavourable conditions. General field studies of the winter conditions of algae are rare. Hurd (1917) found that differences from the summer conditions are slight in the San Juan Island area, except that certain prominent algae, such as Nereocystis, are absent. Johnson and Skutch (1928) found noticeable seasonal variations in the smaller and higher algae. Seasonal changes are more often and conveniently studied on an autecological basis. These studies usually take the form of life cycle studies of individual entities. A good example of this type of study is the work of Parke (1948) on Laminaria saccharina (Linnaeus) Lamouroux.

Successional and repopulation studies are a field in themselves. However, they may throw some light on the role of competition in the establishment of upper and lower limits (Burrows and Lodge, 1951).

An autoecological approach would seem to be preferable in investigating the reasons for the distributions of organisms in the intertidal zone. It seems clear that different factors are limiting in different situations. Generalizations concerning the relationships between organisms and their environment have only limited value.

The present study is mainly descriptive. However, in the descriptions, individual species rather than communities have been emphasized.

ENVIRONMENTAL FACTORS IN JUAN DE FUCA STRAIT

Geological factors.

The substrate seems to affect the organisms living upon it only through its physical aspects. This study is restricted to organisms which require a solid anchorage. The rock must be sufficiently hard to resist rapid erosion, and sufficiently rough to allow attachment. Sand and larger rock fragments, impelled by surf, may scour organisms from adjacent rocks. Suspended material may smother various organisms, or reduce the incident light needed by plants.

The chemical constitution of the substrate does not usually appear to have any nutritive or toxic effect. It has sometimes been suggested that limestone or chalk may affect organisms by raising the pH of the water in the vicinity. However, Boalch (1957) found no significant difference on the open beach between the populations on chalk and those on greensand.

The general geology of the Juan de Fuca Strait area is shown in Fig. 2. The type of beach is mentioned in the descriptions of the stations (Appendix I). In these descriptions, beaches are classified as follows:

1. loose, either of sand or shingle.
2. boulder.
3. rock outcrop.
    a. sandstone or tuff.
    b. fine grained igneous rock, mostly basalt.
    c. gneiss, slate, schist, and quartzite.
    d. conglomerate.
    e. coarse grained igneous rocks, mostly gabbro.

The loose beaches are usually very poor in attached organisms, while the boulders and the outcrops are rich. In choosing the locations for stations, therefore, loose beaches were avoided entirely, and rocky beaches were selected when possible.

The surfaces of the different types of rock listed above have different physical characters, as follows:

1. sandstone and tuff -- eroding surface.
2. fine grained igneous rock -- hard polished surface.
3. coarse grained igneous rock -- hard rough surface.
4. conglomerate, gneiss, schist, slate, and quartzite -- surface of various hardnesses, very rough and irregular.

However, these differences do not appear to be significant in many cases. Highly polished basalt is usually poor in algae. It is not clear if this fact is because the algae could not become attached, or because the agent which polished the rock removes them. Tide pools are largely restricted to areas of sandstone beach.

Figure 2 is based on the Canadian Department of Mines Geological Survey Maps Nos. 17A and 196A. The types of bottom are taken from the Canadian Hydrographic Service chart No. 3607 and the United States Coast and Geodetic Survey chart No. 6300.

The abrasive effect of loose sand was particularly noticeable at Otter Point (Stn. 14). In general, the beaches are more muddy in the eastern portion of the Strait.

Chemical factors.

Salinity.

Herlinveaux (personal communication) and Waldichuk (1957) consider Juan de Fuca Strait oceanographically as a somewhat complicated estuary of the Fraser River. The Fraser River outflow reaches its maximum in early summer. At this time a distinct upper layer of turbid water, with salinity of about 16 ‰, spreads over much of the Strait of Georgia. The main body of water underneath this surface layer is less turbid and more saline. Most of the excess water resulting from a surplus of runoff over evaporation finds its way out to the Pacific Ocean through Haro Strait and the other channels in this area. The two layer system originating in the Strait of Georgia becomes thoroughly mixed in passing through the channels, over the sill south of Victoria, and around Race Rocks. At Race Rocks, the salinity is fairly constant at about 31.35 ‰, ranging from 30.20 ‰ to 32.00 ‰. The mixed water originating in the Strait of Georgia flows outward as the upper layer of a two layer system in the outer portion of Juan de Fuca Strait. It gradually becomes more saline as it entrains water from the lower layer.

The lower layer comes from the Pacific Ocean off Cape Flattery. The salinity of water from this source is influenced by the presence or absence of upwelling at the mouth of Juan de Fuca Strait. Northwesterly winds increase the upwelling, and thus also cause an increase in the salinity of the Strait.

According to Herlinveaux (1957, personal communication), the salinity close to the Canadian shores varies in a pattern determined by the strength of tidal currents. The flood current, flowing in an easterly direction, moves somewhat away from the shore because of Coriolis force. This induces an upwelling of deeper, more saline water. The amount of upwelling, and of the consequent increase in salinity, is proportional to the speed of the current. This effect is not completely reversed by the ebb. Surface water may be moved further inshore, but little change in salinity results, as the lateral salinity gradient is much smaller than the vertical one. Thus, there is a diurnal variation of salinity inshore, with the salinity increasing on the flood tide. Both flood and ebb tides also increase surface salinity by mixing surface and deeper water. There is also a semi-monthly variation, with salinity increasing during the spring tides.

Salinity is not necessarily a conservative property of sea water at the surface. Along the shore it is particularly subject to a decrease through admixture with river water. The rivers of the northern shore of Juan de Fuca Strait contribute about 30×10^8 meter^3 of fresh water a year, with a maximum in the winter. Waldichuk (1957) estimates the fresh water outflow of the Strait of Georgia as 1450.9×10^8 meter^3 a year. These figures indicate that the rivers do not have any significant effect on the system in general. They may have some local effect.

The combined outflow into Port San Juan of the San Juan and Gordon Rivers is the major contribution from the northern shore of Juan de Fuca Strait. It amounts to about 20 X 10^8 meter^3 a year. Salinity analyses of samples taken during the summer at Station 1 show no sign of any freshening of the water. The hydrographic station 2-A (Anon., 1955), occupied by the Pacific Oceanographic Group, was close to Station 1. The surface salinity at this station was determined ten times during the year 1951-1952. Of these only one (29.54 ‰ on October 6, 1951) shows a salinity below 31.00 ‰. Thus, any local freshening of the sea by rivers on the north shore must be very limited.

A westerly wind may also cause upwelling when it blows along the northern shore of the Strait.

The winter and summer distributions of surface salinity in Juan de Fuca Strait are shown in Figures 3 and 4. The 1951-2 and the 1957-8 observations can roughly be related through the continuous daily observations at Race Rocks (Fig. 5). The salinity during these two periods appears to be about the same.

The effect of the summer maximum of Fraser River runoff on the general distribution of salinity is clearly apparent.

The salinity at Muir Creek (Stn. 13), as determined from the samples taken from the beach, shows exceptional variability. The fluctuations of salinity here probably result from the fact that the station is situated close to a sizable stream in a shallow and perhaps poorly flushed bay. Variations at stations subject to surf action, such as Glacier Point (Stn. 10), Sheringham Point (Stn. 12), and Otter Point (Stn. 14) are much smaller.

The salinity of samples taken from the beach along the northern shore in winter is consistent with the general distribution. On the other hand, the summer determinations west of Sheringham Point seem to be appreciably higher than might be expected from the general distribution in June. Many of the beach samples were taken in July and August, when salinity was presumably higher than in June, which is the month of maximum Fraser runoff. Sheringham Point is the effective inner limit of ocean surf in summer. The higher values may result from a mixing up of lower water by the action of surf. However, in this section of the Strait, the higher salinities often appeared to be associated with periods of strong westerly wind of several days' duration. The northwesterly component of winds which parallel the west coast of Vancouver I. is at a maximum in summer (Pickard and McLeod, 1953, fig. 7B). Since the surf certainly does not decrease in winter, the westerly wind is the most probable cause of the higher summer values for salinity along the beach.

Some of the consecutive determinations of salinity made in this investigation are shown in Figure 6. The runs are too short to give a very certain picture of diurnal or semi-monthly variations. The sharp decrease in salinity at Muir Creek on the ebb is probably the consequence of the ebb current sweeping water from Muir Creek itself over the station. At Sandstone Creek, where the surf is quite heavy, there is no marked diurnal variation. Patterns of diurnal variation which might be correlated with upwelling induced by tidal currents or the westerly wind do not appear at either station. There is some indication of a decrease in salinity as the neap tides continue.

Before the gradual disappearance of open coast forms from west to east can be ascribed to a decrease in salinity, the existence of an appropriate salinity gradient must be proved. Such a gradient can be deduced from the June general salinity distribution (Fig. 4), but not from the November one (Fig. 3). It is not clearly apparent in Figure 7, which shows four sets of observations made along the shore. Each set was taken on the same day. None shows any marked gradient, as random variations appear to be greater than any gradient there may be. This figure also shows the average difference between individual determinations of salinity at various stations and the value obtained from Race Rocks on the same day. Most of this data was obtained during the summer. Many of the samples were taken about the end of the ebb tide at the beach, but all samples from Race Rocks are taken at the end of the flood. This difference in method is probably not significant. The determinations at Sandstone and Muir Creeks, where samples were taken at all stages of the tide, appear to be consistent with the other stations. While no definite gradient is apparent along the shore of the outer portion of Juan de Fuca

Strait, the shore stretching north from Victoria sometimes experiences very low salinities of below 29.00 ‰.

<u>Other chemical factors</u>.

Practical considerations permitted only a very few measurements of the dissolved oxygen and pH of the sea water in the area under study. The data obtained showed no exceptional values. It seems very unlikely that either of these water properties are limiting to organisms in the circumstances studied here.

No measurements were made of phosphates, nitrates, or other nutrient substances. The mixing which takes place around Race Rocks and the patterns of upwelling along the shore, suggest that inorganic nutrients are probably never reduced to levels which have been found limiting for phytoplankton. It is unknown whether the same values are limiting for benthic algae.

Physical factors.

Sea temperature.

Winter and summer distributions of surface sea temperature in Juan de Fuca Strait are shown in Figures 8 and 9. The surface temperature at the beach is much more variable than the salinity, when it is considered in relation to the general distribution offshore. These variations in temperature appear to be the consequence of occasional warming of inshore waters. No cooling effects are apparent. This variability is so great that there is little use in attempting to predict sea temperature on the beach from a consideration of the general distribution. However, the data plotted in Figures 9 and 10 show the sea temperatures actually experienced by the intertidal organisms at various stations. The temperatures on the more exposed stations were fairly consistent with the offshore temperatures, ranging from about 9 to 11° C. In more or less enclosed stations the sea may be warmed much more: to 18° at Muir Creek and 22° in Sooke Basin. It is probable that intertidal organisms encounter more extreme temperatures when they are exposed to the air. However, it is possible that sea temperatures may be limiting through effects more subtle than heat or cold death. For instance, changes in average temperatures may effect the balance between respiration and photosynthesis (Krashennikoff, 1926).

Wind.

The appearance of trees and shrubbery at Black Creek, Glacier Point, and Donaldson I. indicates that the prevailing wind is westerly. On the other hand, this may only be the effect of the relative maximum of wind from the northwesterly quadrant in spring and summer (Pickard and McLeod, 1953, fig. 7B) when growth is at a maximum.

As a general rule, the west wind springs up in the afternoon during the summer. Since most daylight low tides occur in the morning, this wind has probably little drying effect on intertidal organisms.

Surf.

Virtually the full force of the ocean swell reaches the Port Renfrew area from the west. Eastward from Port Renfrew the intensity of the swell gradually decreases. It is markedly less at Glacier Point, and usually disappears east of Sheringham Point. No quantitative measurements were obtained of the intensity of the surf. This applies only to the ocean swell coming from the mouth of the Strait. Very heavy surf from local storms can occur in all parts of the Strait.

There is a gradient of surf duration superimposed on the gradient of ocean surf intensity. There is a tendency for the tidal currents to flatten out the swell. The more easterly points generally are reached by surf at time close to slack water. Even at Otter Point, a few heavy swells almost always mark the turn to flood.

Rainfall, humidity, and amount of sunshine.

The average yearly rainfall in the area studied decreases in an easterly direction. It amounts to about 90 inches at Port Renfrew, 30 inches at Race Rocks, and 20 inches in the San Juan Islands. The maximum rainfall is in winter.

The summer of 1957 was exceptionally wet, while that of 1958 was exceptionally dry (Anon., 1957c; 1958a).

It is probable that rainfall has the most effect on intertidal organisms indirectly, through its effect on relative humidity and desiccation. Very heavy rainfall was observed to raise blisters on exposed invidivuals of the order Laminariales, particularly Hedophyllum, but this seemed to have no permanent effect. Heavy rainfall had little effect upon the salinity of tidepools, as the rainwater remained separate as a thin surface layer.

At Observatory Point and Sombrio Point, the fine spray from the heavy surf kept the intertidal organisms moist even on dry days.

Rainfall and humidity are probably roughly related to the amount of cloud cover. This in turn is probably the main factor in differences between amounts of incident light at the various localities studied. Incident light itself was not measured. The average annual number of hours of bright sunshine is about 1400 at Port Renfrew, 1600 at Sooke, 1800 at Race Rocks, 2000 at Victoria, and 2100 in the San Juan Islands (Anon., 1957a).

Tides.

There are a variety of types of tidal curves in the area studied. Figure 10 shows somewhat more than one tidal cycle at Tofino, Port Renfrew, and Victoria. Some much shorter portions of the tidal curves at Sandstone and Muir Creeks are shown in Figure 6. On the open coast at Tofino or Clayoquot the tides are of the mixed semi-diurnal type (defined on page 26). At Victoria, they are markedly declinational. The effect of this is virtually to eliminate the higher low water for much of the tidal cycle. The amplitude of the tides is 13.0 feet at Clayoquot, 11.4 feet at Port Renfrew, 10.2 feet at Sooke, and 9.3 feet at Victoria. The amplitude is taken here as the difference between higher high water and lower low water of large tides, as presented in the tide tables predicted for 1959 by the Canadian Hydrographic Service (Anon., 1958b).

Phase differences are difficult to assess, because of the great differences in form between the various curves. Lower low water at Clayoquot almost always precedes that at the other localities in the area studied. This lag behind lower low water at Clayoquot averages 0.2 hours at Port Renfrew, 1.1 hours at Sandstone Creek, 2.1 hours at Sooke, and 2.6 hours at Victoria. At all these localities, lower low water occurs earlier in the morning as the summer progresses. Consequently, it occurs in the day during the summer, and in the night during the winter.

The limited observations of tidal height at Sandstone Creek and Muir Creek permit some qualitative estimations of the tidal curves at these places. In form, they are roughly intermediate between those of Port Renfrew and Victoria. In amplitude they are very close to Victoria. In the tidal predictions of the Canadian Hydrographic Service, Glacier Point and Becher Bay are referred to Sooke; William Head and Oak Bay to Victoria.

The use of the terms tidal factor and critical tidal factor have been discussed on page 28. The tidal factors noted here (Fig. 11) are derived from an analysis of the mixed semi-diurnal tide. The higher and lower high waters of a day are described as HHW and LHW respectively. Similarly, the higher and lower low waters are given the designations HLW and LLW. In a fourteen day tidal period, including neap and spring tides, each of the above "waters" has a maximum, a minimum, and a mean value. These are designated by prefixing the letters H (for highest), L (for lowest), and M (for mean) to the other three letters. MSL stands for mean sea level. EHHW and ELLW (E for extreme) represent the highest and the lowest tide of the time considered. EHHW and ELLW are the HHHW and LLLW of the two-week tidal period in which they occur. Except for the use of the letter E, this terminology follows Doty (1946).

The mean values listed in Figure 12 cannot properly be found to be critical tidal factors. They are not logically connected with any step on the curves of maximum emergence or submergence. However, they may coincide with these. Mean values of certain tidal factors can be very useful in describing the zonation of organisms.

The tidal data presented below are taken from various sources (Table I). They appear to be consistent with one another. Since the tides at Victoria are mostly of the diurnal type, the tidal factors relating to LHW and HLW are probably not very real. The tidal predictions are listed in the bibliography as Anonymous, 1956, 1957d, 1958b.

Table I — Sources of tidal data.

Figure	Data	Source
6	Sandstone Creek and Muir Creek	Writer's observations. Night values largely interpolated.
10	All data	Hourly coordinates from relevant tide gauges.
12	MSL all localities	Mean of hourly tide gauge readings, June and July, 1957.
	Other factors Sooke, Port Renfrew	Mean of all predicted values, 1959.
	Other factors Victoria, Clayoquot	Mean of all predicted values, 1957.
13, 14	Sooke	Extrapolated from Victoria records.
	Other localities	Tide gauge readings June 18-July 15, 1957.
15-18	All data	Tide gauge readings June 18-July 15, 1957.
19, 20	All data	Predicted values for 1957, each calendar month.

Values for Port Renfrew are shown in Figures 15, 16, 17 and 18 when they are distinct from those for Tofino or Victoria. The tidal factors entered on these figures refer to steps in the Tofino or Victoria curves. Figure 12, 13 and 14 show that various tidal factors are at a different relative height at the various localities. In general, Port Renfrew is intermediate between Tofino and Victoria. However, Figures 15, 16, 17 and 18 all show levels in the middle intertidal zone where the Port Renfrew value is not intermediate. The Sooke tide gauge is in a somewhat enclosed body of water, and the tides recorded there may not be entirely typical of the coast outside at Station 15.

Any critical tidal factors should be apparent in Figure 17 or 18. Figure 17 is relatively simple. LLHW and HLHW are clearly critical tidal factors. The steps in the highest part of the curves are a result of variation in the height of HHHW.

The corresponding critical tidal factors at Port Renfrew are LHHW (8.0 - 8.5) and LLHW (6.0 - 6.5).

Figure 18, except in a first approximation, is not a mirror image of Figure 17. It is confused by the fact that some critical tidal factors are variable in height, and occur at different levels in the two tidal cycles analysed. In this way, steps in two or three adjacent intervals of height may be caused by the same tidal factor. These tidal factors are labelled variable in the table below.

Table II Possible critical tidal factors.

Tofino		Port Renfrew		Victoria	
		from maximum emergence			
HLHW	11.0 - 11.5	LHHW	8.0 - 8.5 (variable)	HLHW	8.5 - 9.0
LLHW	8.0 - 8.5	LLHW	6.0 - 6.5	LLHW	6.0 - 6.5
		from maximum submergence			
HHLW	5.5 - 6.0	HHLW	5.5 - 6.0	LLHW	5.5 - 6.0
HLLW	4.5 - 5.0 (variable)	HLLW	4.0 - 4.5 (variable)	HLLW	5.0 - 5.5 (variable)

It is possible that a great number of emergences and submergences is also a favourable factor for some intertidal organisms. Thus, some animals may utilize the surge of surf in filtering food particles from the water. No distinct steps are evident in Figure 18. However 8.0 - 9.0 (LLHW Tofino, HLHW Victoria) and 5.0 - 6.0 (HHLW Tofino, HHLW Port Renfrew, and HLLW Victoria) are levels where the curves abruptly change slope. All these tidal factors have already been listed as possibly critical above in Table II.

The height of the various tidal factors varies with different times of year. This is shown in Figures 19 and 20. Moreover, the amount by which emergence or submergence may be increased or diminished is also variable. For instance, if the values for LLW on consecutive days are 5.1, 5.3, 5.5, 5.3, 5.1, the duration of maximum submergence just below HLLW will be of the order of two days. If, on the other hand, the values happen to be 5.0, 5.3, 5.5, 5.5, 5.3, 5.0 the duration will be of the order of three days. This effect may be very great with HHHW and LLLW.

Biological factors.

Interrelationships between various populations is undoubtedly a very important factor in the determination of distributional limits of intertidal organisms. However, an effective study of these interrelationships would require a much more precise and sustained investigation than that undertaken here.

Instances of epiphytism or parasitism which are specific to a greater or lesser dègree are noted below in the discussion of the organisms involved. At some stations, particularly Station 1, there appeared to be extensive removal of algal populations through the agency of *Strongylocentrotus purpuratus* and *S. franciscanus*, the sea-urchins.

DISTRIBUTION OF INTERTIDAL ORGANISMS OF JUAN DE FUCA STRAIT.

General.

Marked differences in the intertidal populations were noted at the various stations studied along the coast. These differences were apparent in numbers and wet weight per square meter, in geographical distribution, and in vertical distribution of various species.

The quantitative differences were noted only in a very cursory manner and the orders of magnitude of the quantities involved are indicated in Figure 21. The values for *Fucus* and *Pelvetiopsis* shown for Station 1 were taken from a more sheltered locality, about one hundred yards from the site of the other measurements shown.

A number of the organisms studied, such as *Postelsia* and *Lessoniopsis*, are restricted in varying degree to the more exposed coasts. A few, such as *Sargassum* and *Zostera*, are typical of the more sheltered areas. Others, such as *Nereocystis*, are virtually ubiquitous. A very few, such as *Macrocystis*, are more or less typical of exposed areas, but are not found in the localities of greatest exposure.

The significance of the geographical and vertical distributions presented below depends upon the degree to which the organisms are conspicuous or numerous. If an organism is conspicuous, such as *Macrocystis*, or numerous, such as *Endocladia*, it can be found wherever it occurs. If it is inconspicuous or scattered, it may have been overlooked and not recorded in its full vertical range.

When a significant geographical distribution is too complicated to be expressed conveniently in words, it is presented in one of the figures below. These figures include observations made along the coast between stations (Figure 22) when these observations appear to be important. The vertical distribution of the same organism is also plotted in each figure. The data for each station are placed directly above the position of the relevant station in the map. When the geographical distribution of an organism does not merit a map, but the data on the vertical distribution appear to be of value, the latter distribution is presented by itself. The horizontal scale is the same as that used on the maps, except that the stations with numbers higher than 30 are arranged consecutively, and the intervals between them are reduced. Only vertical distributions in which nine or more measurements of the upper limit have been made are presented. Exceptions are made in cases where the measurements are restricted to a section of the coast studied. The lines of least squares mentioned in the discussion are calculated from the values for upper and lower limits presented below. However, the ordinates used are based on the headland-to-headland distance between stations.

The distribution of organisms along the rocky eastern shore of the entrance to Sooke Harbour appears in some ways to be a small scale model of the distributions which are the object of this investigation (Fig. 25). Some features of this are discussed below in connection with the relevant organisms.

The following systematic treatment is intended to give an adequate taxonomic basis to the distributional information presented. It is not a complete account of all organisms to be found along the coast investigated, or an exhaustive taxonomic discussion of the organisms treated.

When the number of a herbarium specimen is quoted, the prefix UC stands for University of California, UBC for University of British Columbia, and TW for a collection made in this investigation and deposited in the UBC Herbarium.

Systematic Treatment.

Phylum Phaeophyta

Order Laminariales

Family Laminariaceae

LAMINARIA Lamouroux, 1813.

Literature and taxonomy:

Laminaria complanata (Setchell and Gardner) Setchell

Setchell and Gardner, 1903, p. 262 (as *L. saccharina* f. *complanata* Setchell and Gardner); 1925, p. 596, pl. 57.
Scagel, 1957, p. 93.

L. *cuneifolia* J. Agardh f. *cuneifolia*
Agardh, 1867, p. 10 (as *L. cuneifolia*)
Setchell and Gardner, 1903, p. 257. (as *L. bullata* Kjellman); 1925, p. 600, pls. 59a, b, 60. (as *L. cuneifolia*)
Doty, 1947a, p. 39. (as *L. cuneifolia*)
Scagel, 1957, p. 94.

L. cuneifolia f. *angusta* Setchell and Gardner.
Setchell and Gardner, 1903, p. 257 (as *L. bullata* f. *angusta*); 1925, p. 602.
Scagel, 1957, p. 94.

L. cuneifolia f. *subsimplex* Setchell and Gardner
Setchell and Gardner, 1903, p. 257 (as *L. bullata* f. *subsimplex*); 1925, p. 602.
Scagel, 1957, p. 95.

L. platymeris De la Pylaie
De la Pylaie, 1829, p. 53.
Setchell and Gardner, 1925, p. 605.
Guberlet, 1956, pl. opp. p. 40.
Scagel, 1957, p. 95.

L. saccharina f. *linearis* J. Agardh
Agardh, 1867, p. 12.
Setchell and Gardner, 1903, p. 261; 1925, p. 596.
Scagel, 1957, p. 96.

L. saccharina (Linnaeus) Lamouroux f. saccharina.
Lamouroux, 1813, p. 22 (as L. saccharina)
Setchell and Gardner, 1903, p. 261; 1925, p. 595 (as L. saccharina)
Doty, 1947a, p. 39 (as L. saccharina)
Parke, 1948, pls. 5-7 (as L. saccharina)
Scagel, 1948, p. 10, fig. 6. (as L. saccharina)
Scagel, 1957, p. 97.

L. setchellii Silva
Hervey, 1881, p. 98 (as L. andersonii Farlow)
Setchell and Gardner, 1903, p. 255; 1925, p. 605 (as L. andersonii)
Setchell, 1905, p. 105 (as L. andersonii)
Smith, 1944, p. 137, pl. 21, fig. 1 (as L. andersonii)
Silva, 1957, p. 42.
Scagel, 1957, p. 97.

The above list includes all references which apply to the Laminaria material collected. The following four species and forms, which have been reported from British Columbia (Scagel, 1957), were not collected: L. cuneifolia f. amplissima Setchell and Gardner, L. ephemera Setchell, L. saccharina f. membranacea J. Agardh, and L. sinclairii (Harvey ex Hooker f. et Harvey) Farlow, Anderson, and Eaton. All are, however, included in the key below, which is based on all the evidence available.

Setchell and Gardner seem to have misunderstood the description of L. platymeris in their key (1925, p. 545). This key requires that the species should be characterized by: "stipe long, up to 1 m.: stipe compressed from just above the holdfast." De la Pylaie's (1829, p. 52) diagnosis begins "L. stipite brevi, tereti, minuto ..." and below he says "Le stipe est cylindrique et égal dans toute sa longeur... seulment long de 9 à 12 centimétres, sur 6 à 7 millemétres de grosseur traversalement." It is therefore suggested here that the entity which has been described on this coast as *L. platymeris* be placed under *L. cuneifolia* f. *subsimplex* Setchell and Gardner. Only one specimen found in this investigation appears to be this entity (TW 25).

The work of Parke (1948) indicates that the presence or absence of mucilage canals can be the effect of environment. This feature is one of the principal characters used in Setchell and Gardner's key (1925, p. 595). Consequently, the writer has prepared another key, using only gross morphological features. This key is intended as a working field guide to the literature as it now stands after some evaluation in respect to field observations. Some of the entities included may not prove to be taxonomically valid when they are studied more critically. In particular, the distinction between *L. saccharina* f. *saccharina* and *L. cuneifolia* f. *cuneifolia* appears to be a purely arbitrary division of a population which includes every possible intermediate form. However, some young *Hedophyllum sessile* can appear to belong to this population also. Consequently, this consideration alone is inadequate for reduction of *L. cuneifolia* to synonomy under *L. saccharina*.

Key to the species and forms of *Laminaria* found in British Columbia

1 Holdfast discoid, lamina 1 mm. or less thick -- *L. ephemera*

1 Holdfast not discoid -- 2

2 Plants produced from a prostrate rhizome, plants gregarious -- L. sinclairii

2 Plants without rhizome, solitary -- 3

3 Stipe crooked, somewhat flattened; blade orbicular -- L. complanata

3 Stipe straight, blade noticeably longer than broad -- 4

4 Stipe erect, supporting lamina; stipe terete, tapering noticeably -- L. setchellii

4 Stipe not supporting lamina, not terete -- 5

5 Base of lamina cuneate to acute -- L. saccharina (6)

5 Base of lamina cordate to cuneate -- L. cuneifolia (8)

6 Some haptera borne along length of the stipe -- L. saccharina f. linearis

6 All haptera terminal -- 7

7 Lamina so thin that it tears when lifted from the water, diffusely bullate or undulate -- L. saccharina f. membranacea

7 Lamina can support its own weight; bullations in two distinct lines more or less parallel to margin -- L. saccharina f. saccharina

8 Stipe much flattened -- L. cuneifolia f. subsimplex

8 Stipe cylindrical or slightly terete -- 9

9 Lamina more than 40 cm. wide -- L. cuneifolia f. amplissima

9 Lamina less than 40 cm. wide -- 10

10 Stipe more than 4 cm. long; lamina more than 10 cm. wide -- L. cuneifolia f. cuneifolia

10 Stipe less than 4 cm. long; lamina less than 10 cm. wide -- L. cuneifolia f. angusta

Distribution.

The upper limit of Laminaria in the intertidal zone, and the geographical distribution of its various species are presented in Figure 24. L. setchellii is easily identified in the field, and so was noted at some stations where it could not be collected. It probably occurs subtidally, and consequently was not observed at localities other than Salmon Bank (near Station 34). In the intertidal zone at least, it is restricted to more exposed coasts and Boat Pass. Boat Pass is a locality with strong tidal currents. The distributions of the other species of *Laminaria* noted here are made to appear very discontinuous because they occur mostly in the subtidal zone and were seldom collected. Thus *L. saccharina* f. *linearis* was collected only in drift, and *L. complanata* only by dredging.

The upper limit of *Laminaria* shows a definite decrease in height during the transition from open to sheltered coast.

<u>Pleurophycus</u> <u>gardneri</u> Setchell and Saunders, in Saunders, 1901.

Saunders, 1901b, p. 427.
Setchell and Gardner, 1903, p. 264; 1925, p. 607, pl. 80a.
Doty, 1947a, p. 41.
Scagel, 1957, p. 99.

The geographical distribution already recorded (Scagel, 1957, p. 99) extends from the open coast inwards beyond the territory covered in this investigation. The plant is absent from extremely sheltered areas, such as Stations 16, 17, 26 and 28.

The upper limit shows a definite decrease in height during the transition from open to sheltered coast. This is shown in Figure 43.

Cymathere triplicata (Postels and Ruprecht) J. Agardh.

Postels and Ruprecht, 1840, p. 10.
J. Agardh, 1867, p. 30.
Scagel, 1948, p. 10.
Scagel, 1957, p. 99.

There is some variation in this genus. One variant has a thin blade, inconspicuous folds, and an acute base (TW 89). The other has a thick blade, conspicuous folds, and an obtuse, almost cordate base. There are many intermediates between these two extremes, and no evidence was found to warrant segregation into two species.

The geographical distribution of *Cymathere* already recorded (Scagel, 1957, p. 99) extends from the open coast inwards beyond the territory covered in this investigation. It is absent from extremely sheltered areas, such as Stations 16, 17, 26, and 28. It is usually scattered in occurrence, but may occasionally be found in small but almost pure populations. One of these populations is about two hundred meters northwest of Station 15. A smaller one is at Station 9.

Cymathere occurs at about the same level at all stations (Fig. 43).

Costaria costata (Turner) Saunders.

Agardh, 1848, p. 140 (as Costaria mertensii J. Agardh)
Saunders, 1895, p. 57 (as C. mertensii and C. turneri Greville)
Setchell and Gardner, 1925, p. 610.
Okamura, 1925, p. 99, pl. 226 (as C. turneri)
Smith, 1944, p. 138, pl. 22, fig. I.
Doty, 1947a, p. 41 (in part as C. mertensii)
Scagel, 1957, pp. 100, 101 (in part as C. mertensii)

Collections and field observations made during this investigation indicate that Costaria mertensii J. Agardh should be reduced to synonomy under C. costata (Turner) Saunders. There is a disagreement in the literature about the status of these two entities. Setchell and Gardner (1925), Okamura (1925), and Smith (1944) consider that they both belong to one variable species. Saunders (1895) and Doty (1947a) describe them as separate species. The distinguishing features of C. mertensii as described by Saunders and Doty are an amply ruffled blade with a cordate base, smooth and cylindrical stipe, and accessory rhizoids formed along part of the stipe in addition to the terminal ones. The other form, described by these authors as C. costata, has a moderately ruffled lamina with an acute base, costate and distally flattened stipe, and terminal rhizoids only. A range of intermediate forms between these two extremes was found in the present investigation. The specimens TW 63, 164a, b, c, 22, and 214 show the transition from C. costata to C. mertensii.

Costaria has a scattered but widespread geographical distribution in the area studied. The form described as

C. mertensii is found more commonly in sheltered waters. The contrary situation was found by Doty (1947a, p. 41), who states that this variant is found in exposed localities. The upper limit of Costaria is approximately the same at the various stations where it was noted (Fig. 43).

AGARUM (Bory) Postels and Ruprecht.

A. cribrosum Bory
Bory, 1826, p. 193.
Setchell and Gardner, 1925, p. 615, pl. 63.
Scagel, 1957, p. 101.

A. fimbriatum Harvey
Harvey, 1862, p. 166.
Setchell and Gardner, 1925, p. 616, pl. 71.
Scagel, 1957, p. 102.

Both species of this genus appear to be exclusively subtidal in their occurrence. Both were obtained by dredging near Station 36. Since they were never found even in drift along the Vancouver Island shores studied, they would appear to be quite rare there. They seem to have their optimum in more sheltered waters, but the reports from Amphitrite Point and Hazardous Cove (Scagel, 1957) indicate that they can grow in more exposed areas.

Hedophyllum sessile (C. Agardh) Setchell.

Literature and taxonomy.

Agardh, 1824, p. 270 (as L. sessilis)
Agardh, 1848, p. 136 (as L. sessilis)
Harvey, 1862, p. 167 (as L. apoda)
De Toni, 1895, p. 349 (as L. sessilis)
Collins, Holden, and Setchell, 1899, p. 8(A) (as H. sessile); 1899, p. 27(B) (as H. subsessile (Areschoug) Setchell)
Setchell, 1901, p. 121 (as H. sessile); p. 122 (as H. subsessile)
Yendo, 1903 (H. spirale)
Yendo, 1914 (H. bongardianum (Postels and Ruprecht) Yendo).
Setchell and Gardner, 1903, p. 262: 1925, p. 617 (both in part as H. subsessile)
Doty, 1947a, p. 42 (in part as H. subsessile)
Scagel, 1948, p. 10, fig. 8.
Scagel, 1957, pp. 102, 103 (in part as H. subsessile)

All specimens of Hedophyllum found in this investigation are H. sessile (C. Agardh) Setchell.

Four specific names in the genus have been proposed: H. sessile (C. Agardh) Setchell, H. subsessile (Areschoug) Setchell, H. spirale Yendo, and H. bongardianum (Postels and Ruprecht) Yendo. H. sessile is the type species. It has been described as having no stipe in the mature form. It is attached to the substrate by haptera which spring directly from the proximal margin of a more or less simple lamina. According to Setchell (1901, p. 122) H. subsessile is distinguished by the centre of the lamina wearing along its longitudinal axis, so that two new blades are formed from what were the sides of the primary blade. The remains of the proximal margin of the primary blade becomes greatly thickened and comes to resemble a rhizome joining the two new blades. H. spirale was described by Yendo from Japan. It is similar to H. subsessile, but the thickened margin of the primary blade is twisted in a manner resembling *Arthrothamnus*. *H. bongardianum* is a new combination of Yendo's (1914) in which he includes the following entities:

Laminaria bongardiana Postels and Ruprecht
Hafygia bongardiana Areschoug
Arthrothamnus bongardianus J. Agardh
Hafygia ruprechtii Areschoug
Laminaria ruprechtii De Toni
L. crassifolia Postels and Ruprecht
L. nigripes Kjellman
L. digitata Ruprecht
Hedophyllum subsessile (Areschoug) Setchell
Hedophyllum spirale Yendo

The list above appears to be in essence the reduction of *Hedophyllum subsessile* and *Hedophyllum spirale* to synonomy under *L. bongardiana* Postels and Ruprecht. Yendo thought that the forms described in the references above were all different stages in the life cycle of the new entity, or different environmental forms of it. He arranged the published figures in consecutive order from youngest to mature, as follows:

1. Postels and Ruprecht, 1840, pl. 38, fig. d (*L. crassifolia*)
2. ------, 1840, pl. 13 (*L. bongardiana* f. *palmata*)
3. Yendo, 1914, fig. 1.
4. Postels and Ruprecht, 1840, pl. 14 (*L. bongardiana* f. *bifurcata*)
5. Yendo, 1903, pl. 6, fig. 1. (*H. spirale*)
6. Setchell and Gardner, 1903, pl. 20 (*H. subsessile*)

Yendo's contribution (1914) does not appear to be generally accepted. Fritsch (1945, p. 200) still recognizes the three species *H. sessile*, *H. subsessile*, and *H. spirale*. However, there does not appear to have been any published contradiction of Yendo. Herbarium specimen UC 522497, collected in Japan, and originally labelled _Hedophyllum bongardianum_ (P. et R.) Yendo is annotated in Setchell's handwriting as _H. subsessile_. A similar specimen, UC 522496, is not so annotated. The cause of this confusion appears mainly to be the extreme diversity of forms which have been identified as _H. subsessile_. This entity is discussed below, (p. 77), where it is reduced to synonomy under _H. sessile_.

Two more or less generally recognised species have been reported from the area of this investigation, _H. sessile_ and _H. subsessile_. A certain measure of doubt has arisen about the validity of _H. subsessile_. Thus Doty (1947a, p. 42) says "Collections from Cape Arago .... are certainly the same as certain of Setchell's collections .... labelled by him as '_Hedophyllum subsessile_ young! ' " [UC 96831?] .

Hedophyllum sessile is a very variable species. The variation involves the degree and position of the bullations, the amount of splitting of the lamina, and the length of the resulting sections in relation to their width. The extreme forms are one with short, bullate laminae and the other with long, frequently split, smooth laminae. It has been noted that there appears to be some sort of geographical and vertical distribution of these two forms (Setchell and Gardner, 1925, p. 618).

Distribution

The geographical and vertical distributions of _Hedophyllum_ in the area investigated are presented in Figure 25. It does not extend beyond this area towards the Strait of Georgia. Scagel (1957) notes a speciman from Whidbey I., but Hedophyllum was not found at Station 37. In the inner portion of its distribution, it is very scattered, and is restricted to the more open parts of the shore. It is thus usually restricted to the tips of such points as Albert Head, Clover Point, Ten Mile Point, and Gordon Head. Towards the open coast, it occurs in all rocky bays. Thus, Hedophyllum of a perfectly healthy appearance is present at Muir Creek, where the sea temperature may be as high as 16° C., and the salinity as low as 29.50 ‰. The plants in the vicinity of Victoria often appear to be in poor shape, suffering from necrosis of the distal portions of the lamina.

Both the upper and the lower limits of Hedophyllum definitely decrease in height during the transition from the open to the sheltered coast. The limits close to the entrance of Sooke Harbour appeared to be lowered in a similar manner. However, the plants are so scattered that it is difficult to be sure of this. Hedophyllum very seldom occurs below low water mark or in tide pools.

Variability and life cycle of Hedophyllum sessile.

As described on page 7, cultures were made of zoospores taken from fertile sporophytes of Hedophyllum sessile collected during the winter of 1957-58. The purpose of these cultures was to follow the life cycle of Hedophyllum, and to experiment with the effect of salinity, inorganic nutrients, and source of the sea water on the growth of the plants.

The morphology of the gametophytes and young sporophytes of Hedophyllum conforms to the pattern already described in the literature for other genera of the order Laminariales (Papenfuss, 1951, p. 145).

Young sporophytes were obtained first, in 26 days, in culture Number 1, containing plain Sooke water, with nothing added. Sporophytes next appeared, a day or two afterwards, in culture Number 2 containing Sooke water with inorganic nutrients added. Eventually, all the cultures produced sporophytes except the one containing Vancouver Harbour water and nutrient stock (Number 5). The sporophytes did not seem to be able to progress beyond the stage where they were a monostromatic layer of cells. Most of the young sporophytes were finally killed when the temperature of the cultures was raised to 18°C.

Quantitative growth of the gametophytes, as distinct from their progress towards formation of mature gametangia, did not seem to be enhanced by the presence of added nutrients. Two months after the initiation of the cultures, they were ranked on a basis of growth as indicated by the depth of the brown tint evident on the slides. The culture ranked first had the densest growth (Table III).

Table III Amount of growth in Hedophyllum cultures

Culture No.	Rank.
1. (Sooke water)	2
2. (Sooke water + nutrients)	4
3. (Sooke water + nutrients and salt)	6
4. (Vancouver water)	1
5. (Vancouver water + nutrients)	5
6. (Vancouver water + nutrients and salt)	3

These experiments indicate that there is no chemical factor in Vancouver Harbour water which prevents the growth of Hedophyllum gametophytes and very young sporophytes. This suggests that the factor which excludes Hedophyllum from the Strait of Georgia operates upon the larger sporophyte. This suggestion is reinforced by the fact that the sporophytes in localities close to the limits of the plant's distribution are often in poor shape. This is in contrast to some other algae, such as Lessoniopsis (see p. 83 below).

As noted above, the larger sporophytes of Hedophyllum are very variable in their morphology. The rough proportions of the bullate and smooth forms in populations of Hedophyllum at various times and places are shown in Figure 26. The rapid changes some of these populations undergo indicate that these two forms are not distinct entities, but are stages in development or are variants caused by differing environmental factors. When vertical differences were noted in mixed populations, the bullate individuals were always above the smooth.

The specimens of Hedophyllum collected can be classified fairly well under one of the nine classifications. Different parts of a few large plants (TW 110) may fall into different categories. These nine variants are illustrated in Figure 27. They can be described as follows:

1. Lamina unsplit, plane, and completely smooth.

2. Lamina with two lines of bullations submarginal, more or less plane, not split more than once or twice.

3. Lamina smooth at the margins, bullate to a greater or less distance from the longitudinal axis, not split more than once or twice.

4. Lamina bullate at distal end, smooth at proximal end; may be split several times.

5. Lamina bullate at proximal end, smooth at distal end.

6. Lamina entirely smooth, split many times, extensively furled at base.

7. Lamina broad, long, smooth or with a very few bullations scattered irregularly, usually not split.

8. Lamina entirely bullate, short in relation to breadth, divided several times, extensively furled at base.

9. Lamina eroded down to the proximal margin, greater or lesser regeneration of the blade occurring at the ends of the resulting strip of lamina.

The detailed distribution of these variants was studied. Changes were noted in a few marked plants. From these studies it was found that the bullation of areas of the lamina is closely correlated with direct exposure to sunshine. Presumably it is the result of sunburn or drying. The regenerated blades of variant No. 9 are, however, initially bullate in any habitat. The splitting of the blade is the mechanical result of wave action. The shortness of bullate blades in relation to breadth is perhaps the result of a slight brittleness of extensively bullate blades.

The actual distribution of these variants in the field is complicated by the fact that a Hedophyllum plant may be protected from the sun by a variety of factors. These include cloudy weather, shading by overhangs, or being exposed only at night through the nature of tidal patterns. Thus the plants are usually smooth at Port Renfrew, under overhangs, and during the winter. Smooth plants were generally more common in the summer of 1957, which was unusually wet, than in the summer of 1958, which was unusually dry.

Another complicating factor is the phenomenon of distal erosion of the plant. Parke (1948) found that in Laminaria saccharina material is continuously being eroded from the distal end of the lamina while new tissue is being continuously added to the proximal end. The result of this process is that no portion of the lamina is more than nine months old, although the plant may live for three years. The same phenomenon was found to occur in Hedophyllum. One of the plants observed is shown in Figure 28. The growth rates found in the somewhat limited experiments at Station 33 ranged up to about 20 cm. of tissue added and 10 cm. eroded away per month. Since few plants are more than 50 cm. long, the tissue in the lamina of this genus may be changed in much less than nine months. Thus changes in the weather conditions from month to month may change the patterns of bullation on the plants.

The young sporophytes (category Number 1 above) appear in the largest numbers about July, although plants of young appearance can be found at almost any time of year. Further development of the plant depends on its environment. If it is in a position exposed to sun, it quickly develops into Number 8. Some intermediate forms were found which indicated that it probably passes through Number 2 and Number 3 very quickly before it becomes Number 8. Young specimens of Number 8 are often no more than a few centimeters high. If the plant is sheltered from the sun, it remains in Number 1 form until it reaches a greater size, about 10 centimeters in length. Then it becomes Number 2. These lines of bullations apparently do not have the same origin as those bullations which are not arranged in lines. The movements of marks made on a number of plants, of which one is shown in Figure 28, and the pattern of regeneration discussed below, indicate that the origin of new tissue is somewhat localized on the two sides of the proximal end of the lamina. In some cases, the sides of the lamina grow more quickly than does the area closer to the longitudinal axis. This might set up stresses which cause the two lines of bullations. In any case, the bullations become diffuse as the plant reaches its full size. If the plant is subject to wave action, the lamina is split repeatedly, and the plant can then be classed under category Number 6. If it is in a very sheltered position, the lamina remains relatively entire, and the plant falls into category Number 7.

The conditions affecting the development of the plant may change after the plant has developed. The weather may change from generally sunny to generally cloudy. In this case, the new tissue is smooth, while distal erosion gradually removes the bullate tissue. While this is happening, the plant can be classed under category Number 4. The reverse change in weather could not produce the rare form Number 5. This may be the result of some accident protecting the distal end of the lamina while leaving the proximal end exposed. The lamina of another plant might do this, or a temporary submergence in a neighbouring tide pool.

The *Hedophyllum* zone is never exposed to sunlight after the end of August, as the low tides occur during the night. The entire population develops the habit described as Number 6. The storms of the season tear away many of the mature plants. These are replaced to some extent by small plants. It is uncertain if these are the result of active sporulation at this time, or have remained small because they were shaded by the larger plants until these latter were torn away.

The mature plants towards the upper limit of the *Hedophyllum* zone were found to be fertile in November, 1957. By December they were fertile at all levels. The sori covered most of the functionally ventral side of the lamina, but only isolated spots on the dorsal side. By the end of January, many of the laminae had been almost entirely eroded away. It is not known to what extent these dates are typical. This portion of the life cycle was studied for only one season, but probably this was fairly typical.

In spring regeneration begins at both ends of the narrow strip remaining of the previous year's lamina. These new laminae are at first much furled and are always bullate. This is described as category Number 9. The regenerated laminae become larger and more plane. They become smooth, or remain bullate, in relation to environment, as in the first year. They develop new haptera from their new margins. The remains of the previous year's lamina decays or is eroded away. The two new laminae may become two distinct plants, but they usually remain as one complex plant associated with a massive holdfast. By careful scrutiny, the remains of the old lamina can usually be found well into the summer. The marked plants used in studying this stage of the life cycle happened all to be in a locality sheltered from both sun and surf. They changed from Number 9, through Numbers 8, 3, 2 almost to Number 7.

It is not known how long the average Hedophyllum sporophyte survives. The very heavy attrition of mature plants observed during the winter indicates that few live more than about two years. The life cycle discussed above is diagrammed in Figure 29.

Yendo's (1903) discussion of the life cycle of H. spirale indicates that it is much the same as the one described above for H. sessile. H. spirale sporophytes also appear in the early summer. They quickly develop two submarginal lines of bullations. Eventually the centre of the lamina is eroded away. Many small sporophytes last over the winter in an early stage of development.

The second year stage of Hedophyllum sessile described above is almost exactly the same as the entity which has been described as H. subsessile (Areschoug) Setchell. The writer has examined the very heterogeneous collection of specimens identified as H. subsessile and deposited in the herbarium of the University of California. Some appear to be Laminaria bongardiana Postels and Ruprecht. The specimens which appear to be the basis for the description of H. subsessile are UC96835 (top and bottom), 96836, 96832, and 96833. These are all from the Phycotheca Boreali-Americani, and all were collected from one locality at one time: the west shore of Amaknak I., June 23, 1899. On the whole, these have a more robust "rhizome" than have the specimens collected in Juan de Fuca Strait by the writer. However, UC96836 (on paper) is very similar to some of the collections made in this investigation. UC96836 (in envelope, larger fragment) shows that the new lamina is the result of regeneration, as in H. sessile. Although there are some differences between these Alaska plants of Hedophyllum and the ones studied here, these differences are inadequate as the basis for a separate species. Hedophyllum subsessile (Areschoug) Setchell is therefore reduced to synonomy under H. sessile (C. Agardh) Setchell. This is based only on Setchell's description and specimens. It was not possible to examine Areschoug's type material.

The life cycle of Hedophyllum sessile described above and presented in Figure 29 is based on a small number of field experiments and more extensively on field observations. It agrees with the great majority of the latter. However, extremely rare occurrence of bullate Hedophyllum in tide pools indicates that it is not a complete explanation.

Family *Lessoniaceae*.

Dictyoneurum *californicum* Ruprecht.

Ruprecht, 1852, p. 80.
MacMillan, 1902, p. 213.
Smith, 1944, p. 139, pl. 22, fig. 2.
Scagel, 1957, p. 104.

MacMillan's report (1902) of this alga from Juan de Fuca Strait is definitely confirmed. It was found growing attached to rock at Station 2. Its upper limit was found to be -1.6 feet. It was found in drift at Providence Cove and Station 3. Since drift specimens were found only up to a distance of about 100 yards from Station 2, it is probable that *Dictyoneurum* grows very close to the places where it is found in quantity in drift. *Dictyoneurum* has not been reported from Neah Bay by Rigg and Miller (1947) or from Oregon by Doty (1947a). However, there is no doubt that the material collected in this investigation is the same entity as that described from the Monterey Peninsula (Smith, 1944).

Nereocystis luetkeana (Mertens) Postels and Ruprecht

Postels and Ruprecht, 1840, p. 9, pls. 8, 9.
Smith, 1944, p. 139, pl. 24.
Scagel, 1957, p. 104.

Nereocystis is ubiquitous throughout the area investigated. It occurs both in such exposed localities as Station 1, and in such sheltered ones as Station 16. It is absent from one or two miles of coast east of Magdalena Point and also west of Otter Point, probably because of a lack of a suitable solid substrate.

The upper limits of *Nereocystis* shown in Figure 43, except for the one from Station 2, represent small plants which never reach maturity. Mature plants are attached in the subtidal zone and normally are always floating offshore.

On exposed coasts, a short form may be found in the lower tidepools.

<u>Postelsia</u> <u>palmaeformis</u> Ruprecht.

Ruprecht, 1852, p. 19.
Myers, 1925.
Smith, 1944, P. 142.
Scagel, 1957, p. 105.

<u>Postelsia</u> occurs only at Station 1 and at about one half of a mile west of there, close to the Cerantes Rocks, in the area investigated. It does not occur at Station 4, where the surf is very heavy. The reports of this alga from Friday Harbour and Puget Sound noted by Scagel (1957) are questionable.

<u>Postelsia</u> has a higher intertidal range than any other member of the order Laminariales. At Station 1, its upper limit is at 8.9 feet, and its lower limit is at 5.6 feet (Fig. 30).

The distribution of this alga is very sharply defined. The sporophytes appear to be robust and in good shape wherever they do grow. This indicates that the factor which limits it is not operative upon the mature sporophyte. The plants are restricted to the steep sides and tops of points with a maximum of surf. Myers (1925) has cultured the gametophyte and young sporophytes in water taken from San Francisco Bay. This suggests that an ordinary chemical factor is not limiting to the distribution of <u>Postelsia.</u> It is still possible that a rhythm or interaction of chemical factors may be involved.

Macrocystis integrifolia Bory

Bory, 1826b, p. 10.
Scagel, 1948, p. 7, figs. 10-20.
Womersley, 1954, p. 120.
Scagel, 1957, p. 106.

This plant is very scattered in its distribution along the coast studied. A fair number of plants were found in the vicinity of Station 15. A very few plants were also found at three other localities: about one kilometer west of Otter Point, about 200 meters east of Sheringham Point, and at Station 8. Scagel (1957) notes that *Macrocystis* is restricted to open coast areas not directly exposed to heavy surf. This is a very limited habitat in the coast studied here, as there are no islands or headlands to give shelter from the surf of heavy storms. *Macrocystis* is much more common in the vicinity of Neah Bay, which has more shelter.

Macrocystis is characteristically subtidal in distribution, with an upper limit at about 0 feet (Fig. 30).

The reports of *Macrocystis* from Gordon Head, Esquimalt, Victoria, and Whidbey Island mentioned by Scagel (1957) are probably erroneous, deriving from drift, which may be moved a long way from its source. The writer has found drift *Macrocystis* both at Victoria and in the San Juan Islands.

Lessoniopsis _littoralis_ (Farlow and Setchell) Reinke

Reinke, 1903, p. 25.
Smith, 1944, p. 145, pl. 27.
Scagel, 1957, p. 107.

The detail of the geographical distribution of _Lessoniopsis_ is shown in Figure 34. The alga forms a conspicuous and continuous zone as far into the Strait as Point San Simon (Station 6). A few individuals occur on a point about a hundred yards west of Station 9. A large colony occurs at Glacier Point (Station 10) and along the coast immediately to the west of it. East of Glacier Point, the distribution is intermittent. The plant becomes more and more restricted to rock surfaces with an aspect facing the surf directly, as it approaches the eastern limits of its distribution. One small, isolated colony occurs at Station 18 (Fig. 23). This is a situation which is relatively sheltered from surf. No _Lessoniopsis_ occurs on the southern shore of Donaldson Island, which is much more exposed. Tidal currents flow very strongly through the channel between Donaldson Island and the mainland. The channel is 35 fathoms deep; so much upwelling may occur. However, it is difficult to suggest a factor which is operative on one side of the channel and not on the other.

The individual plants of _Lessoniopsis_ at the limits of its distribution appear to be just as healthy as any others. Changes in salinity do not have much effect on the plants. It grows off the mouth of a sizeable creek just west of Glacier Point. The plants here must occasionally endure much freshening of the sea water, since they are perennials.

The upper limit of Lessoniopsis decreases appreciably in height from about 5.0 feet at Stations 1 and 4 to 2.8 feet at Stations 9 and 18.

Family Alariaceae

Pterygophora californica Ruprecht

Ruprecht, 1852, p. 17.
Frye, 1918, p. 65.
Smith, 1944, p. 148, pl. 29.
Scagel, 1957, p. 107.

Pterygophora is a subtidal plant throughout the area studied, so its distribution could not be followed precisely. Its upper limit is very close to low water west of Jordan River. It is lower in more sheltered waters. A number of drift stipes was all that could be seen of it at Gordon Head. It can be dredged from a depth of three to five fathoms on Salmon Bank.

ALARIA Greville, 1820

Literature and taxonomy.

Alaria marginata Postels and Ruprecht var. *marginata*
Postels and Ruprecht, 1840, p. 11 (as *A. marginata*)
Saunders, 1901a, p. 561 (as *A. curtipes*)
Setchell and Gardner, 1903, p. 275; 1925, p. 640, pl. 28 (both as *A. marginata*)
Yendo, 1919, p. 93, pl. 6 (as *A. marginata*)
Smith, 1944, p. 147, pl. 28 (as *A. marginata*)
Doty, 1947a, p. 43 (as *A. marginata*)
Scagel, 1948, p. 10, fig. 5 (as *A. marginata*); 1957, p. 108 (as *A. marginata*)

A. marginata var. *musaeformis* Postels and Ruprecht
Postels and Ruprecht, 1840, p. 11.

A. nana Schrader
Schrader, 1903, p. 157, pls. 23-27.
Yendo, 1919, p. 118, pl. 13.
Setchell and Gardner, 1925, p. 636.
Smith, 1944, p. 146.
Scagel, 1957, p. 108.

A. tenuifolia f. *amplior* Setchell and Gardner
Setchell and Gardner, 1903, p. 274.
Scagel, 1957, p. 109.

A. tenuifolia f. *tenuifolia* Setchell, in Collins, Holden and Setchell
Collins, Holden and Setchell, 1901, p. 45 (as *A. tenuifolia*)
Yendo, 1919, p. 97, pl. 8 (as *A. pylaii* (Bory) Greville).
Scagel, 1948, p. 10 (as *A. tenuifolia*); 1957, p. 109.

A. valida f. *longipes* Setchell and Gardner
Setchell and Gardner, 1903, p. 279.
Scagel, 1957, p. 110.

A. valida Kjellman and Setchell f. *valida*
Setchell and Gardner, 1903, p. 278, pl. 21 (as *A. valida*)
Scagel, 1957, p. 110.

The taxonomy of Alaria is in some confusion by reason of the variability of the genus and the inadequacy of some of the descriptions. Variations caused by changes in environment and age have not been studied extensively (Yendo, 1919, p. 1). Yendo notes a number of these variations in a qualitative manner. The relative length of stipe and rachis varies with age, and the length of the stipe is greater in shade, deep water, and less saline water (p. 10-11). The angle formed by the merging of the lamina with the main axis varies with the rate at which the individual is growing at the time (p. 13). The lamina tends to be thinner and broader in deeper, quieter, or less saline water (p. 13-14). The general shape of the lamina is a poor criterion, because most of this is usually worn away in mature individuals (p. 14). It is also noted that a study of herbarium material while the student is out of touch with field conditions is particularly dangerous, because there is a strong bias in collection towards small and perhaps immature specimens, and because specimens may become distorted upon drying.

There is a marked disagreement between Yendo (1919) and Setchell and Gardner (1925) about cryptostomata characters. The only moderately constant characters which can at present be used in a key are those concerning the gross morphology of the fertile sporophyll. These include number, shape of the base, proportion of length to breadth, thickness in relation to that of the lamina, and topography of the sorus.

The degree of tapering in the rachis and of robustness in the stipe are also sometimes useful. These criteria also have the additional advantage that they exclude immature forms, and a few peculiar specimens which may be infertile hydrids.

Key to the species and forms of *Alaria* found in British Columbia.

1 Sporophylls noticeably thicker than the lamina; surface of the sporophylls smooth; sori covering the greater part of the sporophyll, except a narrow even margin, and a small area near the distal end: sorus with distinct boundaries -- 2

1 Sporophylls not noticeably thicker than the lamina: surface of the sporophylls may be rough; sorus generally restricted to the proximal half or less of the sporophyll, sometimes with indistinct boundaries, particularly in the case of the distal one -- 4

2 The base of the majority of sporophylls cordate and asymmetrical -- *A. marginata* Postels and Ruprecht

2 The base of the majority of sporophylls acute and symmetrical -- *A. valida* Kjellman and Setchell -- 3

3 Stipe more than six centimeters long -- *A. valida* f. *longipes*

3 Stipe less than six centimeters long-- *A. valida* f. *valida*

4 Sporophylls more or less pinnately arranged, becoming more crowded distally, some of the proximal spaces being more than one centimeter long; stipe and rachis more than 10 centimeters long; less than 20 sporophylls -- *A. tenuifolia* -- 5

4 Sporophylls crowded so that arrangement is not apparent; stipe and rachis less than ten centimeters long; more than 20 sporophylls; rachis evenly tapering along its whole length -- *A. nana*

5 Sporophylls longer than the maximum breadth of the lamina, and more than one third that distance in breadth -- *A. tenuifolia* f. *amplior*

5 Sporophylls not reaching above dimensions -- *A. tenuifolia* f. *tenuifolia*

This key is designed mainly for use in the field. The thickness of the sporophylls and the taper of the rachis may be changed by pressing and drying.

It is not too realistic to consider the forms very carefully when the species themselves are in doubt, but they are included for the sake of completeness.

Alaria marginata Postels and Ruprecht

While Postels and Ruprecht (1840) do not provide an illustration of this entity, their description (p. 11) is quite detailed. That part of it which deals with the sporophylls is as follows:

> ".... : pinnis linearibus, apice at basi rotundatis, stipitatis, coriaceis, margine integerrimus, planis, fascia nitida cinctis. ...."

The parallel Russian description is merely a translation of this. There seems little doubt that this is the entity illustrated in Yendo (1919, pl. 6 and below, Fig. 33). The illustrations by Setchell and Gardner (1925, pl. 28) and Scagel (1948, fig. 5) are very similar to each other. They differ from Yendo in that the bases of the sporophylls are broad, but not cordate, the sori are not shown, and the base of the lamina is more obtuse. The illustration by Smith (1944, pl. 28) is again different. The sori cover only a part of the sporophylls, the sporophylls are less crowded, and the base of the lamina is acute. Finally Postels and Ruprecht (1840, p. 11) describe another variety, musaeformis. The description of this entity seems to be inadequate. It seems to be based on "lamina pinnatifida", which would seem to be simply the tattered appearance most Alaria laminae assume when they have been partly worn away.

Thus, while there is no doubt that the form with cordate bases of the sporophylls is A. marginata, opinion differs about where the line should be drawn between A. marginata and

A. valida Kjellman and Setchell (p. 95, below). There seems to have been a tendency to identify some of these as *A. valida* when they are actually *A. marginata* (Doty 1947a, p. 32).

Some of the variants seem to be different stages in the life cycle of the same entity. The only way to prove this conclusively is to follow the progress of marked plants. This could not be brought to a successful conclusion in this investigation. However, an examination of the material collected permitted some tentative explanations. The criteria used to distinguish a younger plant from an older one were the presence of a greater proportion of infertile sporophylls, less extensive sori on the fertile sporophylls, fewer sporophylls, and smaller sporophylls. A relatively smooth stipe, with no traces of previous sporophylls was also taken as an indication of a younger plant. Only plants which were fertile to some degree were considered. The size of the plant itself does not appear to be a reliable criterion.

The confusion between *A. marginata* and *A. valida* seems to obtain from it being possible for young forms of *A. marginata* to be very similar to an older *A. valida*. Thus Figure 34 much resembles the type of *A. valida* f. *valida* pictured by Setchell and Gardner (1903, pl. 21). The sporophylls seem usually to develop cordate bases after they are almost entirely fertile. However, the development of *A. marginata* is extremely variable and a great number of variants appear occasionally.

There is another type of variation in *A. marginata*, in the arrangement of the sporophylls. One extreme, called variant Number 1 in this discussion, has the origins of the sporophylls grouped closely together (Fig. 33). The base of the lamina is often broad. In variant Number 2, the sporophylls are more widely spaced and more or less pinnately arranged (Fig. 35). These do not seem to be part of the same developmental sequence, since young and mature individuals of both types were found, and there appeared to be a rough geographical distribution of these two variants. (Fig. 41). However, a complete range of intermediates between the two was found. It was decided that formal description of variant Number 2 as a new entity was not justified. It may be an environmental effect.

Alaria nana Schrader

This is a fairly distinct species by virtue of its characteristic position high in the intertidal zone on exposed coasts. The young and the old forms are shown in Figure 37. The old form may occasionally key out in the key on page 88 as *A. valida* f. *longipes* but the two entities are on a basis of arrangement and number of sporophylls quite distinct. *A. nana* characteristically has a robust, erect stipe. The lamina is usually almost entirely worn away.

Alaria tenuifolia Setchell

This species is found in more sheltered waters. The sporophylls are very variable in shape. Material collected of this species was inadequate to permit any deductions about its development. The sporophylls of *Alaria tenuifolia* f. *amplior* often have a cordate base, but they are quite distinct from *A. marginata*. (Figs. 39, 33).

Alaria valida Kjellman and Setchell

As noted above (p.), until A. valida is seen in its type locality (Whidbey Island), there is a tendency to identify some A. marginata as A. valida. The writer has examined the material filed under A. valida in the Herbaria of the University of British Columbia and of the University of California. UC 463988, 463989 (Sooke) and UBC 176 (Nr. Hope Island) are definitely A. marginata. UC 633999 (Table Island) is immature, but could well be A. marginata. UC 395392 (Neah Bay) is mounted so that the sporophylls can not be seen. It could well be A. valida. Except for the co-type from Unga, Alaska (UC 96671), the known distribution of A. valida is restricted to the more sheltered portions of Juan de Fuca Strait and Queen Charlotte Strait (UBC 205).

Two forms of A. valida have been described, A. v. f. valida (in Setchell and Gardner, 1903, p. 278) and A. v. f. longipes Setchell and Gardner (1903, p. 279). The illustration of A. v. f. valida (pl. 21) is a good likeness of the type specimen, UC 96663. However, the thick sporophylls have not bee indicated too well. There is a co-type, UC 96671, from Unga, Alaska, which appears to be a different entity. The stipe is very robust, tapering sharply at the top, where the sporophylls are crowded. It resembles the older individuals of A. nana (Fig. 40,a), but is much larger. The type specimen of A. v. f. longipes is not labelled, but appears to be

UC 96666. It appears to be the younger individual of *A. v.* f. *valida*. It can be confused with *A. tenuifolia* (Figs. 41 and 43), but they may be distinguished by sporophyll thickness. Usually the sorus of *A. valida* covers more of the sporophyll than does that of *A. tenuifolia*.

Distribution of *Alaria*.

The geographical distribution of the various species of *Alaria* is presented in Figure 41. *A. nana* occurs in localities most exposed to surf. *A. tenuifolia* may be found in the more sheltered localities north and east of Race Rocks. *A. valida* and *A. marginata* both occur on more or less open coasts. *A. marginata* is characteristic of the more exposed, and *A. valida* of the more sheltered localities. These latter two species are the most easily confused of those present on the coast.

Alaria nana occupies a distinct zone high in the intertidal zone (Fig. 41). This zone is definitely lower in the more easterly stations. The other species have an upper limit low in the intertidal zone. At Station 29, *A. tenuifolia* occupies a zone above one of the species with thicker sporophylls, either *A. valida* or *A. marginata*.

The distinct distributions of the various species of *Alaria* eliminates the possibility that these species are merely different stages in the development of the same entity. There still remains the possibility that they are the effect of different environments on the same entity. A number of individuals were collected which appear to be intermediate between the two species. Examples of these are TW 10, 260, 313 (intermediate between *A. nana* and *A. marginata*); TW 111, 117 (Between *A. marginata* and *A. tenuifolia*); TW 118, 251 (between *A. valida* and *A. tenuifolia*); TW 8, 231 (between *A. marginata* and *A. valida*); and TW 262 (between *A. tenuifolia* and *A. nana*). Some of these came from the Race Rocks area, where the distributions of the four species come together.

Egregia menziesii (Turner) Areschoug subsp. *menziesii*.

Areschoug, 1876, p. 67 (as *E. menziesii*)
Setchell and Gardner, 1903, p. 271: 1925, p. 647.
Smith, 1944, p. 149, pl. 30, fig. 1.
Scagel, 1948, p. 10, 1957, p. 111.
MacMillan, 1902.

Egregia extends in from the open coast to Goose Island and Whidbey Island (Scagel, 1957). It becomes very scattered towards the limits of its geographical distribution. Thus, while it was not found at Gordon Head (Stn. 32) in this investigation, there is no reason to doubt the report from here noted by Scagel (1957). The upper limit of *Egregia* decreases slightly in height in an easterly direction. The statement by MacMillan (1902) that *Egregia* is the highest of all Laminariales is difficult to understand, since *Postelsia*, *Alaria nana*, and *Hedophyllum* are all higher in their upper limits.

Order Chordariales.

Family Corynophlaeaceae

<u>Leathsia</u> <u>difformis</u> (Linnaeus) Areschoug.

Areschoug, 1947, p. 376.
Setchell and Gardner, 1903, p. 249, pl. 45, figs. 65, 66 (in part as <u>L. amplissima</u> Setchell and Gardner); pl. 513, pl. 40, fig. 52.
Smith, 1944, p. 114, pl. 15, fig. 2.
Doty, 1947a, p. 34.
Scagel, 1957, p. 77.

The vertical distribution of L. difformis is shown in Figure 43. The alga is of frequent but scattered occurrence, often on the flat tops of rocks, or epiphytic on <u>Rhodomela</u>. <u>Leathsia</u> is very common at Station 13.

Family Chordariaceae

<u>Heterochordaria</u> <u>abietina</u> (Ruprecht) Setchell and Gardner.

Setchell and Gardner, 1903, p. 251, pl. 18, fig. 16 (as <u>Chordaria</u> <u>abietina</u> Ruprecht); 1925, p. 550, pl. 36, figs. 18, 19 and pl. 91.
Kylin, 1940, p.42.
Smith, 1944, p. 98, pl. 14, fig. 3.
Doty, 1947a, p. 33.
Scagel, 1957, p. 80.

The vertical distribution of <u>Heterochordaria</u> is shown in Figure 43. The alga has a scattered but widespread distribution on rocks throughout the range. It is particularly common at Station 23.

Order Desmarestiales.

Family Desmarestiaceae.

Desmarestia intermedia Postels and Ruprecht

Postels and Ruprecht, 1840, p. 13, pl. 26.
Pease, 1917, p. 385 (as *D. aculeata*)
Setchell and Gardner, 1925, p. 564.
Doty, 1947a, p. 35.
Blinks, 1957, p. 269.
Scagel, 1957, p. 82.

D. munda Setchell and Gardner

Setchell and Gardner, 1924, p. 7; 1925, p. 567, pl. 89.
Smith, 1944, p. 121, pl. 17, fig. 1.
Doty, 1947a, p. 35.
Blinks, 1951, p. 269.
Scagel, 1957, p. 84.

Desmarestia is a variable genus, the taxonomy of which is in some confusion (Scagel, 1957, p. 85). The flattened forms in the area studied are definitely *D. munda*. However, among the filiform species, the distinction between *D. media* Setchell and Gardner and *D. intermedia* is not clear. The material collected was identified as *D. intermedia* mostly on the basis of the fasciculate branching mentioned by Setchell and Gardner (1925, p. 564).

The ecological relationships between *D. intermedia* and *D. munda* are not apparent. The two species are often found together (Figure 43), and appear to reach the same height in the intertidal zone. The extreme acidity of the cell sap of *Desmarestia* (Blinks, 1951, p. 269) makes it extremely vulnerable to desiccation. This factor probably limits the upward extension of the plant into the intertidal zone. Both species are common at Station 9.

Order Fucales.

Family Fucaceae.

Fucus distichus (Linnaeus) emend. Powell.

Literature and taxonomy.

Agardh, 1820, p. 92 (as _F. evanescens_); p. 97 (as _F. furcatus_)
Harvey, 1862, p. 163.
Setchell and Gardner, 1903, p. 281 (as _F. evanescens_)
Gardner, 1922, p. 16, pls. 1-17 (as _F. furcatus_), p. 36, pls. 35-59 (as _F. evanescens_)
Smith, 1944, p. 152, pl. 32, fig. 2 (as _F. furcatus_ C. A. Agardh)
Doty, 1947a, p. 44 (as _F. furcatus_ and _F. evanescens_)
Silva, 1953, p. 227 (as _F. gardneri_)
Scagel, 1957, p. 114 (as _F. evanescens_), p. 116 (as _F. gardneri_)
Powell, 1957a, 1957b (as _F. distichus_ (L.) emend Powell.)

The taxonomy of the species of _Fucus_ on the Pacific coast of North America is in some confusion. The genus is extremely variable, many of the past descriptions have been inadequate, and the genus has not yet been studied critically on this coast from an ecological point of view.

Fucus furcatus and _F. evanescens_ were described by Agardh from specimens which were said to have been collected from North Pacific shores by Chamisso (Gardner, 1922, p. 6). Gardner (1922) described 13 forms of _F. furcatus_ and deals with 21 forms of _F. evanescens_. Some of the latter are described by himself, the rest by Kjellman (1877, 1889), Setchell and Gardner (1903), and Stroemfelt (1886). Smith (1944) referred all _Fucus_ in the Monterey Peninsula to _F. furcatus_ f. _luxurians_ Gardner. Doty (1947a) makes no comment on the forms of _F. furcatus_ but states that the forms of *F. evanescens* are indistinct, except for *F. evanescens* f. *stellatus* Gardner. Silva (1953) redescribed *F. furcatus* as *F. gardneri* on the grounds that the former name is a homonym of the previous *F. furcatus* Esper. Silva did not make the transfers of the various forms of *F. furcatus* C. A. Agardh. Scagel (1957) made most of these transfers, while noting (p. 118) that the validity of the various forms is questionable. Powell (1957a) reduced all hermaphroditic species of *Fucus* which possess caecostomata to synonomy under *Fucus distichus* (L.) emend Powell. *F. furcatus* and *F. evanescens* are among the species so reduced.

The 34 forms of *F. distichus* which Gardner has described or noted from the Pacific coast of North America should be reduced to synonomy, and not transferred to *F. distichus*. The genus is so variable that as they stand they are more of a hindrance than a help in identifying specimens of *Fucus*. Doty's comments (1947a, p. 45) throw sufficient doubt on the validity of the forms of *F. evanescens*. The collections made in this investigation were with some doubt identified as *F. evanescens* f. *robustus* Setchell and Gardner, *F. furcatus* f. *typicus* Gardner, *F. furcatus* f. *abbreviatus* Gardner, *F. furcatus* f. *reflexus* Gardner, *F. furcatus* f. *rigidus* Gardner, and *F. furcatus* f. *variabilis* Gardner, according to Gardner's descriptions. The occurrence of these collections was then plotted against time and place in a manner similar to Figure 26. The occurrence of these forms appeared to have no relationship either to time or place. This throws sufficient doubt on the validity of the forms of _F_. _fucatus_ C. A. Agardh as described by Gardner.

Powell (1957a) describes four subspecies of _F_. _distichus_: _F_. _distichus_ subsp. _distichus_ (Linnaeus) emend. Powell, _F_. _distichus_ subsp. _anceps_ (Harvey et Ward ex Carruthers) Powell, _F_. _distichus_ subsp. _edentatus_ (De la Pylaie) Powell, and _F_. _distichus_ subsp. _evanescens_ (C. Agardh) Powell. However, it was decided not to describe the material collected to subspecies, until more extensive comparisons are made of North American and European populations of _Fucus distichus_.

Distribution.

The upper and lower limits of _Fucus distichus_ are shown in Figure 43. _Fucus_ forms a prominent zone on the beach at almost all localities except those most exposed to surf. In such exposed localities (Stn. 10) a very scattered dwarf form with a very robust stipe sometimes occurs. Its appearance is similar to _Pelvetiopsis_, and it has some resemblance to _F_. _distichus_ subsp. _anceps_.

Pelvetiopsis limitata (Setchell) Gardner f. _limitata_
Gardner, 1910, p. 127 (as _P_. _limitata_ and _P_. _l_. f. _typica_)
Setchell and Gardner, 1925, p. 703 (as _P_. _limitata_ and _P_. _l_. _typica_)
Smith, 1944, p. 155 (as _P_. _limitata_)
Doty, 1947a, p. 45 (as _P_. _limitata_ and _P_. _l_. f. _typica_)
Scagel, 1957, p. 122

Pelvetiopsis was collected only at Station 1 of the Vancouver Island coast studied. It occupies a zone immediately above _Fucus_, between 8.9 and 9.8 feet. The alga may also occur at Stations 2, 3 and 4.

Family Cystoseiraceae.

Cystoseira geminata C. Agardh.

C. Agardh, 1824, p. 286.
Setchell and Gardner, 1903, p. 285; 1925, p. 706
(as Cystophyllum geminata (Agardh) J. Agardh)
Fensholt, 1955, p. 313, figs. 1-10, 35-39.
Scagel, 1956, p. 122, figs. 7-14.
Scagel, 1957, p. 122.

Cystoseira has a very scattered occurrence along the more exposed coasts studied. This distribution of this alga is shown in Figure 44. It was found to be most abundant close to Station 15.

Family Sargassaceae

Sargassum muticum (Yendo) Fensholt.

Yendo, 1905, p. 158.
Fensholt, 1955, p. 313, figs. 11-16, 40-51.
Scagel, 1956, p. 5, figs. 1-6.
Scagel, 1957, p. 123.

Sargassum usually forms a continuous zone near low water mark in very sheltered areas, such as Stations 16 and 17. The distribution of this alga is shown in Figure 44.

Phylum Rhodophyta

Sub Class Bangiophycidae

Order Bangiales

Family Bangiaceae.

Porphyra schizophylla Hollenberg, in Smith and Hollenberg.

Smith and Hollenberg, 1943, p. 213, figs. 6, 7.
Smith, 1944, p. 173, pl. 39, fig. 4; pl. 40, fig. 4.
Doty, 1947b, p. 161.

Porphyra perforata J. Agardh

Agardh, 1883, p. 69.
Hus, 1900, p. 63; 1902, p. 202, pl. 20, figs. 4-10.
Setchell and Gardner, 1903, p. 289.
Kylin, 1925, p. 7.
Smith, 1944, p. 172, pl. 39, fig. 5.
Doty, 1947b, p. 161.
Scagel, 1957, p. 130.

The vertical distribution of *Porphyra* is shown in Figure 45. Two zones of the algae in the intertidal zone are apparent. The plants in the upper zone are usually in very poor shape during the summer. Collections (TW1171-1173) from this zone at Stations 4, 10, and 14 agree reasonably well with the description of *P. Schizophylla* Hollenberg. However, many specimens do not fit the description very well. The excentric striations of the gelatinous matrix which parallel the inner faces of the cells and the other distromatic *Porphyras* reported from this area is not clear. Moreover, one collection (TW1248) from the upper *Porphyra* zone is monostromatic, with very thick layers of mucilage.

The lower zone consists mainly of *Porphyra perforata*. The lower zone also includes a number of distromatic individuals, some of which seem to be related to *P. schizophylla* as noted above.

Sub Class Florideophycidae.

Order Cryptonemiales.

Family Endocladiaceae.

<u>Endocladia</u> <u>muricata</u> (Harvey) J. Agardh.
Agardh, 1847, p. 10.
Setchell and Gardner, 1903, p. 297 (as <u>E</u>. <u>m</u>. f. <u>compressa</u> and <u>E</u>. <u>m</u>. f. <u>inermis</u>)
Kylin, 1925, p. 28.
Smith, 1944, p. 211, pl. 47, figs. 3, 4.
Doty, 1947b, p. 166.
Scagel, 1957, p. 160.

<u>Endocladia</u> <u>muricata</u> shows some variability. Some individuals have flattened branches and some have reduced spines. These variants were described by Setchell and Gardner (1903) as <u>E</u>. <u>m</u>. f. <u>compressa</u> and <u>E</u>. <u>m</u>. f. <u>inermis</u> respectively. The types were collected from tide pools in the vicinity of Friday Harbour. These variants were noted in the material collected. TW1022 is an example of the form with flattened branches, and TW1001 of that with reduced spines. The alga was never found in tide pools. The variants, as found on the open beach, do not seem to be sufficiently distinct to be revived as taxonomic entities.

<u>Endocladia</u> is common throughout the area studied, but is absent from very sheltered areas, such as Stations 16, 17, 26 and 28. The vertical distribution of <u>Endocladia</u> is shown in Figure 45.

Order Gigartinales.

Family Gigartinaceae.

Gigartina agardhii Setchell and Gardner

Setchell and Gardner, 1933, p. 290, pl. 64.
Smith, 1944, pl. 69, fig. 2.

G. corymbifera (Kutzing) J. Agardh

Agardh, 1876, p. 202.
Setchell and Gardner, 1933, p. 275, pls. 53, 54.
Smith, 1944, p. 281, pl. 66.
Scagel, 1957, p. 185.

G. cristata (Setchell) Setchell and Gardner

Setchell and Gardner, 1933, p. 289, pl. 63.
Smith, 1944, p. 283, pl. 69, fig. 1.
Doty, 1947b, p. 180.
Scagel, 1957, p. 185.

G. mamillosa (Goodenough and Woodward) J. Agardh.

Agardh, 1851, p. 278.
Setchell and Gardner, 1933, p. 285.
Doty, 1947b, p. 180.
Scagel, 1957, p. 187.

G. papillata (C. Agardh) J. Agardh, in C. Agardh.

Agardh, 1846, p. 19.
Setchell and Gardner, 1933, p. 287, pl. 61.
Smith, 1944, p. 283, pl. 70, fig. 2.
Scagel, 1957, p. 188.

Gigartina is a very variable genus in need of further study.

G. corymbifera has an upper limit of 1.4 feet at Station 32. The other four species occur at intermediate heights in the intertidal zone. The vertical distribution of species of the mid-intertidal *Gigartina* is shown in Figure 45.

Iridaea heterocarpa Postels and Ruprecht

Postels and Ruprecht, 1840, p. 18.
Kylin, 1925, p. 28.
Setchell and Gardner, 1937, p. 170. (as *Iridophycus heterocarpum*)

Smith, 1944, p. 291, pl. 73, fig. 1. (as *Iridophycus heterocarpum*)
Doty, 1947b, p. 183. (as *Iridophycus heterocarpum*)
Scagel, 1957, p. 191.

Much of the *Iridaea* collected was sterile and so difficult to determine to species. *I. heterocarpa* appeared to be the most common species. The upper limit of the *Iridaea* zone is shown in Figure 45.

Order Rhodymeniales.

Family Rhodymeniaceae.

Halosaccion glandiforme (Gmelin) Ruprecht.
Ruprecht, 1851, p. 279.
Setchell and Gardner, 1903, p. 43.
Kylin, 1925, p. 43.
Smith, 1944, p. 298, pl. 73, figs. 6, 7.
Doty, 1947b, p. 186.
Scagel, 1957, p. 194.

The vertical distribution of *Halosaccion* is shown in Figure 45. The alga occurs either in a solitary habit, or in dense patches. The gregarious habit is more common on the open coast (Stns. 1 to 5). *Halosaccion* grows on rocks or epiphytically on *Odonthalia* and *Rhodomela*.

Order Ceramiales

Family Ceramiaceae.

Callithamnion pikeanum var. *laxum* (Setchell and Gardner) Doty.

Setchell and Gardner, 1903, p. 339 (as *Ceratothamnion pikeanum* f. *laxum*)
Gardner, 1927, p. 407, pl. 88 (as *Callithamnion laxum* (Setchell and Gardner) Setchell and Gardner)
Doty, 1947b, p. 191.
Scagel, 1957, p. 207 (as *Callithamnion laxum* Setchell and Gardner, in Gardner)

C. *pikeanum* var. *pacificum* (Harvey) Setchell and Gardner, in Gardner.

Harvey, 1862, p. 175 (as *Callithamnion arbuscula* var. *pacifica*)
Gardner, 1927, p. 406, pl. 87, figs. 2, 3.
Doty, 1947b, p. 191.
Scagel, 1957, p. 207.

C. *pikeanum* Harvey var. *pikeanum*.

Harvey, 1853, p. 230 (as *C*. *pikeanum*)
Kylin, 1925, p. 56 (as C. *pikeanum*)
Gardner, 1927, p. 405, pl. 57, fig. 1 (as *C*. *pikeanum*)
Smith, 1944, p. 318, pl. 81, fig. 2 (as *C*. *pikeanum*)
Doty, 1947b, p. 191 (as *C*. *pikeanum*)
Scagel, 1957, p. 208.

These three varieties seem to belong to one species, *C*. *pikeanum*. In the area studied, *C*. *pikeanum* includes all *Callithamnion* plants which have at least the first three orders of branches heavily corticated, and a distribution in the intertidal zone. The three varieties are distinguished mainly on a basis of their general habit. *C*. *p*. var. *pikeanum* has a group of relatively unbranched percurrent axes, with bushy secondary branches distinct from one another and mostly of equal length. *C*. *p*. var. *pacificum* has a pyramid-like form, since the secondary branches are not distinct from one another, and decrease in length distally. *C. p.* var. *laxum* usually has the secondary branches loosely arranged. These habits are well shown in Gardner's photographs.

The vertical distribution of *C. pikeanum* is shown in Figure 45.

Family Rhodomelaceae.

Rhodomela larix (Turner) C. Agardh.

Agardh, 1822, p. 376.
Setchell and Gardner, 1903, p. 330.
Kylin, 1925, p. 75.
Smith, 1944, p. 374, pl. 97, fig. 1.
Doty, 1947b, p. 196.
Scagel, 1957, p. 241.

The vertical limits of Rhodomela are shown in Figure 45. They are very variable, because the plant often forms a belt around tide pools and is frequently associated with water seepage.

Odonthalia floccosa (Esper) Falkenberg.

Falkenberg, 1901, p. 607.
Kylin, 1925, p. 75.
Smith, 1944, p. 375, pl. 97, fig. 2.
Doty, 1947b, p. 197.
Scagel, 1957, p. 242.

Some individuals of this species may be confused with Rhodomela, but the latter can usually be distinguished by the blunt tips and spiral arrangement of its branchlets. O. floccosa is the higher of the two species of Odonthalia encountered in the intertidal zone. Its upper limit is shown in Figure 45.

Odonthalia washingtoniensis Kylin

Kylin, 1925, p. 76.
Doty, 1947b, p. 197.
Scagel, 1957, p. 245.

This species has a somewhat scattered distribution, mainly in the hollows between boulders at about low water mark.

Phylum Chlorophyta

Order Ulotrichales

Family Monostromaceae.

Monstroma fuscum var. blytii (Areschoug) Collins.

Collins, 1903, p. 12.
Setchell and Gardner, 1920, p. 243.
Scagel, 1957, p. 34.

Monstroma zostericola Tilden

Tilden, 1900, p. 388 (IV)
Setchell and Gardner, 1903, p. 209 (as M. leptodermum Kjellman)
Setchell and Gardner, 1920, p. 238, pl. 14, figs. 12, 13.
Smith, 1944, p. 43.
Doty, 1947a, p. 11.
Scagel, 1957, p. 36.

Family Ulvaceae

Enteromorpha intestinalis (Linnaeus) Link

Link, 1820, p. 5.
Setchell and Gardner, 1903, p. 212; 1920, p. 252.
Smith, 1944, p. 49, pl. 5, figs. 4-6.
Doty, 1947a, p. 14.
Scagel, 1957, p. 39.

Enteromorpha linza (Linnaeus) J. Agardh

Agardh, 1883, p. 134.
Setchell and Gardner, 1920, p. 262, pl. 12, figs. 1-4 (as Ulva linza Linnaeus)
Smith, 1944, p. 44, pl. 3, figs. 4, 5.
Doty, 1947a, p. 18, pl. 1, figs. 7-9.
Scagel, 1957, p. 41.

Enteromorpha angusta (Setchell and Gardner) Doty.

Setchell and Gardner, 1920, p. 264, pls. 22, 26, fig. 1 (as Ulva angusta Setchell and Gardner)
Smith, 1944, p. 45, pl. 4, figs. 1-3.
Doty, 1947, p. 20, pl. 1, figs. 1-6.

Enteromorpha vexata (Setchell and Gardner) Doty.

Setchell and Gardner, 1920, p. 271, pl. 17, figs. 4-7 (as Ulva vexata Setchell and Gardner)
Doty, 1947a, p. 21, pl. 1. figs. 12-14.

Ulva lactuca Linnaeus

Linnaeus, 1753, p. 1163.
Setchell and Gardner, 1920, p. 265.
Smith, 1944, p. 45, pl. 3, figs. 6, 7.
Scagel, 1957, p. 44.

Ulva taeniata (Setchell) Setchell and Gardner.

Setchell and Gardner, 1920, p. 273, pl. 23.
Smith, 1944, p. 48, pl. 3, figs. 1-3.
Doty, 1947a, p. 8, pl. 2, figs. 11, 12: pl. 4, figs. 3, 4.

Ulva lobata (Kutzing) Setchell and Gardner

Setchell and Gardner, 1920, p. 268.
Smith, 1944, p. 46, pl. 4, figs. 4, 5.
Doty, 1947a, p. 10.

Monostroma zostericola is epiphytic on Phyllospadix. The specimen collected of Enteromorpha intestinalis probably came from a tide pool. E. vexata is epiphytic on Egregia. Specimens of the rest of the members of the Ulotrichales listed above were collected from the zone presented as miscellaneous Ulotrichales in Figure 46. The taxonomic heterogeneity of this zone probably contributes to the great variability of its upper limit.

Order Schizogoniales.

Family Prasiolaceae

Prasiola meridionalis Setchell and Gardner

Setchell and Gardner, 1920, p. 278, pl. 17, fig. 3, pl. 19, fig. 8, pl. 20, fig. 1.
Smith, 1944, p. 53, pl. 2, figs. 10-15.
Doty, 1947a, p. 22.
Scagel, 1957, p. 47.

Rosenvingiella constricta (Setchell and Gardner) Silva

Gardner, 1917, p. 384, pl. 32, fig. 5 (as *Gayella constricta* Setchell and Gardner)
Setchell and Gardner, 1920, p. 280, pl. 21, figs. 5-10 (as *Gayella constricta*)
Smith, 1944, p. 54, pl. 2, figs. 8, 9. (as *Gayella constricta*)
Silva, 1957, p. 41.
Scagel, 1957, p. 47.

It is possible that *Ronsenvingiella constricta* is a stage in the development of *Prasiola meridionalis* (Scagel, 1957, p. 47). The two entities are certainly extremely closely associated in their occurrence in the field. They characteristically occupy the same zone. Material collected from Station 15 was *Prasiola* only in January, but mixed *Prasiola* and *Rosenvingiella* in June.

The vertical distribution of *Prasiola* and *Rosenvingiella* is shown in Figure 46. At all stations the zone is found, it is limited to the top of a single boulder or outstanding rock outcrop. It is probable that these algae obtain nutrients from bird droppings rather than from the sea water. The boulders covered by the plants seem to be those places where sea birds can overlook a large area of water at high tide and yet be out of reach of heavy spray.

Order Cladophorales.

Family Cladophoraceae

Spongomorpha coalita (Ruprecht) Collins

Collins, 1909, p. 361.
Setchell and Gardner, 1920, p. 230, pl. 16, fig. 4, pl. 32.
Smith, 1944, p. 65, pl. 6, fig. 1.
Doty, 1947a, p. 24.
Scagel, 1957, p. 57.

S. mertensii (Ruprecht) Setchell and Gardner

Setchell and Gardner, 1920, p. 227.
Doty, 1947a, p. 24, pl. 6, figs. 10-12.
Scagel, 1957, p. 57.

S. spinescens Kutzing

Kutzing, 1849, p. 418.
Setchell and Gardner, 1920, p. 229.
Doty, 1947a, p. 25, pl. 5, figs. 1, 5, 6.
Scagel, 1957, p. 58.

The upper and lower limits of *Spongomorpha* spp. are shown in Figure 46. The alga has a common but scattered occurrence at most stations. It is very common at Station 14. The most frequently encountered species was *S. coalita*, which can generally be recognized by its particularly rope-like habit.

Order Siphonales

Family Codiaceae.

Codium fragile (Suringar) Hariot.

Hariot, 1889, p. 32.
Setchell and Gardner, 1920, p. 171, pls. 28, 29.
Smith, 1944, p. 75, pl. 9, fig. 5.
Taylor, 1945, p. 72.
Doty, 1947a, p. 30.
Silva, 1951, p. 96.
Scagel, 1957, p. 64.

C. setchellii Gardner

Gardner, 1919, p. 489, pl. 42, figs. 11, 12.
Smith, 1944, p. 75, pl. 9, fig. 4.
Doty, 1947a, p. 30.
Taylor, 1945, p. 68.
Silva, 1951, p. 83.
Scagel, 1957, p. 65.

The upper limits of these two species of Codium are shown in Figure 46. Codium Setchellii is restricted to more shaded situations than is C. fragile. Codium is particularly common at Station 15.

Divison Tracheophyta

Sub Division Pteropsida

Class Angiospermae

Sub Class Monocotyledonae

Family Naiadaceae

Phyllospadix scouleri Hooker

Hooker, 1840, (2): 171.
Morong, 1893, p. 65, pls. 73, 74.
Taylor, 1909, p. 30.
Jepson, 1951, p. 67.

All fruiting *Phyllospadix* collected belonged to the species *P. scouleri*.

The geographical and vertical distribution of *Phyllospadix* is shown in Figure 47. The plant is found on the rocky shores of more exposed coasts. The factor which restricts it to exposed coasts does not seem to be salinity, since the plant can be found in tidepools which are much freshened by the inflow of fresh water streams.

Zostera marina Linnaeus

Linnaeus, 1753, p. 968.
Morong, 1893, p. 62, pls. 69, 71.
Taylor, 1909, p. 29.
Jepson, 1951, p. 66.

Fertile specimens of *Zostera* were not found, but *Z. marina* is the only species reported from British Columbia. *Zostera* forms a zone with an upper limit of about 1.0 feet on sandy or muddy beaches in the most sheltered sections of the area studied.

The geographical distribution of *Zostera* is shown in Figure 47. The *Phyllospadix* and *Zostera* zones seem almost to merge at the entrance to Sooke Harbour. At Bentinck I. and Gordon Head (Stn. 32) the two plants occupy adjacent bays.

Phyllum Mollusca

Class Lamellibranchiata

Order Filibranchiata

Family Mytilidae

Mytilus californianus Conrad

Johnson and Snook, 1927, p. 427, fig. 387.
Young, 1941.
Coe and Fox, 1942.
Fox and Coe, 1943.
Young, 1945.
Rao, 1953a.
Rao, 1953b.
Segal, Rao, and James, 1953.
Dehnel, 1956.

Mytilus californianus is one of the classic examples of an organism which is restricted to open exposed coasts. It is the most thoroughly investigated of such organisms on the Pacific coast of North America. Young (1941) found that the sex cells and larvae are unfavourably affected by salinities of less than 29.6 ‰. However, he thinks that this is not a complete explanation of the geographical distribution of the animal. Baird and Drinnan (1957, working with *M. edulis*) and Rao (1953b) found that the flesh/shell weight ratio was less with those animals which are higher in the intertidal zone. This suggests that starvation may be the limiting factor at higher levels. However, Fox and Coe (1943) found that the calcium from ingested food is inadequate for the formation of the shell. The element must be actively absorbed from the sea water. Baird and Drinnan (1957) mention that there is a possibility that this absorption is favoured by many short submergences as opposed to a few longer ones. Thus, there may be an increase of shell weight up to the point in the middle intertidal zone where the combined action of tide and waves causes a maximum number of short submergences. Young (1941, 1945) notes that there is a great variability between individuals in responses to various stimuli. Partly for this reason, there is much that is still uncertain about the physiological basis of the ecology of this animal.

The vertical and geographical distribution of Mytilus spp. is shown in Figure 48. The records for Stations 13 and 31 are not certain, as they occur on isolated boulders off-shore, where the animals could not be examined critically. The record from Station 13 is probably M. californianus, while that from Station 31 is probably M. edulis. The geographical distribution of M. californianus extends into the approaches of the Strait of Georgia beyond the area investigated. It is found on the southern approaches of Saturna I., but not at Station 36. This inner limit is not too inconsistent with the 29.6 ‰ isohaline (Figure 4.) The upper levels of M. californianus on the open coast often appeared to be denuded on areas of rock which rise above the general level of their immediate vicinity. This may be the effect of crushing by driftwood impelled by surf. In other situations, the upper limit appeared to be raised in places shaded by overhangs.

M. edulis Linnaeus
Johnson and Snook, 1927, p. 428, fig. 388.

M. edulis is characteristic of more sheltered shores (Fig. 48). The vertical limits of the animal are 5.4 and 3.8 feet at Station 17.

Phylum Arthropoda

Sub Phylum Crustacea

Class Cirripedia

Shelford, 1930.
Towler, 1930.
Worley, 1930.
Rice, 1930.
Moore, 1935.

Order Thoracica

Family Chthamalidae

Chthamalus dallii Pilsbry

Johnson and Snook, 1927, p. 269.
Cornwall, 1955, p. 36.

Chthamalus dallii is the highest ranging of the intertidal barnacles in the area investigated. Thus, the upper limit of acorn barnacles shown in Figure 46 is probably the upper limit of *C. dallii*.

Family Scalpellidae

Mitella polymeris (Sowerby).

Johnson and Snook, 1927, p. 261, figs. 212, 221.
Cornwall, 1955, p. 40.

The vertical and geographical distribution of *Mitella* is shown in Figure 49. *Mitella* is usually found in clusters, particularly in crannies oriented up and down the slope of the beach, where the surge of water resulting from wave action is concentrated.

DISCUSSION.

There does not appear to be any distinct phytogeographical boundary in the area studied. The inner limits of various open coast organisms found along the southwest shore of Vancouver Island are usually distinct from one another. These inner limits for a number of the more prominent forms are Postelsia (Stn. 1), Pelvetiopsis (Stn. 1?), Macrocystis (Stn. 15), Lessoniopsis (Stn. 18), Alaria nana (Stn. 23), Mytilus californianus (Stn. 27), Mitella (opposite Trial Is.), Phyllospadix (Stn. 32), and Hedophyllum (Stn. 32).

An inspection of the various upper and lower limits plotted above shows that they vary both in their slope and their variability. Four groups are apparent. First, some are so variable that no pattern can be observed in them (for instance, upper Spongomorpha, Fig. 46.). Second, some are much more variable in the westerly portion of their distribution (for instance, upper Endocladia, Fig. 45.). Third, some have a definite and even slope down from west to east (for instance, upper Phyllospadix, Fig. 47.). Fourth, some are virtually constant at all stations (for instance, upper Cymathere, Fig. 43.).

Most of what is known of the physical environment of the southwest coast of Vancouver Island is either measured at Port Renfrew, Sooke, and Victoria, or is known only as qualitative comparisons of the stretches of coast between Sooke and the other two localities. For instance, tidal factors are measured at Port Renfrew, Sooke, and Victoria; and surf is heavy on the coast from Port Renfrew to Sooke, while it is very slight along the coast from Sooke to Victoria. This situation makes it desirable to compare the observed, or failing that, the interpolated heights of a limit at these three localities. A quantitative means of comparing the characters of a limit along the two stretches of coast, Port Renfrew -- Sooke and Sooke -- Victoria, is also needed.

The 36 limits used (28 upper and 8 lower) were measured at nine or more stations throughout the area studied. The lower limits seem to fall into the same four groups as do the upper limits, so both types were treated together.

Each limit, measured to the nearest one tenth of a foot, as y, was plotted against the headland to headland distance between stations listed in Table IV as x. The unit used for this headland to headland distance is arbitrary, the minimum distance between stations being 1 and the total distance from Station 1 to Station 34 being 100. The unit is about a mile. A straight line to represent each limit was calculated by the method of least squares. Data from Stations 16, 17, 26 and 28 were not used in these calculations. The Y-variance of the data from this line of least squares was calculated for the entire coast from Station 1 to 34, and for the two sections Stations 1-15 and 18-34.

This approach assumes that a line joining the heights actually measured for a limit at each station is linear.

The data were not tested for linearity. However, the standard deviation of the data because of errors in measurement was calculated independently as about 0.6 feet (page 6, above). This would mean that a perfectly linear limit would have a variance of 0.36 from errors of measurement. This should be the minimum variance found, if the figure for the standard deviation is valid, and the limits are linear. Actually, the minimum variance should be less, as some of the data are mean values. The minimum variance for the whole stretch of coast is the upper limit of Cymathere, which is 0.26. The modal variance is between 0.40 and 0.50. Thus the line of least squares is a good approximation of the less variable limits, which are the ones discussed in detail below.

Table IV. Headland to headland distances of stations. (x)

Station	Distance	Station	Distance	Station	Distance
1	0	11	29	24	58
2	6	12	30	25	63
3	7	13	33	27	67
4	8	14	37	29	68
5	15	15	41	30	71
7	20	18	44	31	77
8	24	20	47	32	80
9	25	22	51	33	88
10	26	23	55	34	100

The difference between the variances along the two stretches of coast, Stations 1-15 and Stations 18-34, was tested at the 95 per cent level of significance by means of the F. ratio. Four limits were found to have a significantly greater variance of the stretch of coast from Port Renfrew to Sooke. These limits are listed in Table V. It is probable that a few more limits actually belong in this group, for instance the upper limit of <u>Halosaccion</u>, (Fig. 45) but the difference was not found to be significant. This is because the boundary between the more and the less variable parts of the limit is probably closer to Station 13 than Station 15. Also, all cases where the data plotted are mean values of more than two measurements occur in the western stretch of coast. Both these factors tend to reduce the variance of the limits along the coast from Port Renfrew to Sooke, and so reduce the difference between that variance and the variance along the coast from Sooke to Victoria. However, the existence of this group of limits, which are more variable in the western portion of their distribution, is clearly shown by those levels where the difference was found to be significant. The total of all the variances along the western stretch of coast is significantly greater than the total for the eastern portion. In no case was the variance for the eastern stretch of coast significantly greater than that for the western stretch.

<u>Table V.</u> <u>Limits which are more variable on exposed coasts.</u>
The degrees of freedom are listed in brackets after each variance.

Limit	Organism	Total variance	(f)	Variance(f) Stns.1-15		Variance(f) Stns.18-34		Linear constants m	b
Upper	Acorn barnacles	1.95	(23)	3.34	(12)	0.47	(10)	-0.044	11.6
Upper	<u>Endocladia</u>	1.55	(25)	2.71	(13)	0.32	(11)	-0.032	9.2
Upper	<u>Prasiola</u>	5.87	(9)	10.12	(5)	0.74	(3)	-0.079	17.5
Lower	<u>Prasiola</u>	3.64	(9)	6.45	(5)	0.18	(3)	-0.059	13.9

The divisions made between the other three groups were arbitrary. All limits with a variance of more than 1.50, with no significant difference between the variances of the two sections of coast were placed in the group of variable limits. This group includes 11 limits (Table VI). The variance of 1.50 corresponds to a standard deviation of 1.2 feet, about twice that determined in connection with errors of measurement.

Table VI. Limits which are very variable along the entire coast.

Limit	Organism	Total variance	(f)	m	b
Upper	Nereocystis	4.30	(15)	-0.006	1.2
Upper	Rhodomela	3.77	(12)	-0.027	5.8
Upper	Porphyra schizophylla	3.32	(9)	-0.092	15.2
Upper	Gigartina	3.29	(14)	+0.001	7.4
Upper	Halosaccion	2.64	(13)	-0.065	7.8
Upper	Callithamnion	2.62	(9)	-0.059	7.5
Upper	Leathsia	2.51	(8)	-0.002	4.8
Lower	Mitella	2.06	(16)	+0.004	4.3
Upper	Spongomorpha	1.82	(20)	-0.007	4.6
Upper	Misc. Ulotrichales	1.77	(12)	-0.000	4.8
Lower	Fucus	1.69	(23)	-0.038	6.5

Among the less variable limits, some have a definite slope down from Port Renfrew to Victoria and some do not have a definite slope. Those limits with a slope numerically greater than -0.010 were placed in the group having a definite slope. The remainder were placed in the group having no definite slope. No positive slopes greater than +0.010 were found. A slope of -0.010 means that the Y-intercept of the line of least squares is one foot lower at Station 34 than at Station 1. In the case of the lower limit of Porphyra perforata, which was not measured over the entire coast covered, a definite slope is counted as one which causes the level of the limit at the easternmost station measured to be one foot or more lower than the level at the westernmost station measured. Thus, the lower limit of P. perforata is counted as having no definite slope, as a slope of -0.010 does not cause the level at Station 33 to be as much as one foot lower than the level at Station 3. Thirteen limits were found to have a definite slope (Table VII) and eight have no definite slope (Table VIII).

Table VII. Slightly variable limits which have a definite slope.

Limit	Organism	Total variance	(f)	m.	b.
Lower	Gigartina	1.43	(10)	-0.053	6.2
Upper	Mytilus californianus	1.09	(14)	-0.046	9.3
Upper	Laminaria	0.48	(14)	-0.049	3.0
Upper	Hedophyllum	0.45	(26)	-0.034	5.8
Upper	Egregia	0.64	(12)	-0.031	3.9
Upper	Pleurophycus	0.36	(13)	-0.025	2.1
Lower	Hedophyllum	0.38	(25)	-0.024	2.8
Upper	Fucus	1.22	(23)	-0.022	8.1
Upper	Phyllospadix	0.33	(21)	-0.020	2.5
Lower	Mytilus californianus	1.06	(16)	-0.018	4.4
Upper	Heterochordaria	0.93	(11)	-0.017	4.2
Upper	Odonthalia	0.60	(14)	-0.013	3.1
Upper	Porphyra perforata	1.03	(19)	-0.017	7.0

Table VIII. Slightly variable limits which have no definite slope.

Limit	Organism	Total variance	(f)	m.	b.
Lower	Porphyra perforata	0.52	(15)	-0.010	4.7
Upper	Costaria	0.73	(11)	-0.009	2.4
Upper	Alaria	0.48	(25)	-0.006	2.8
Upper	Desmarestia	0.94	(16)	-0.006	2.1
Lower	Endocladia	0.75	(22)	-0.006	5.4
Upper	Iridaea	0.67	(14)	-0.006	3.0
Upper	Mitella	1.07	(17)	-0.002	8.4
Upper	Cymathere	0.26	(9)	-0.002	1.4

The four groups delimited above are not exhaustive. No levels were found which have a noticeable positive slope, a significantly greater variance in the easterly portion of their distribution, or which have a noticeable difference of slope in the two portions of their distribution. It is possible that more accurate measurements would reveal examples of these missing types of limits, but it seems probable that there are very few of them.

The environmental factor responsible for the greater variability on the open coast of the limits shown in Table V is probably very closely connected with the direct action of surf. The climatic and hydrographic conditions typical of the open coast are relatively constant over a distance of miles, but the action of surf may change greatly over a distance of yards. This group of limits is a small one and consists of limits in the upper part of the intertidal zone. Thus, surf was found to have a definite effect on some limits. Only some limits are affected, and the effect is to make the limits more variable rather than to raise them uniformly. Thus, adding a fixed amount to limits to allow for wave action (Johnson and Skutch, 1928) is unwise.

The very variable limits (Table V) are probably so for a variety of reasons. Many are small and scattered organisms which suffer from greater errors of measurement (p. 31 above) than the larger ones. If they were measured more accurately, some could probably be placed in the other groups. Some are probably not linear. The upper limit of Rhodomela, which is often associated with tide pools and water seepage, is probably an example of a limit governed by a factor which is not in a linear relationship to the headland to headland distance between stations.

The limits listed in Tables VII and VIII are the ones most suitable for use in testing the hypothesis of tidal factors. They have been shown to be relatively invariable and unaffected by the direct action of surf. While it is possible that the other limits are precisely the ones which are the more affected tidal factors, Tables VII and VIII contain more than one half of all the limits studied. If the hypothesis has any general use, it must explain these also.

The observed values of each limit for Stations 1, 15, and 30 and also the Y-intercepts of the relevant lines of least squares at these three points were used. Any cases where one of these values or intercepts fell within one half a foot of a tidal factor shown in Figures 13 and 14 were noted. If a limit is determined by a tidal factor, it should coincide with that factor at all three of the stations studied. When one of these three-fold coincidences could be achieved by using a mixture of observed values and intercepts, for example if the Y-intercept at Station 1 and the observed values at Stations 15 and 30 all coincided with a single factor, this was accepted.

Out of the 20 limits taken, four coincided with a tidal factor. These were upper Demarestia and upper Cymathere (LLLW), upper Porphyra perforata (LLHW), and upper Mitella (HLHW). It is not impossible that these are simple coincidences, but it is easy to see why LLLW may be an important critical tidal factor. Some algae, of which Desmarestia is a very good example (p.101, above, Muenscher, 1915a) cannot survive even a few minutes of drying. Even on the open coast, there are occasionally calm, sunny days. Over the period of a month or two, such a day would probably coincide with a low tide. Thus an alga which can not survive any degree of drying would probably be limited by LLLW, in spite of the usually dampening effect of surf and a moist climate. A number of limits parallel LLLW but are a little distance above it: upper Costaria (b = 2.4), Alaria (not nana) (b = 2.8), and Iridaea (b = 3.0). These may be plants which are slightly more resistant to drying, or which are smaller and can be more sheltered by other plants. Since some time is required for a plant to dry, limits dependent on LLLW should be a little way above it, rather than at exactly the same level. These limits which are a little way above LLLW are well approximated by MLLW. This latter is often quoted as a critical tidal factor, even though it is not strictly one, not being connected with any sudden increase in maximum emergence.

Apart from the case of LLLW, the hypothesis of critical tidal factors does not seem to be generally useful either as an explanation or as a detailed description of intertidal limits. It is probable that in some cases a tidal factor may have an important effect. The time of settling of reproductive bodies has already been suggested (p.25 above) as an example of such a special case. However, the hypothesis has so far been used as a general explanation or description, and should be judged as such.

Most of the limits listed in Table VIII have been discussed in connection with LLLW as a critical tidal factor (p. 132, above). The others retain such a constant height in such different environments that they are probably associated with some mean rather than an extreme value of some factor in the environment. One such mean value is the percentage of time a level is exposed (Fig. 15). A possible mechanism by which the percentage of time exposed might limit an organism involves nutrients. It would not make much difference to the nutrition of an animal or plant if in a particular day it is exposed for a maximum of six or twelve hours. However, a change from 50% exposure to 55% exposure might make a great deal of difference to the feeding of the one or the absorption of nutrients by the other. The concentration of nutrients in the seawater around British Columbia coasts is relatively high and is probably not often limiting to phytoplankton. However, the surface to mass ratio of a benthic alga is much smaller than that of a phytoplankter. In addition, an intertidal alga is exposed for a portion of the time, during which it cannot absorb nutrients. So nutrients may very well be limiting to intertidal benthic algae.

The slightly variable limits which have a distinct slope (Table VI) are the most difficult of all to explain. The same sort of slope seems also to occur in the subtidal zone as in the case of the upper limit of *Pterygophora*. In the case of *Laminaria*, an upper limit appears to start in the low intertidal zone at Station 1 and cross low water mark into the subtidal zone in the San Juan Islands (Fig. 24). These examples indicate that some factor may be involved which is not peculiar to the intertidal zone. The only environmental factor which appears to have a regular gradient from Port Renfrew to Victoria is rainfall. Humidity and incident light may also be associated with this factor. Trevarthen (Chapman, 1957) has shown how the restrictions placed on photosynthesis by desiccation and lack of light may limit an intertidal alga in its upper and lower levels respectively (p. 26, above). Increased light towards Victoria, if it occurs, could easily cause a lowering of lower limits, both in the intertidal and the subtidal zones. Desiccation as a hindrance to photosynthesis would work over a relatively long period, so that mean values of surf and humidity are involved. This should result in a relatively even downward slope. This effect of desiccation should not be confused with desiccation as a directly lethal factor. This latter should be effective more through extreme values of surf and humidity, and would result in a much more variable limit. This does not explain the lowering of upper limits once they are in the subtidal zone.

This discussion has dealt mainly with upper limits. The formation of lower limits is less well understood. In some cases they may be dependent on the upper limit of a competitive form in a lower zone. The general pattern of those lower limits which were observed seemed to be that the lower limit had a similar but numerically lesser slope. Thus, the zone of an organism becomes lower and narrower towards Victoria. There are exceptions to this: both the Fucus and Gigartina zones appear to become wider towards Victoria. The limits of both zones are quite variable, so this is not certain. No instances were found in which a zone low in the intertidal zone on the open coast tends to rise towards mean sea level in more sheltered waters (p. 23, above).

This investigation has been of a preliminary nature. A more detailed investigation would require more accurate measurements of the vertical distributions involved, more quantitative measurements of factors of the physical environment, and a better understanding of the taxonomy and physiology of the organisms studied. If errors in measurement of heights resulting from differences between the actual and predicted tides could be eliminated, the levels would probably be accurate to the nearest one or two tenths of a foot. This would permit comparisons, not only with tidal factors, but also with the percentage exposure of a level. Quantitative measurements of what appear to be the three most important factors in the environment: surf, nutrients, and light, are lacking. It is not certain what aspect of surf favours the open coast forms, or what are the limiting values of nutrients for benthic algae. Some of the problems raised by the variability of a number of the intertidal organisms would be most easily attacked following the progress of numbers of marked plants to ascertain developmental series, and correlation of the variations with the fine detail of their physical environment. This work is technically much easier than transplanting and culturing experiments, and so should precede them.

SUMMARY AND CONCLUSIONS.

1. The physical environment of the intertidal zone between Port Renfrew and Victoria is described. This stretch of coast is a transition from an open oceanic coast to a sheltered one.

2. The vertical and geographical distributions of the more conspicuous intertidal organisms along this stretch of coast are described. The occurrence of *Dictyoneurum californicum* Ruprecht from British Columbia is confirmed. *Porhphyra schizophylla* Hollenberg, *Gigartina agardhii* Setchell and Gardner, *Enteromorpha angusta* (Setchell and Gardner) Doty, *E. vexata* (Setchell and Gardner) Doty, *Ulva taeniata* (Setchell) Setchell and Gardner, and *U. lobata* (Kutzing) Setchell and Gardner are recorded for the first time from British Columbia.

3. Variability in *Hedophyllum*, *Laminaria*, *Costaria*, *Cymathere*, *Alaria*, and *Fucus* is discussed. *H. subsessile* (Areschoug) Setchell is reduced to synonomy under *H. sessile* (C. Agardh) Setchell. *Costaria mertensii* J. Agardh is reduced to synonomy under *C. costata* (Turner) Saunders. The 34 forms of *Fucus distichus* (Linnaeus) emend, Powell listed by Gardner (1922) under the two former species *F. furcatus* C. Agardh and *F. evanescens* C. Agardh are reduced to synonomy.

4. Evidence is presented that different factors or combinations of factors in the physical environment limit the geographical distributions studied.

5. The vertical distributions of a number of organisms are discussed. Differences in the variability of various limits are emphasized. The hypothesis of critical tidal factors is criticized. The importance of certain mean values, rather than extreme values, of certain factors in the physical environment is suggested.

BIBLIOGRAPHY

Agardh, C.A. -1820. Species algarum ... Vol. 1, pt. 1: Fucoideae, pp. 1-168, Lundae (not seen).

______ -1822. Species algarum ... Vol. 1, pt. 2, pp. 169-531, Lundae (not seen).

______ -1824. Systema algarum ... xxxviii 312 pp., Lund (not seen).

______ -1846. Icones algarum ineditae. Ed. Nova. 4 pp., 20 pls., Lund (not seen).

Agardh, J.G. -1847. Nya alger från Mexico. Öfvers. K. Svensk. Vetensk. -Akad. Förhandl. 4:5-17 (not seen).

______ -1848. Species genera et ordines algarum ... Vol. 1 viii + 363 pp. Lund.

______ -1851. Species genera et ordines algarum ... Vol. 2, pt. 1, xii + 351 pp., Lund (not seen).

______ -1867. De Laminarieis. Lunds Univ. Årsskr. 4:1-36 (not seen).

______ -1876. Species genera et ordines algarum ... Vol. 3, pt. 1. Epicrisis systematis floridearum. vii + 724 pp. Lund (not seen).

______ -1883. Till algernes systematik, nya bidrag. Afd. 3. Lunds Univ. Årsskr. 19:1-177, 4 pls. (not seen).

Anon., -1955. Physical and chemical data record Juan de Fuca Strait Project 1951-52. Pacific Oceanographic Group, Fish. Res. Bd. Canada 182 pp. Nanaimo, B.C.

______ -1956. Pacific coast tide and current tables 1957. Canadian Hydrographic Service Tidal Publication No. 10, 199 pp. Ottawa.

______ -1957a. Atlas of Canada rev. ed., Dept. of Mines and Tech. Surveys, Geographical Branch. 110 pls., Ottawa.

______ -1957b. Data Report No. 11 British Columbia Inlet Cruises, 1957. Institute of Oceanography, University of British Columbia. iii + 60 pp., Vancouver, B.C.

______ -1957c. Monthly meteorological summary [ies] for Victoria, B.C. Meteorological Division, Department of Transport, Canada. Mss.

______ -1957d. Pacific coast tide and current tables 1958. Canadian Hydrographic Service Tidal Publication No. 10, 197 pp., Ottawa.

Anon., -1958a. Monthly meteorological summary [ies] for Victoria, B.C. Meteorological Division, Department of Transport, Canada, Mss.

______ -1958b. Pacific coast tide and current tables 1959. Canadian Hydrographic Service Publication No. 10, 197 pp., Ottawa.

Areschoug, J.E. -1847. Enumeratio phycearum in maribus scandinaviae crescentium. Sectio prior. Nova Acta Reg. Soc. Sci. Upsaliensis 13:223-382, 9 pls. (not seen).

______ -1876. De tribus Laminarieis et de Stephanocystide osmundaceae (Turn.) Trev. observationes praecursorias. Bot. Notiser. 3:65-63 (not seen).

Baird, R.H. and R.E. Drinnan - 1957. The ratio of shell to meat in Mytilus as a function of tidal exposure to air. Cons. Int. Explor. Mer. Jour. 22:329-336, 4 figs.

Baker, S.M. -1910. On the causes of the zoning of brown seaweeds on the sea shore II. The effect of periodic exposure on the expulsion of gametes and on the germination of the oospore. New Phyt. 9:54-67, 1 fig., 4 tables.

Beveridge, W.A. and V.J. Chapman -1950. The zonation of marine algae at Piha, New Zealand, in relation to the tidal factor (Studies in intertidal zonation 2) Pacific Science 4:188-201, 14 figs.

Blackman, F.E. -1905. Chromatic adaptation. Facts and theories concerning the adaptations of plants to differences in illumination. New Phyt. 3:237-242.

Blinks, L.R. -1951. Physiology and biochemistry of algae in G.M. Smith, ed., Manual of Phycology, Chap. 14, pp. 263-291. Chronica Botanica, Malden, Mass.

Boalch, G.T. -1957. Marine algal zonation and substratum in Beer Bay, South-East Devon. Jour. Mar. Biol. Ass. U.K. N.S. 36:519-528, 4 figs.

Bory de Saint-Vincent, J.B. -1826a. Iridea Dict. Class. Hist. Nat. 9:15-16. Paris (not seen).

______ -1826b. Macrocyste Dict. Class. Hist. Nat. 10:8-10. Paris (not seen).

Brown, L.B. -1915. Experiments with marine algae in fresh water. Publ. Puget Sound Biol. Sta. 1:31-34, pl.3.

Burrows, E.M. and S. Lodge -1951. Autecology and the species problem in Fucus. Jour. Mar. Biol. Ass. U. K. N.S. 30:161-176, 6 figs., 1 table.

Burrows, E.M., E. Conway, S.M. Lodge, and H.T. Powell -1954. The raising of intertidal algal zones on Fair Isle. Jour. Ecol. 42:283-288, 5 figs.

Carnahan, J.A. -1952. Intertidal zonation at Rangitoto Island, New Zealand (Studies in intertidal zonation 4) Pacific Science 6:35-46. 8 figs.

Chapman, V.J. -1942. Zonation of marine algae on the sea-shore. Proc. Linn. Soc. 154:239-253.

Chapman, V.J. -1946. Marine algal ecology. Bot. Rev. 12:628-672.

______ -1957. Marine algal ecology Bot. Rev. 23:320-350, 2 figs.

Coe, W.R. and D.L. Fox -1942. Biology of the California sea-mussel (Mytilus californianus) I Influence of temperature, food supply, sex, and age on the rate of growth. Jour. Ex. Zool. 90:1-30, 6 figs.

Coleman, J. -1933. The nature of the intertidal zonation of plants and animals. Jour. Mar. Biol. Ass. U.K. N.S. 18:435-476, 15 figs., 7 tables.

______ -1942. Some intertidal enigmas. Proc. Linn. Soc. 154:232-234.

Collins, F.S. -1903. The Ulvaceae of North America. Rhodora 5:1-31, pls. 41-43 (not seen).

______ -1909. The green algae of North America. Tufts College Studies (Sci. Ser.) 2:79-480, 18 pls.

______, I. Holden, and W.A. Setchell -1895-1919. Exsiccati Fasicles 1-46 and A-E. Phycotheca Boreali-Americana. Malden, Mass.

Cornwall, I.E. -1955. The barnacles of British Columbia. B.C. Prov. Mus. Handbook No. 7. 69 pp. Victoria, B.C.

De la Pylaie, A.J.M.B. -1829. Flore de l'île de Terre-neuve et des îles Saint-Pierre et Miclon. 128 pp. Paris.

De Toni, G.B. -1895. Sylloge algarum omnium hucusque cognitarum Vol. 3 Fucoideae. xvi + 638 pp. Padua.

Dehnel, P.A. -1956. Growth rates in latitudinally and vertically separated populations of Mytilus californianus. Biol. Bull. 110:43-53, 4 figs.

Delf, E.M. -1942. The significance of the exposure factor in relation to zonation. Proc. Linn. Soc. 154:234-239.

Doty, M.S. -1946. Critical tidal factors that are correlated with the vertical distribution of marine algae and other organisms along the Pacific coast. Ecol. 27:315-328, 6 figs.

______ -1947a. The marine algae of Oregon Pt. 1. Chlorophyta and Phaeophyta. Farlowia 3:1-65, 10 pls.

______ -1947b. The marine algae of Oregon. Pt. 2. Rhodophyta. Farlowia 3:159-215, pls. 11-14.

______ -1957. Rocky intertidal surfaces in J.W. Hedgepeth ed., Treatise on marine ecology and paleoecology. Vol. 1 Ecology Geol. Soc. Am. Memoir 67, Chap. 18:535-586, 18 figs., 1 pl.

______ and J.G. Archer -1950. An experimental test of the tide factor hypothesis. Am. Jour. Bot. 37:458-464, 2 figs., 3 tables.

Ekman, S. -1935. Tiergeographie des Meeres. Akademische verlangsgesellschaft m.b.h. xii + 542 pp., Leipzig.

Evans, R.G. -1947. The intertidal ecology of selected localities in the Plymouth neighbourhood. Jour. Mar. Biol. Ass. U.K. N.S. 27:173-218, 13 figs., 3 tables.

Falkenberg, P. -1901. Die Rhodomelaceen des Golfes von Neapel und der Angrenzenden Meeres-Abschnitte. Fauna und Flora des Golfes von Neapel, etc. Monographie 26. xvi + 754 pp., 10 figs., 24 pls. Berlin (not seen).

Feldmann, J. -1938. Recherches sur la végétation marine de la Méditerranée. La Côte des Albères. Rev. Alg. 10:1-339, 20 figs., pls. 1-20.

Fensholt, D.E. -1955. An emendation of the genus Cystophyllum (Fucales) Am. Jour. Bot. 42:305-322, 51 figs.

Forbes, E. and R. Godwin-Austen -1859. The natural history of the European Seas. viii + 306 pp. London (not seen).

Fox, D.L. and W.R. Coe -1943. Biology of the California sea-mussel (Mytilus californianus) II Nutrition, metabolism, growth, and calcium deposition. Jour. Ex. Zool. 93:205-249, 3 figs.

Fritsch, F.E. -1945. The structure and reproduction of the algae. Vol. 2. xiv + 939 pp. Cambridge Univ. Press.

Frye, T.C. -1918. The age of Pterygophora californica. Publ. Puget Sound Biol. Sta. 2:65-71, 1 pl.

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

______ -1922. Photosynthesis in some of the red and brown algae as related to depth and light. Publ. Puget Sound Biol. Sta. 3:177-193, pls. 31-33, 9 tables.

Gardner, N.L. -1910. Variations in nuclear extrusion among the Fucaceae. Univ. California Publ. Bot. 4:121-136, 2 pls.

______ -1917. New Pacific coast marine algae I. Univ. California Publ. Bot. 6:377-416, pls. 31-35.

______ -1919. New Pacific coast marine algae IV. Univ. California Publ. Bot. 6:487-496, pl. 42.

______ -1922. The genus Fucus on the Pacific coast of North America. Univ. California Publ. Bot. 10:1-180, pls. 1-60.

______ -1927. New Rhodophyceae from the Pacific coast of North America V. Univ. California Publ. Bot. 13: 403-434, pls. 84-93.

Gislén, T. -1943. Physiographical and ecological investigations concerning the littoral of the northern Pacific Section 1. A comparison between the life-conditions in the littoral of central Japan and California Lunds Univ. Årsskr. Ser. 2 39(5):1-64, 7 figs., 4 pls.

Grubb, V.M. -1936. Marine algal ecology and the exposure factor at Peveril Point, Dorset. Jour. Ecol. 24:392-423, 7 figs., pl. 19, 13 tables.

Guberlet, M.L. -1956. (Illustrated by E.L. Curtis) Seaweeds at ebb tide. Univ. Washington Press xvi + 182 pp., Seattle.

Hariot, P. -1889. Algues, in Mission scientifique du Cap Horn, 1882-1883. Vol. 5. Botanique. 109 pp., 9 pls. Paris.

Harvey,W.-1853. Nereis boreali-americana. Pt. II Rhodospermae. Smithsonian Contrib. to Knowledge 4 (Art 5):1-258, pls. 13-36 (not seen).

______ -1862. Notice of a collection of algae made on the northwest coast of North America, chiefly at Vancouver Island, by David Lyall, Esq., M.D., R.N., in the years 1859-61. Jour. Proc. Linn. Soc. 6:157-176(not seen).

Hedgepeth, J.W. -1953. An introduction to the zoogeography of the northwestern Gulf of Mexico with reference to the invertebrate faunas. Publ. Inst. Mar. Sci. Univ. Texas Vol. 3(1):109-224, 45 figs. (not seen).

______ ed., -1957. Treatise on marine ecology and paleoecology. Vol. 1 Ecology. Geol. Soc. Am. Mem. 67 viii + 1296 pp.

Herlinveaux, R.H. -1954. Tidal currents in Juan de Fuca Strait. Jour. Fish Res. Bd. Canada 11:799-815, 9 figs., 4 tables.

______ -1957. On tidal currents and properties of the sea water along the British Columbia coast. Prog. Rep. Pacific Coast Stations Fish. Res. Bd. Canada 108:7-9, 3 figs.

Hervey, A.B. -1881. Sea mosses xv + 281 pp., 20 pls., Boston (not seen).

Hooker, H.J. -1840. Flora boreali-americana or The Botany of the northern parts of British America Vol. 2. 327 pp. H.G. Bohn, London.

Hurd, A.M. -1917. Winter condition of some Puget Sound algae. Publ. Puget Sound Biol. Sta. 1:341-348.

Hus, H.T.A. -1900. Preliminary notes on west-coast Porphyras. Zoe 5:61-70.

______ 1902. An account of the species of Porphyra found on the Pacific coast of North America. Proc. California Acad. Sci. Ser. 3, Botany 2(6):173-241, 3 pls.

Hutchins, L.W. -1947. The bases for temperature zonation in geographical distribution. Ecol. Mon. 17:325-335, 8 figs.

Jepson, W.L. -1951. A manual of the flowering plants of California. Univ. California Press. 1238 pp. Berkeley and Los Angeles.

Johnson, D.S. and A.F. Skutch -1928. Littoral vegetation on a headland of Mt. Desert Island, Maine. I. Submersible or strictly littoral vegetation. Ecol. 9:188-215, pls. 8-13, 2 charts.

Johnson, M.E. and H.J. Snook -1927. Seashore animals of the Pacific coast. MacMillan xiv + 659 pp. New York.

Kanwisher, J. -1957. Freezing and drying of intertidal algae. Biol. Bull. 113:275-285, 5 figs.

Kitching, J.A. -1935. An introduction to the ecology of intertidal rock surfaces on the coast of Argyll. Proc. Roy. Soc. Edin. 58:351-374, 7 figs., 4 tables, 1 pl.

Kjellman, F.R. -1877. Om Spetsbergens marina Klorofyllförande Thallophyten, II. Bihang till Kgl. Sv. Vet.-Akad. Handl., Vol. 4, no. 6. Stockholm (not seen).

______ -1889. Om Beringshafvets Algflora Kgl. Svensk. Vetensk. Ak. Handl., 23 (8):1-58, 7 pls. (not seen).

Klugh, A.B. and J.R. Martin -1927. The growth rate of certain marine algae in relation to depth of submergence. Ecol. 8:221-231, 4 figs., 7 tables.

Knudsen, M. -1901. Hydrographical tables G.E.C. Gad, 63 pp., Copenhagen (not seen).

Krashennikoff, T. -1926. Échanges gazeux chez les algues brunes de la région arctique découvertes à mer basse. C.R. Acad. Sci. Paris 182:939-941, 2 tables.

Kützing, F.T. -1849. Species algarum ... vi 922 pp. Leipzig.

Kylin, H. -1925. The marine algae in the vicinity of the Biological Station at Friday Harbour, Wash. Lunds Univ. Årsskr. N.F. Avd. 2, Bd. 21, Nr 9, K. Fysiogr. Sällsk. Handl. N.F. Bd. 36, Nr 9:1-87, 47 figs.

______ -1940. Die Phaeophyceenordnung Chordariales. Lunds Univ. Årsskr. N.F. Avd. 2, Bd. 36, Nr 9, K. Fysiogr. Sällsk. Handl. N.F. Bd. 51, Nr 9: 67 pp., 30 figs., 8 pls.

Lami, R. -1934. Nébulosité et brumes régionales comme facteurs possibles de la répartition géographique des algues marines Rev. Alg. 7:181-182.

Lamouroux, J.V. -1813. Essai sur les genres de la famille des Thallasiophytes non articulées. Ann. Mus. d'Hist. Nat. 20:21-47, 115-139, 267-293, pls. 7-13. Paris (not seen).

Lorenz, J.R. -1863. Physikalische Verhältnisse und Vertheilung Organismen im Quarnerichen Golfe. xii + 379 pp., 33 figs. Kais. Kön. Hog und Stadtsdr. Vienna (not seen).

Link, H.P. -1820. Epistola ... de algis aquaticis in genera disponendis. in Nees von Esenbeck, C.G.D. (Ed.), Horae physicae berolineses, No. 1, 8 pp., 1 pl. Bonn (not seen).

Linnaeus, C. -1753. Species plantarum 1:(1-12), 1-560: 2:(1-31), 561-1200. Holmiae (not seen).

Lubimenko, V. -1925. Sur l'adaptation chromatique chez les algues marines C.R. Acad. Sci. Paris 181:730-732.

MacMillan, C. -1902. The kelps of Juan de Fuca. Postelsia 1:193-220, pls. 22-26.

Moore, H.B. -1935. The biology of Balanus balanoides IV. Relation to environmental factors. Jour. Mar. Biol. Assoc. U.K. N.S. 20:279-307, 11 figs., 5 tables.

Morong, T. -1893. The Naiadaceae of North America. Mem. Torrey Bot. Club 3(2):1-65, pls. 20-74.

Morton, J.E. -1954. The crevice faunas of the upper intertidal zone at Wembury. Jour. Mar. Biol. Ass. U.K. N.S. 33:187-224, 7 figs.

Muenscher, W.L.C. -1915a. Ability of seaweeds to withstand desiccation. Publ. Puget Sound Biol. Sta. 1:19-23.

______ -1915b. A study of the algal associations of San Juan Island. Publ. Puget Sound Biol. Sta. 1:59-84.

______ -1916. Distribution of shore algae on Shaw Island. Publ. Puget Sound Biol. Sta. 1:199-210.

Myers, M.E. -1925. Contributions toward a knowledge of the life histories of the Melanophyceae. A preliminary report. Univ. California publ. Bot. 13:109-124, pls. 8-9.

Okamura, K. -1907-1942. Icones of Japanese Algae. 7 vols. 345 pls. Kazamashobo Tokyo.

______ -1932b. The distribution of marine algae in Pacific waters. Rec. Ocean. Work in Japan 4(1):30-150.

Osterhout, W.J.V. -1906a. The resistance of certain marine algae to changes in osmotic pressure and temperature. (Preliminary communication) Univ. California Publ. Bot. 2(8):227-228.

______ -1906b. The rôle of osmotic pressure in marine plants (Preliminary communication) Univ. California Publ. Bot. 2(9):229-230.

Papenfuss, G.F. -1942. Studies of South African Phaeophyceae I Ecklonia maxima, Laminaria pallida, Macrocystis pyrifera. Am. Jour. Bot. 29:15-24, 59 figs.

______ -1951. Phaeophyta in G.M. Smith, ed., Manual of phycology, Chronica Botanica, Malden, Mass. Chap 7, pp. 119-158, figs. 29-37.

Parke, M. -1948. Studies on British Laminariaceae I. Growth in Laminaria saccharina (L.) Lamour. Jour. Mar. Biol. Assoc. U.K. N.S. 27:651-709, 10 figs., 8 tables, pls. 5-12.

Pease, V.A. -1917. North Pacific Coast species of Desmarestia. Publ. Puget Sound Biol. Sta. 1:383-394, pls. 83, 84.

Pickard, G.L. -1957. Tables for conversion of chlorosity to salinity. Ms.

______ and D.C. McLeod -1953. Seasonal variations of temperature and salinity of surface waters of the British Columbia coast. Jour. Fish. Res. Bd. Can.10: 125-145, 8 figs., 5 tables.

Pilsbry, H.A. -1916. The sessile barnacles (Cirripedia) contained in the collections of the U.S. National Museum. U.S. Nat. Mus. Bull. 60:1-222 (not seen).

Pomerat, C.M. and E.R. Reiner -1942. The influence of surface angle and of light on the attachment of barnacles and other sedentary organisms. Biol. Bull. 82:14-25, 6 tables, 3 figs.

Pomerat, C.M. and C.M. Weiss -1946. The influence of texture and composition of surface on the attachment of sedentary marine organisms. Biol. Bull. 91:57-65, 5 figs., 3 tables.

Postels, A. and F. Ruprecht -1840. Illustrationes algarum in itinere circa orbem ... Exsecuto in Oceano Pacifico imprimis septentrionali ad littora Rossica Asiatico-Americana collectarum. iv + 22 + [2] pp., 40 pls. St. Petersburg.

Powell, H.T. -1957a. Studies on the genus Fucus L. I Fucus distichus L. emend. Powell. Jour. Mar. Biol. Ass. U.K. N.S. 36:407-432, 1 fig., 2 pls.

______ -1957b. Studies in the genus Fucus L. II. Distribution and ecology of forms of Fucus distichus L. emend. Powell in Britain and Ireland. Jour. Mar. Biol. Ass. U.K. N.S. 36:663-693, 4 pls., 5 figs.

Rao, K.P. -1953a. Rate of water propulsion in Mytilus californianus as a function of lattitude. Biol. Bull. 104:171-181, 5 figs.

Rao, K.P. -1953b. Shell weight as a function of intertidal height in a littoral population of Pelecypods. Experientia 9:465-466, 1 fig.

Reinke, J. -1903. Studien zur vergleichenden Entwicklungsgeschichte der Laminariaceen. 67 pp., 15 figs. Kiel.

Rice, L. -1930. Peculiarities in the distribution of barnacles in communities and their probable causes. Publ. Puget Sound Biol. Stat. 7:249-257, 4 graphs.

Ricketts, E.F. and J. Calvin -1952. Between Pacific tides. 3rd. ed., rev. by J.W. Hedgpeth, Stanford Univ. Press. xiii + 501 pp.

Rigg, G.B. -1913. Is salinity a factor in the distribution of Nereocystis Luetkeana? Bull. Torr. Bot. Club. 40:237-242, 1 fig.

______ -1917. Seasonal development of bladder kelp. Publ. Puget Sound Biol. Sta. 1:309-318.

______ and R.C. Miller -1949. Intertidal plant and animal zonation in the vicinity of Neah Bay, Washington. Proc. Calif. Acad. Sci. 4th. Ser. 26:323-351, 8 figs., 2 tables.

Ruprecht, F.J. - 1851. Tange des ochotskischen Meeres in A.T. von Middendorf, Reise in den aussersten Norden und Osten Sibiriens während der Jahre 1843 und 1844. Bd. 1 (2): Botanik, pp. 191-435, pls. 9-18. St. Petersburg (not seen).

______ -1852. Neue oder unvollständig bekannte Pflanzen aus dem nördlichen Theile des stille Oceans. Mem. de l'Acad. St. Petersburg Sci. Nat. 7:57-82, 8 pls. (not seen).

Saunders, de A. -1895. A preliminary paper on Costaria with a description of new species. Bot. Gaz. 20:54-58, pl. 7.

______ -1901a. A new species of Alaria. Minn. Bot. Studies 2:561-562, pl. 33.

______ -1901b. Papers from the Harriman Alaska expedition XXV. The algae of the expedition. Proc. Wash. Acad. Sci. 3:391-486, pls. 10-26.

Scagel, R.F. -1948. An investigation on marine plants near Hardy Bay, B.C. Rep. Prov. Dept. Fish. No. 1:1-70, 26 figs., 11 tables. Victoria, B.C.

______ -1956. Introduction of a Japanese alga, Sargassum muticum into the North-east Pacific. Fish. Res. Pap. Washington Dept. Fish. 1(7):49-58, 14 figs.

Scagel, R.F. -1957. An annotated list of the marine algae of British Columbia and Northern Washington (Including keys to genera) Nat. Mus. Canada Bull. No. 150, Biol. Ser. No. 52. vi + 289 pp., 1 fig. Ottawa.

Scholander, P.F., W. Flagg, V. Walters, and L. Irving -1953. Climatic adaptation in arctic and tropical poikilotherms. Physiol. Zool. 26:57-92, 12 figs., 9 tables.

Schrader, H.F. -1903. Observations on Alaria nana sp. nov. Minn. Bot. Studies Ser. 3:157-165, 4 pls.

Schreiber, E. -1930. Untersuchungen über Parthenogenesis, Geschlechtsbestimmung und Bastardierungsvermogen bei Laminarien. Planta 12:331-353, 12 figs. (not seen).

Segal, E., K.P. Rao, and T.N. James -1953. Rate of activity as a function of intertidal height within populations of some littoral molluscs. Nature 172:1108-1109, 2 figs.

Setchell, W.A. -1893. On the classification and geographical distribution of the Laminariaceae Trans. Conn. Acad. Sci. 9:333-375.

______ -1901. Notes on algae I Zoe 5:121-129.

______ -1905. Regeneration among kelps. Univ. California Publ. Bot. 2:138-169, pls. 15-17.

______ -1917. Geographical distribution of marine algae. Science 45:197-204.

______ -1920a. The temperature interval in the geographical distribution of marine algae. Science 52:187-190.

______ -1920b. Stenothermy and zone-invasion Am. Nat. 54: 385-397.

______ -1935. Geographical elements of the marine flora of the north Pacific Ocean. Am. Nat. 69:560-577, 11 figs.

______ and N.L. Gardner -1903. Algae of northwestern America. Univ. California Publ. Bot. 1:165-418, pls. 17-27.

______ and ______ -1920. The marine algae of the Pacific coast of North America. Pt. II. Chlorophyceae. Univ. California Publ. Bot. 8(2):139-375, pls. 9-33.

______ and ______ -1924. Phycological contributions VII Univ. California Publ. Botany 13:1-13.

______ and ______ -1925. The marine algae of the Pacific coast of North America. Pt. III. Melanophyceae. Univ. California Publ. Bot. 8(3):383-898, pls. 34-107.

Setchell, W.A. and N.L. Gardner -1933. A preliminary survey of Gigartina, with special reference to its Pacific North American species. Univ. California Publ. Bot. 17(10):255-340., pls. 46-65.

______ and ______ -1937. Iridophycus in the northern hemisphere. Proc. Nat. Acad. Sci. 23:169-174.

Shelford, V.E. -1930. Geographic extent and succession in Pacific North American intertidal (Balanus) communities. Publ. Puget Sound Biol. Sta. 7:217-223, 1 chart.

Silva, P.C. -1951. The genus Codium in California with observations on the structure of the walls of the utricles. Univ. California Publ. Bot. 25(2):79-114, pls. 1-6, 32 figs.

______ -1953. The identity of certain Fuci of Esper. Wasmann Jour. Biol. 11(2):221-232.

______ -1955. The eighth International Botanical Congress, Phyc. News Bull. (8) 24:9-16.

______ -1957. Notes on Pacific coast marine algae. Madroña 14(2):41-51.

Smith, G.M. -1944. Marine algae of the Monterey Peninsula, California. Stanford Univ. Press. ix + 622 pp.

______ -1947. On the reproduction of some Pacific coast species of Ulva. Am. Jour. Bot. 34:80-87, 38 figs.

______ and G.J. Hollenberg -1943. On some Rhodophyceae from the Monterey Peninsula, California. Am. Jour. Bot. 30:211-222, 30 figs.

Southward, A.J. and A.J. Orton -1954. The effects of wave-action on the distribution and numbers of the commoner plants and animals living on the Plymouth breakwater. Jour. Mar. Biol. Ass. U.K. N.S. 33:1-19, 7 figs., 3 tables.

Stephenson, T.A. -1942. The causes of the vertical and horizontal distribution of organisms between tide marks in South Africa. Proc. Linn. Soc. 153:219-232.

______ and A. Stephenson -1949. The universal features of zonation between tide-marks on rocky coasts. Jour. Ecol. 37:289-305, 4 figs., 8 pls.

Strickland, J.D.H. -1957. Standard methods of seawater analyses. Vol. 1, Fisheries Res. Bd. Canada, Pacific Oceanographic Group [2] + 9+8+19+9+10+14+9+7+13 pp., 9 tables.

Stroemfelt, H.F.G. -1886. Om algenvegetationen vid Islands kuster. Akademisk afhandling, Upsala. 89 pp., 3 pls. Göteborg (not seen).

Taylor, N. -1909. Zosteraceae in North American Flora 17(1): 29-30. New York Botanical Garden.

Taylor, W.R. -1945. Pacific marine algae of the Allan Hancock expedition to the Galapagos Islands. Allan Hancock Pacific Expeditions. 12. ix + 528 pp. 100 pls.

Tilden, J.E. -1894-1902. American Algae. Centuries I-VI, St. Paul.

Towler, E.D. -1930. An analysis of the intertidal barnacle communities of the San Juan Archipelago. Publ. Puget Sound Biol. Sta. 7:225-232, 6 graphs.

Tully, J.P., ed., -1950. Manual of oceanographic methods. Fish. Res. Bd. Can., Pacific Oceanographic Group. 3+15+20+15+10+13+1+4+3+3+2+1+7+6+6+2+12+8 pp. Nanaimo, B.C.

Waldichuk, M. -1957. Physical oceanography of the Strait of Georgia, British Columbia. Jour. Fish. Res. Bd. Canada 14(3):321-486, 70 figs., 25 tables.

Womersley, H.B.S. -1954. The species of Macrocystis with special reference to those on southern Australian coasts. Univ. California Publ. Bot. 27:109-132, 8 pls., 1 map.

______ -1956. The marine algae of Kangaroo Island IV. The algal ecology of American River Inlet. Aust. Jour. Mar. Freshwater Res. 7:64-87, 4 figs., 7 pls., 2 tables.

Worley, L.G. -1930. Correlation between salinity, size and abundance of intertidal barnacles. Publ. Puget Sound Biol. Sta. 7:233-240, 5 figs.

Yendo, K. -1903. Hedophyllum spirale sp. nov., and its relation to Thallassiophyllum and Arthrothamnus. Bot. Mag. 17: 165-173, pl. 6. Tokyo.

______ -1905. Preliminary list of Japanese Fucaceae. Bot. Mag. 19:158. Tokyo (not seen).

______ -1914. Notes on algae new to Japan II. Bot. Mag. 28 (333):263-281. Tokyo.

______ -1919. A monograph on the genus Alaria. Jour. Coll. Sci. Imp. Univ. Tokyo 43(1):1-145, pls. 1-19.

Young, R.T. -1941. The distribution of the mussel (Mytilus californianus) in relation to the salinity of its environment. Ecol. 22:379-386, 7 tables.

______ -1945. Stimulation of spawning in the mussel (Mytilus californianus) Ecol. 26:58-69.

Zanefeld, J.S. -1937. The littoral zonation of some Fucaceae in relation to desiccation. Jour. Ecol. 25:431-468, 12 figs., pl. 22, 11 tables.

APPENDIX I Description of Stations.

Stations are described on a basis of locality, aspect, and physiography. A place name is termed official when it may be found on any of the Canadian Hydrographic Service Chart Nos. 3607, 3642, or 3647, United States Coast and Geodetic Survey Chart No. 6380, or Canadian National Topographic Series map Nos. 92B/5, 92B/6, 92C/8, or 92C/9. In some cases common usage is very much at variance with these official names. For instance, Station 9 (Rockbottom Creek) is locally known as Sandstone Creek, and is identified as such on a highway sign. In cases where the official name is virtually unknown, the common name is used in the text above. The equivalence of common and official name is always noted below. Some stations do not occur in the immediate vicinity of a named feature of the landscape. In these cases, the station is related to such a feature, for instance Station 33, near Deadman Bay. The name of the feature used in these instances is always an official name. Positions of stations are also given to the nearest ten seconds of latitude and longitude.

Station 1. Botany Beach (unofficial) and Observatory Point (unofficial)
48°31'30"N. 124°26'50"W.
Facing southwest.
A sandstone shelf (Botany Beach) immediately west of a sandstone point (Observatory Point). Many tidepools and potholes.

Station 1a. Waadah Island (official).
48°23'10"N. 124°36'00"W.
Facing north.
Series of parallel rocky ridges running roughly north-south.

Station 1b. Mukkaw Bay (official).
48°18'10"N. 124°39'50"W.
Facing west.
Boulder and rock outcrop in a sandy beach.

Station 2. Minute Creek (official).
48°30'20"N. 124°19'40"W.
Facing south.
Rocky point just west of the mouth of the creek.

Station 3. Sombrio River (official).
48°29'40"N. 124°18'10"W.
Facing southwest.
Conglomerate shelf and large conglomerate boulders, about 800 meters east of the mouth of Sombrio River.

Station 4. Sombrio Point (official).
48°29'10"N. 124°17'30" W.
Facing southwest.
Conglomerate overlying basalt.

Station 5. Magdalena Point (official).
48°27'30"N. 124°12'10"W.
Facing south.
Rocky shelf and a large boulder about 500 meters east of the point itself.

Station 6. San Simon Point (official).
48°26'00"N. 124°06'20"W.
Facing southwest.
The more easterly of the two points. Basalt.

Station 7. Pete Wolf Creek (official).
48°26'10"N. 124°05'50"W.
Facing southeast.
Sandstone cliff and boulders about 300 meters west of the creek mouth.

Station 8. Desolation Creek (official) commonly called Black Creek.
48°25'10"N. 124°01'40"W.
Facing southwest.
Spit just east of the creek mouth, composed of small boulders and shingle, with a few large boulders.

Station 9. Rockbottom Creek (official) commonly called Sandstone Creek.
48°24'40"N. 124°00'30"W.
Facing south.
Sandstone shelf, with some tidepools and potholes, and a few large boulders. About 700 meters east of the creek mouth.

Station 10. Glacier Point (official) commonly called Point no Point.
48°23'40"N. 123°59'10"W.
Facing southwest.
Small island joined to the mainland by a bridge. Basalt.

Station 11. Flea Beach (unofficial).
48°22'50"N. 123°56'30"W.
Facing southeast.
A small rocky point to the east of a long sandy beach.

Station 12. Sheringham Point (official).
48°22'40"N. 123°55'10"W.
Facing west.
Basalt cliff about 200 meters west of the lighthouse.

Station 13. Muir Creek (official).
48°22'50"N. 123°52'20"W.
Facing south.
Sandstone shelf strewn with many boulders, about 800 meters west of the mouth of the creek.

Station 14. Otter Point (official).
48°21'20"N. 123°49'20"W.
Facing south.
Basalt point.

Station 15. Muir Point (official).
48°21'30"N. 123°45'00"W.
Facing south.
Boulder beach, with a few very large boulders.

Station 16. West of Cooper Cove.
48°23'20"N. 123°45'00"W.
Facing south.
Shingle beach.

Station 17. 17-Mile Point (unofficial).
48°23'10"N. 123°38'50"W.
Facing south.
Rocky point.

Station 18. West of Iron Mine Bay.
48°20'10"N. 123°47'10"W.
Facing south.
Rocky point forming the west side of Iron Mine Bay, and opposite to Donaldson Island.

Station 19. Donaldson Island (official).
48°20'00"N. 123°42'10"W.
Facing south.
Rocky shore.

Station 20. East of Iron Mine Bay
48°19'50"N. 123°40'40"W.
Facing southwest.
Rocky.

Station 21. Beechey Head (official).
48°18'50"N. 123°39'10"W.
Facing southwest.
Rocky point.

Station 22. Smythe Head (official).
48°19'10"N. 123°36'10"W.
Facing west.
Rocky point.

Station 23. Great Race Rock (official).
48°17'50"N. 123°31'40"W.
Facing south.
Rocky shore with some small boulders.

Station 24. William Head (official).
48°20'30"N. 123°31'40"W.
Facing south.
Levels were taken from a length of rocky shore.

Station 25. Albert Head (official).
48°23'20"N. 123°28'50"W.
Facing south.
Rocky point.

Station 26. Dyke Point (official), commonly known as View Royal.
48°27'00"N. 123°26'10"W.
Facing southwest.
Rocky point.

Station 27. Saxe Point (official).
48°25'10"N. 123°23'40"W.
Facing south.
Rocky point.

Station 28. Portage Inlet (official).
48°27'40"N. 123°25'10"W.
Facing north.
Rocky shore, mud at the level of low tide.

Station 29. Ogden Point Breakwater (official).
48°24'50"N. 123°23'30"W.
Facing west.
At the seaward extremity of the breakwater.

Station 30. Clover Point (official).
48°24'10"N. 123°21'00"W.
Facing west.
Gently sloping rocky shore.

Station 31. Cadboro Point (official) commonly called Ten-Mile Point.
48°27'00"N. 123°16'10"W.
Facing southeast.
Levels were taken from a length of rocky shore.

Station 32. Gordon Head (official).
48°29'40"N. 123°18'20"W.
Facing north.
Levels were taken from a length of rocky shore.

Station 33. Near Deadman Bay.
48°30'20"N. 123°07'30"W.
Facing southwest.
Rocky shore about 400 meters south of the bay, below Mt. Dallas.

Station 34. Goose Island (official).
48°27'30"N. 122°57'20"W.
Facing southwest.
Rocky shore.

Station 35. Brown Island (official).
48°32'20"N. 123°00'20"W.

Station 36. Camp Bay (official).
48°44'38"N. 123°11'10"W.
Facing southeast.
Shingle beach and rock outcrops.

Station 37. Admiralty Head (official).
48°09'20"N. 123°11'10"W.
Facing southwest.
Shingle beach.

APPENDIX II

Systematic list of specimen material deposited in the Herbarium of the University of British Columbia.

Phylum Phaeophyta.

Order Laminariales

Family Laminariaceae.

Laminaria complanata (Setchell and Gardner) Setchell.
TW 274.

L. cuneifolia f. *angusta* Setchell and Gardner
TW 125.

L. cuneifolia J. Agardh f. *cuneifolia*
TW 172, 287, 334.

L. cuneifolia f. *subsimplex* Setchell and Gardner
TW 25, 215, 293.

L. saccharina f. *linearis* J. Agardh
TW 66a-c.

L. saccharina (Linnaeus) Lamouroux f. *saccharina*
TW 45-47, 127, 294, 311.

L. setchellii Silva
TW 74, 81, 87, 106, 140, 149, 162, 167, 191, 242, 287.

Pleurophycus gardneri Setchell and Saunders
TW 56, 82.

Cymathere triplicata (Postels and Ruprecht) J. Agardh
TW 65, 50, 63, 93, 121-123, 142, 164a-c, 214, 265.

Costaria costata (Turner) Saunders.
TW 22, 50, 63, 91, 93, 121-123, 142, 164a-c, 214, 265.

Agarum cribrosum Bory
TW 332.

A. fimbriatum Harvey
TW 333.

Hedophyllum _sessile_ (C. Agardh) Setchell
TW 2-4, 9, 11, 16-18, 20, 27, 29, 35, 38-42, 52, 58, 67-69, 71, 80, 83-85, 90, 97, 100, 109, 110, 113, 115, 116, 123, 135, 136, 138, 145-147, 151, 165, 177, 178, 192, 195, 197-200, 212, 213, 216a-b, 219, 223, 224, 226-230, 236-238, 247, 250, 254, 258, 263, 264, 270, 271, 273, 289, 290, 292, 295-297, 299, 308, 312, 317.

Family Lessoniaceae

Dictyoneurum _californicum_ Ruprecht
TW 156-158, 239, 240, 245.

Nereocystis _luetkeana_ (Mertens) Postels and Ruprecht
TW 64.

Postelsia _palmaeformis_ Ruprecht
TW 161, 234, 246, 284.

Macrocystis _integrifolia_ Bory
TW 126, 173, 277.

Lessoniopsis _littoralis_ (Farlow and Setchell) Reinke
TW 72, 75, 154, 163, 285.

Family Alariaceae

Pterygophora _californica_ Ruprecht
TW 129.

Alaria _marginata_ Postels and Ruprecht var. _marginata_
TW 1, 5, 6, 8, 12, 37, 48, 57, 60-62, 76, 78, 99, 101-105, 117, 124, 130-132, 137, 144, 152, 153, 155, 179, 180, 190, 220, 243, 248, 253, 255, 259, 261, 268, 269, 272, 281, 282, 298, 314, 318.

_A._ _nana_ Schrader
TW 2, 7, 10, 15, 19, 73, 79, 119, 166, 168, 169, 233, 244, 249, 260, 280, 283, 313, 315, 316.

_A._ _tenuifolia_ f. _amplior_ Setchell and Gardner
TW 232.

_A._ _tenuifolia_ Setchell f. _tenuifolia_
TW 111, 112, 114, 208-210, 218, 257, 309, 310.

_A._ _valida_ f. _longipes_ Setchell and Gardner
TW 118, 221, 251, 279.

_A._ _valida_ Kjellman and Setchell f. _valida_
TW 231.

Alaria sp.
TW 119, 141, 202, 204-207, 209, 262, 325, 329.

Egregia menziesii (Turner) Areschoug subsp. *menziesii*
TW 23, 30, 31, 54, 55, 171a,b, 203, 319-321, 323, 324, 326-328, 330, 331.

Order Chordariales.

Family Corynophlaeaceae

Leathesia difformis (Linnaeus) Areschoug.
TW 610-619, 621-623.

Family Chordariaceae

Heterochordaria abietina (Ruprecht) Setchell and Gardner.
TW 628-634, 636-643.

Order Desmarestiales.

Family Desmarestiaceae

Desmarestia intermedia Postels and Ruprecht.
TW 654-656.

D. munda Setchell and Gardner.
TW 651-653.

Order Fucales.

Family Fucaceae

Fucus distichus (Linnaeus) emend. Powell
TW 405, 407-413, 415, 417-420, 423, 424, 426-431, 433-437, 439-451, 453-460, 462, 464-468, 470-473, 476, 478-482.

Pelvetiopsis limitata (Setchell) Gardner f. *limitata*.
TW 400-402, 404.

Family Cystoseiraceae

Cystoseira geminata C. Agardh
TW 483-487.

Family Sargassaceae

Sargassum muticum (Yendo) Fensholt.
TW 488-490.

Phylum Rhodophyta

Sub Class Bangiophycidae.

Order Bangiales.

Family Bangiaceae

Porphyra schizophylla Smith and Hollenberg
TW 1171-1173, 1179, 1181, 1193-1196.

P. perforata J. Agardh
TW 1182-1185, 1187, 1188, 1190, 1197-1199, 1202.

Porphyra sp.
TW 1174, 1175, 1180, 1191, 1192, 1204-1217, 1221-1223, 1228, 1229, 1231, 1237, 1240, 1242-1244, 1248.

Sub Class Florideophycidae

Order Cryptonemiales.

Family Endocladiaceae.

Endocladia muricata (Harvey) J. Agardh.
TW 999-1024.

Order Gigartinales.

Family Gigartinaceae.

Gigartina agardhii Setchell and Gardner
TW 1025-1029.

G. corymbifera (Kützing) J. Agardh
TW 1044, 1045.

G. cristata (Setchell) Setchell and Gardner
TW 1030-1039.

G. mamillosa (Goodenough and Woodward) J. Agardh.
TW 1054-1057.

G. papillata (C. Agardh) J.G. Agardh.
TW 1046-1053.

Gigartina sp.
TW 1040, 1041, 1058-1067.

Iridaea heterocarpa Postels and Ruprecht
TW 1266, 1285, 1286, 1307, 1310.

Iridaea sp.
TW 1250, 1251, 1252b, 1254-1256, 1260, 1263, 1265, 1268-1274, 1276-1284, 1287-1290, 1292-1295, 1297-1300, 1304-1306.

Order Rhodymeniales.

Family Rhodymeniaceae.

Halosaccion glandiforme (Gmelin) Ruprecht.
TW 934-967.

Order Ceramiales.

Family Ceramiaceae.

Callithamnion pikeanum var. laxum (Setchell and Gardner) Doty.
TW 969, 970, 974, 976, 991, 997.

Callithamnion pikeanum var. pacificum (Harvey) Setchell and Gardner
TW 980-990, 992, 993, 995, 996.

Callithamnion pikeanum Harvey var. pikeanum
TW 968, 971-973, 975, 977-979, 994, 998.

Family Rhodomelaceae

Rhodomela larix (Turner) C. Agardh.
TW 1070-1092.

Odonthalia floccosa (Esper) Falkenberg.
TW 1093-1128.

Odonthalia washingtoniensis Kylin
TW 1129-1140.

Phylum Chlorophyta

Order Ulotrichales.

Family Monostromaceae.

Monostroma fuscum var. *blytii* (Areschoug) Collins.
TW 762, 763.

M. zostericola Tilden
TW 769.

Monostroma sp.
TW 1220, 1224, 1227.

Family Ulvaceae

Enteromorpha intestinalis (Linnaeus) Link.
TW 764.

E. linza (Linnaeus) J. Agardh.
TW 759, 760, 769, 771, 772.

E. angusta (Setchell and Gardner) Doty.
TW 756, 770.

E. vexata (Setchell and Gardner) Doty.
TW 767, 768.

Enteromorpha sp.
TW 765, 1225, 1245-1247.

Ulva lactuca Linnaeus
TW 751, 752, 758.

U. taeniata (Setchell) Setchell and Gardner.
TW 749.

U. lobata (Kützing) Setchell and Gardner.
TW 750, 753-755, 761.

Ulva sp.
TW 1186, 1218, 1219, 1226, 1230, 1233-1236, 1238, 1239, 1241.

Order Schizogoniales.

Prasiola meridionalis Setchell and Gardner
TW 744, 745, 747a, 748.

Rosenvingiella constricta (Setchell and Gardner) Silva
TW 743, 747b.

Order Cladophorales.

Family Cladophoraceae.

Spongomorpha coalita (Ruprecht) Collins
TW 721, 722, 724, 737, 741.

Spongomorpha mertensii (Ruprecht) Setchell and Gardner.
TW 732, 733, 736, 738, 742.

Spongomorpha spinescens Kützing
TW 723, 726-731, 735.

Spongomorpha sp.
TW 734.

Order Siphonales.

Family Codiaceae

Codium fragile (Suringar) Hariot.
TW 708-720, 757.

Codium setchellii Gardner
TW 700-707.

Division Tracheophyta

Sub Division Pteropsida

Class Angiospermae

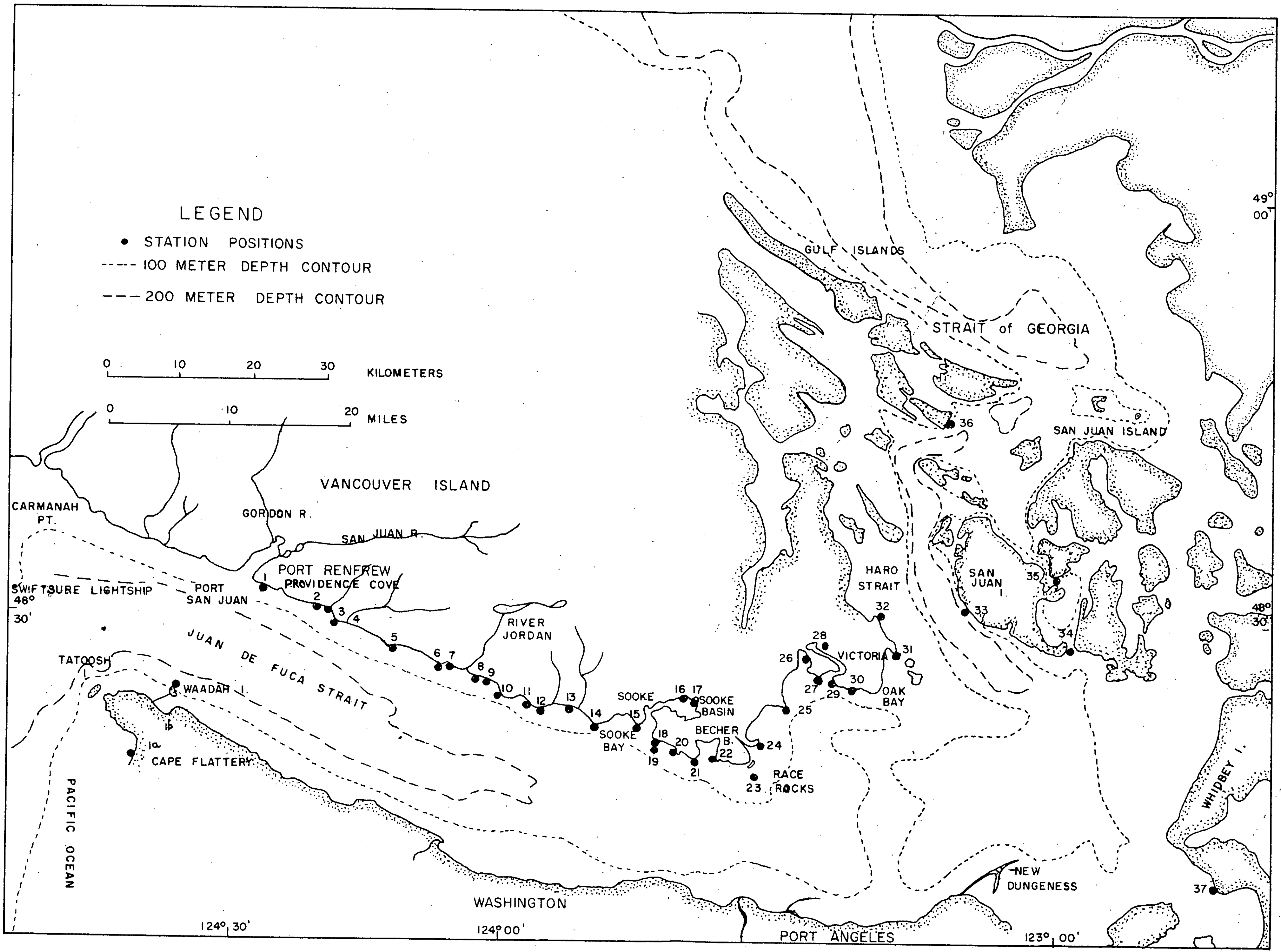
Sub class Monocotyledonae

Family Naiadaceae

Phyllospadix scouleri Hooker
TW 500-520.

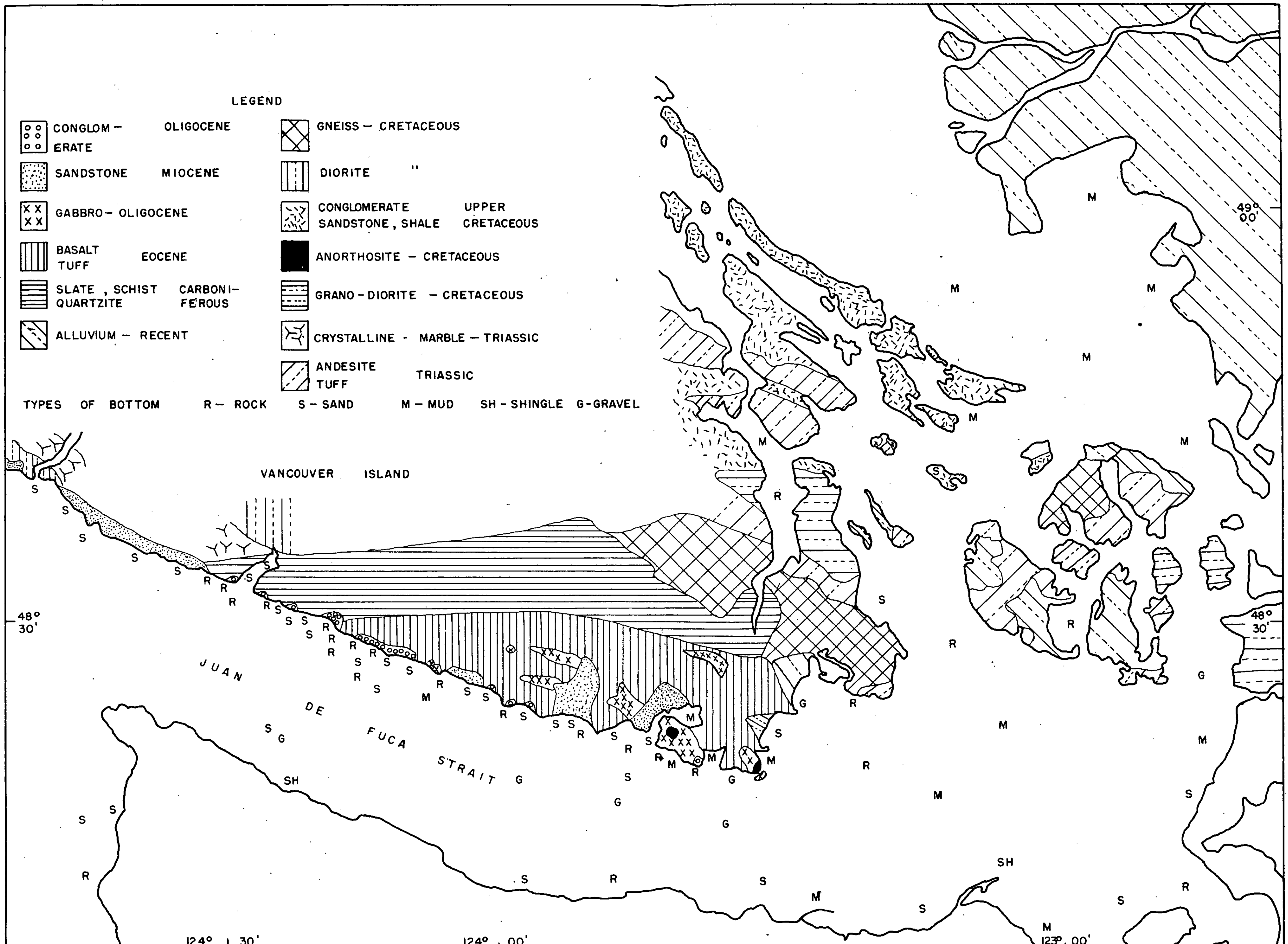
Zostera marina Linnaeus
TW 521-523.

Figure 1. Topography of Juan de Fuca Strait.



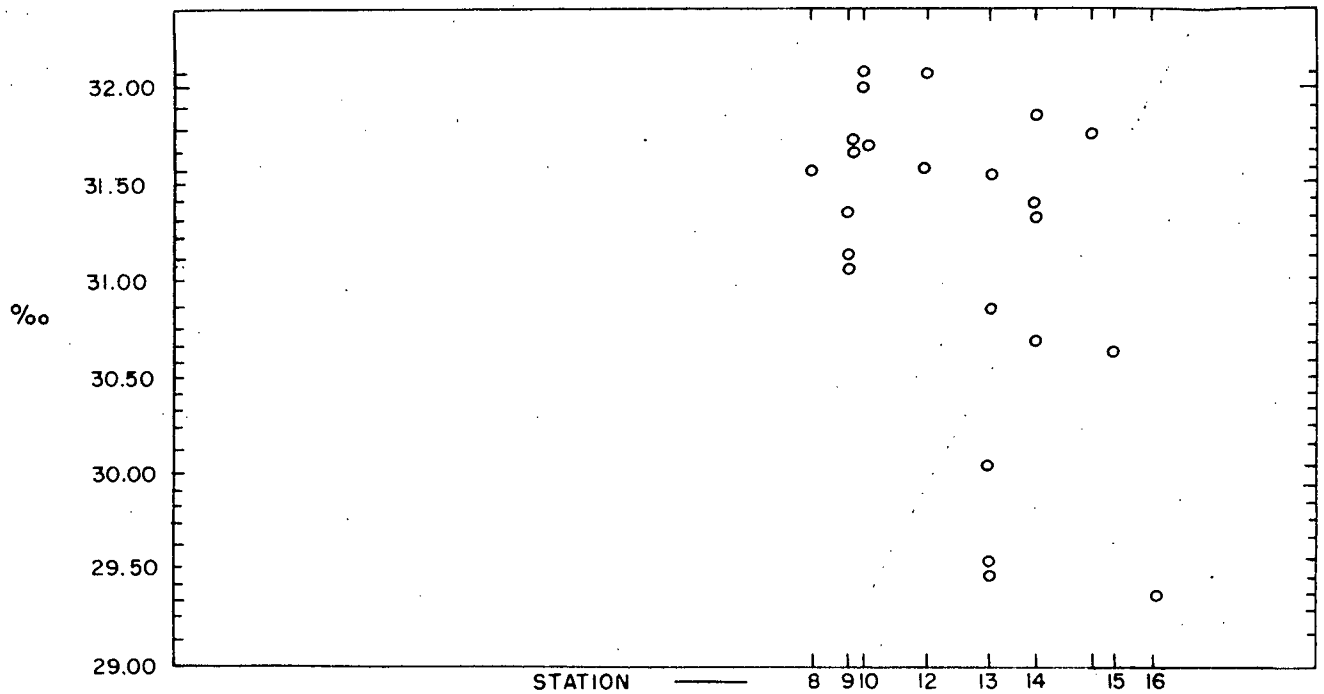
LEGEND
STATION POSITIONS
100 METER DEPTH CONTOUR
200 METER DEPTH CONTOUR
0 10 20 30 KILOMETERS
0 10 20 MILES
VANCOUVER ISLAND
CARMANAH PT.
GORDON R.
SAN JUAN R.
PORT RENFREW
PROVIDENCE COVE
SWIFTSURE LIGHTSHIP
PORT SAN JUAN
48° 30'
RIVER JORDAN
JUAN DE FUCA STRAIT
TATOOSH
WAADAH I.
CAPE FLATTERY
PACIFIC OCEAN
SOOKE
SOOKE BASIN
SOOKE BAY
BECHER B.
RACE ROCKS
VICTORIA
OAK BAY
HARO STRAIT
GULF ISLANDS
STRAIT of GEORGIA
SAN JUAN ISLAND
SAN JUAN I.
49° 00'
WHIDBEY I.
NEW DUNGENESS
WASHINGTON
PORT ANGELES
124° 30'
124° 00'
123° 00'

Figure 2. Geology of Juan de Fuca Strait.

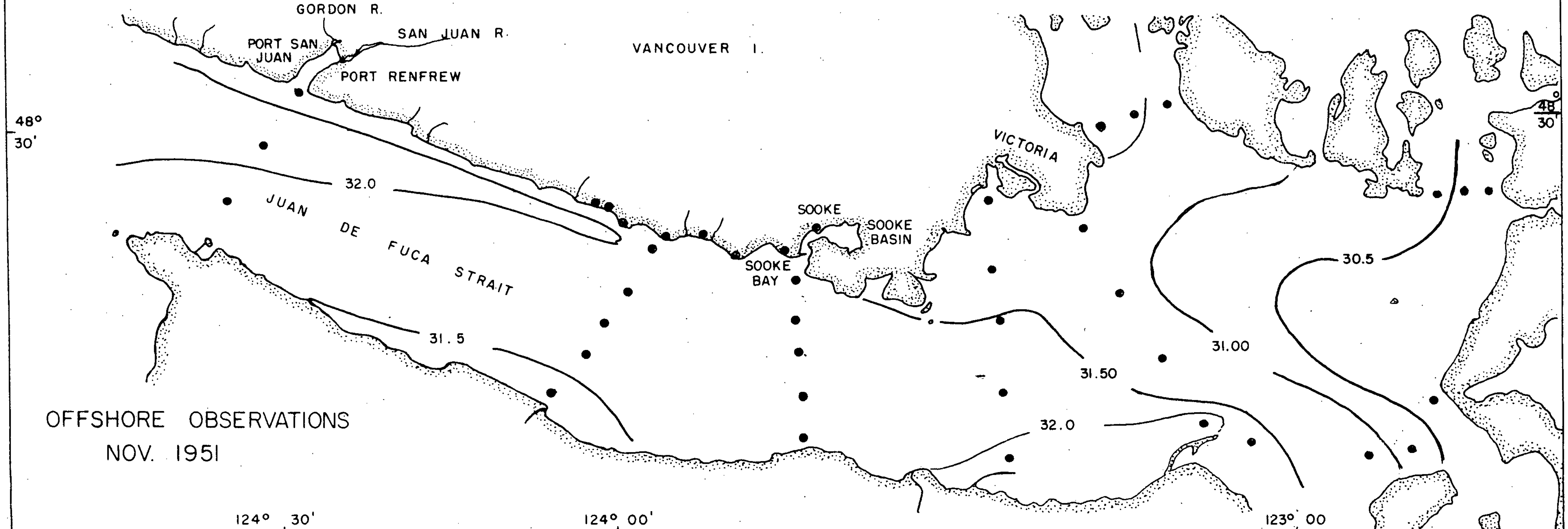


LEGEND
CONGLOM - ERATE OLIGOCENE
SANDSTONE MIOCENE
GABBRO - OLIGOCENE
BASALT TUFF EOCENE
SLATE, SCHIST QUARTZITE CARBONIFEROUS
ALLUVIUM - RECENT
GNEISS - CRETACEOUS
DIORITE "
CONGLOMERATE SANDSTONE, SHALE UPPER CRETACEOUS
ANORTHOSITE - CRETACEOUS
GRANO-DIORITE - CRETACEOUS
CRYSTALLINE - MARBLE - TRIASSIC
ANDESITE TUFF TRIASSIC
TYPES OF BOTTOM R - ROCK S - SAND M - MUD SH - SHINGLE G - GRAVEL
VANCOUVER ISLAND
JUAN DE FUCA STRAIT
49° 00'
48° 30'
124° 30'
124° 00'
123° 00'

Figure 3. Winter surface salinity distribution of Juan de Fuca Strait.

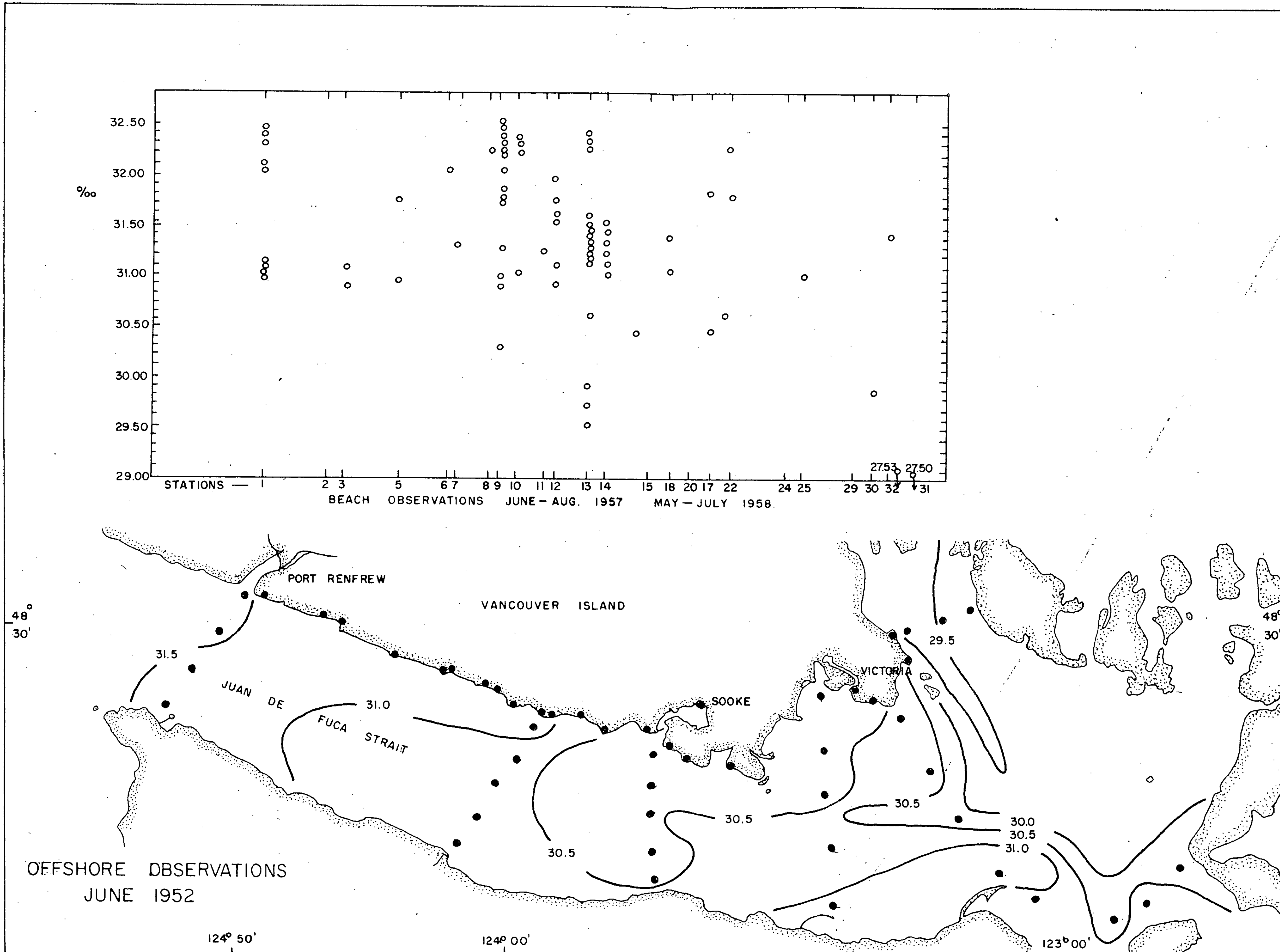


BEACH OBSERVATIONS SEPT. '57 — APRIL '58



OFFSHORE OBSERVATIONS
NOV. 1951

Figure 4. Summer surface salinity distribution of Juan de Fuca Strait.



32.50
32.00
31.50
31.00
30.50
30.00
29.50
29.00
‰
STATIONS — 1 2 3 5 6 7 8 9 10 11 12 13 14 15 18 20 17 22 24 25 29 30 32 31
27.53
27.50
BEACH OBSERVATIONS JUNE – AUG. 1957 MAY — JULY 1958
PORT RENFREW
VANCOUVER ISLAND
JUAN DE FUCA STRAIT
SOOKE
VICTORIA
31.5
31.0
30.5
30.0
29.5
48° 30'
124° 50'
124° 00'
123° 00'
OFFSHORE OBSERVATIONS
JUNE 1952

Figure 5. Monthly mean surface salinities at Race Rocks.

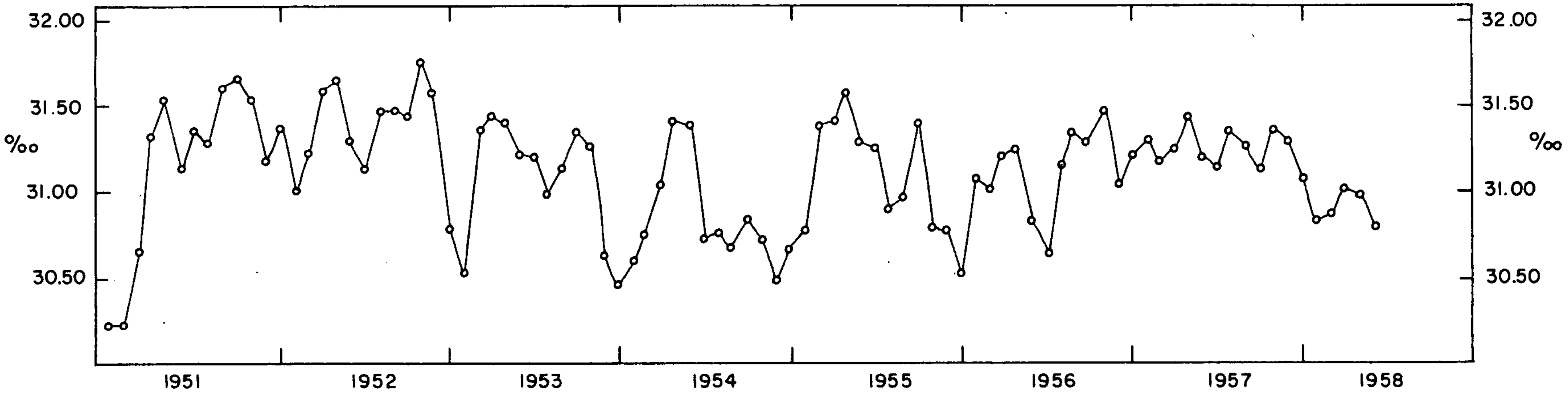
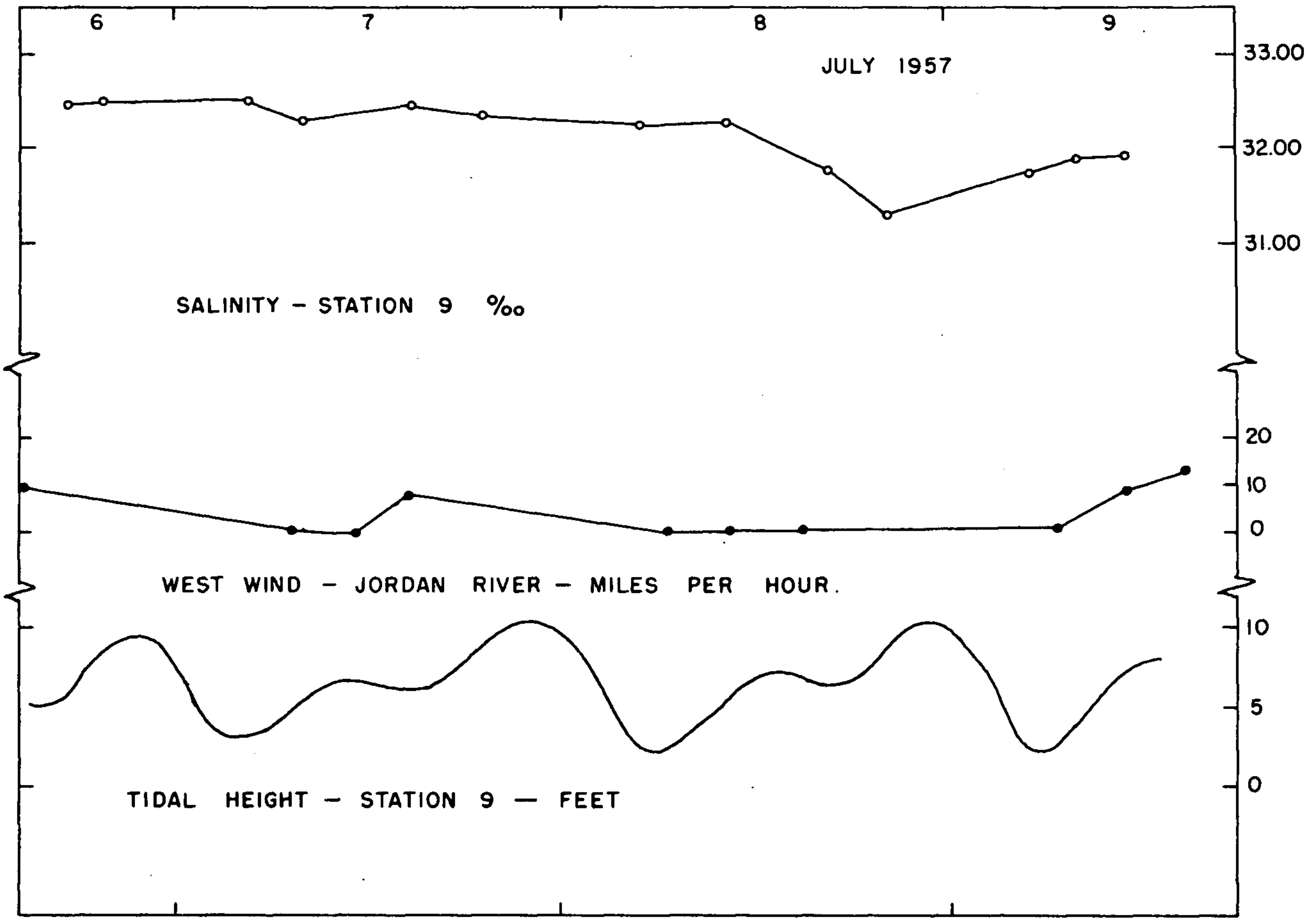

32.00
31.50
31.00
30.50
‰
1951
1952
1953
1954
1955
1956
1957
1958

Figure 6. Diurnal variations in salinity at Stations 9 and 13, compared with wind and tide.


6
7
8
9
JULY 1957
33.00
32.00
31.00
SALINITY - STATION 9 ‰
20
10
0
WEST WIND - JORDAN RIVER - MILES PER HOUR.
10
5
0
TIDAL HEIGHT - STATION 9 — FEET

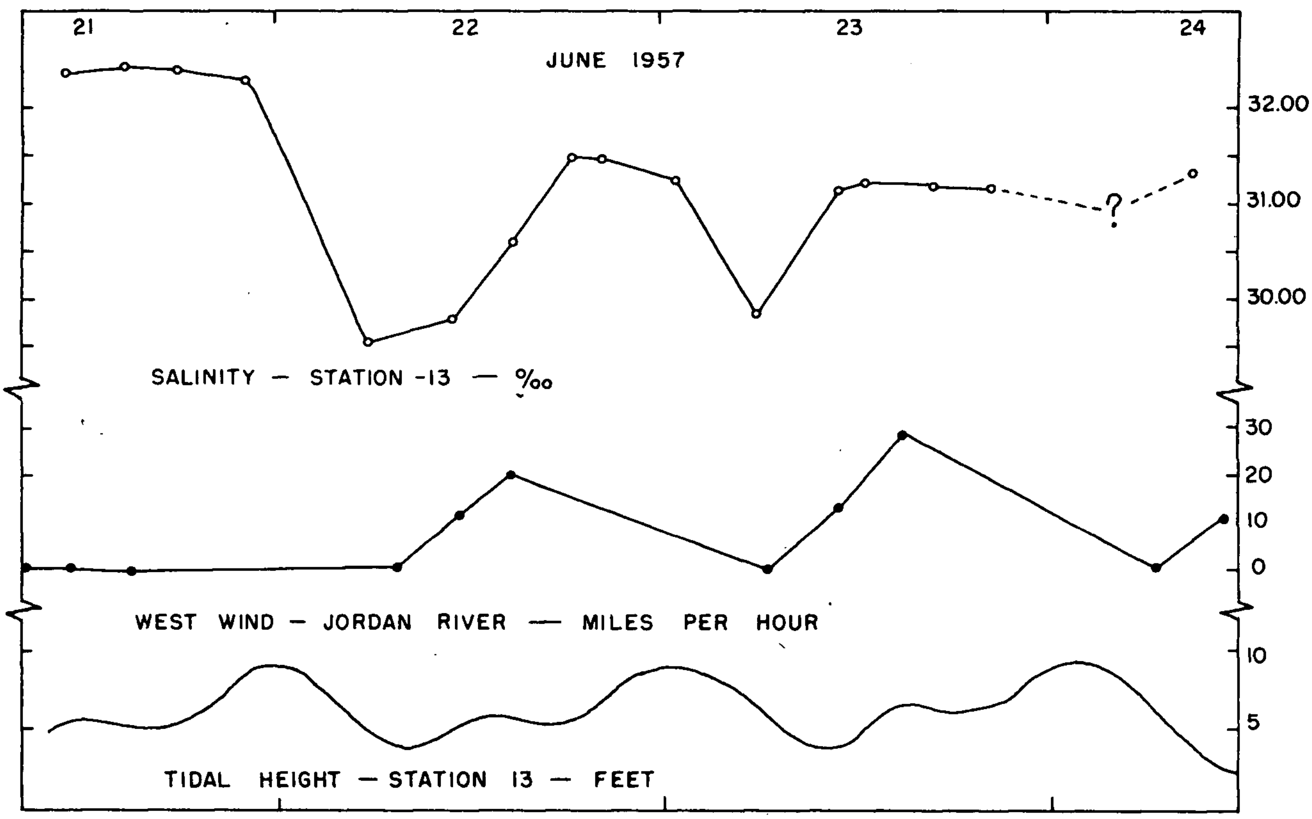

21
22
23
24
JUNE 1957
32.00
31.00
30.00
?
SALINITY - STATION -13 — ‰
30
20
10
0
WEST WIND - JORDAN RIVER — MILES PER HOUR
10
5
TIDAL HEIGHT - STATION 13 — FEET

Figure 7. Salinity differences along the north shore of Juan de Fuca Strait.

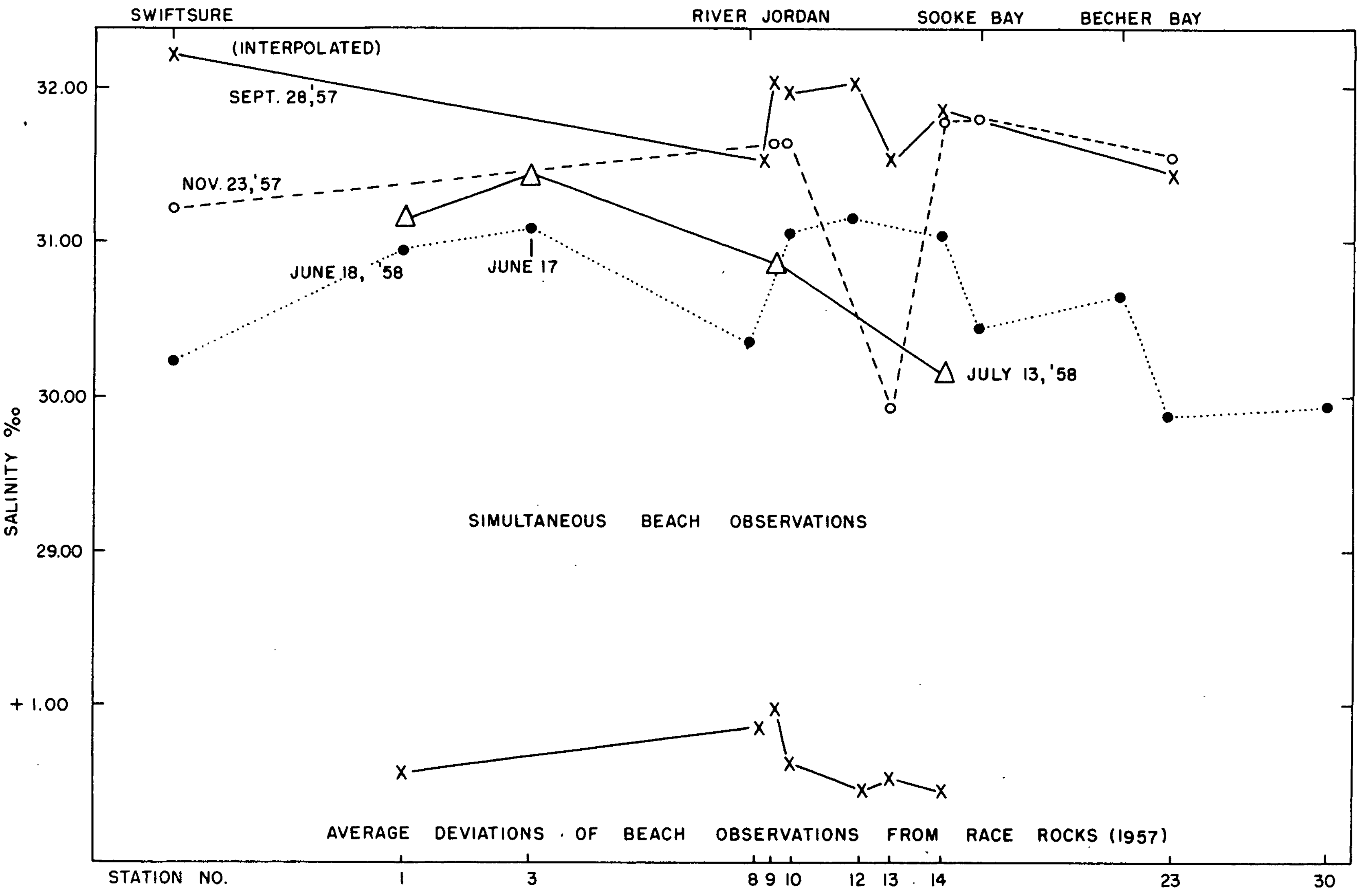
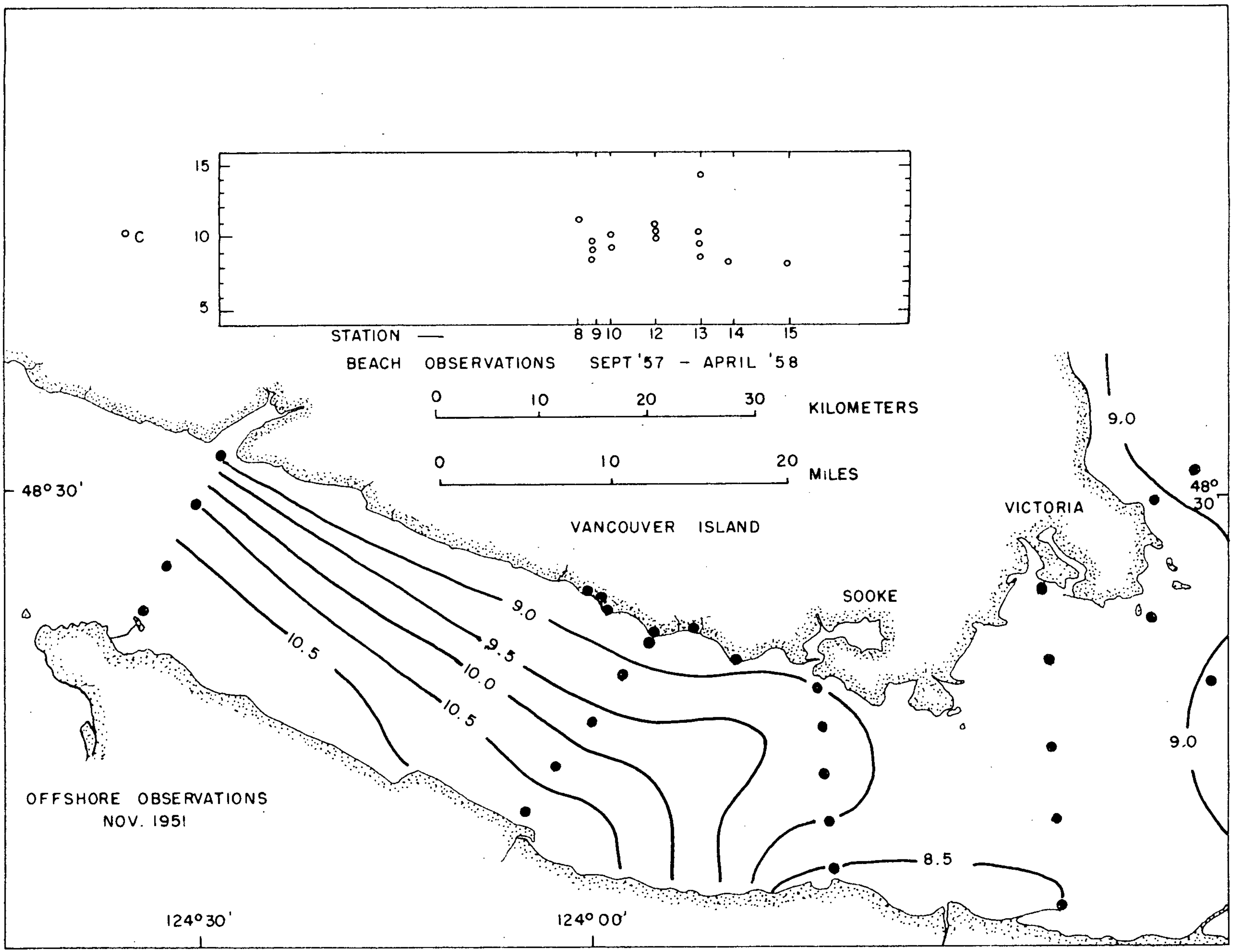
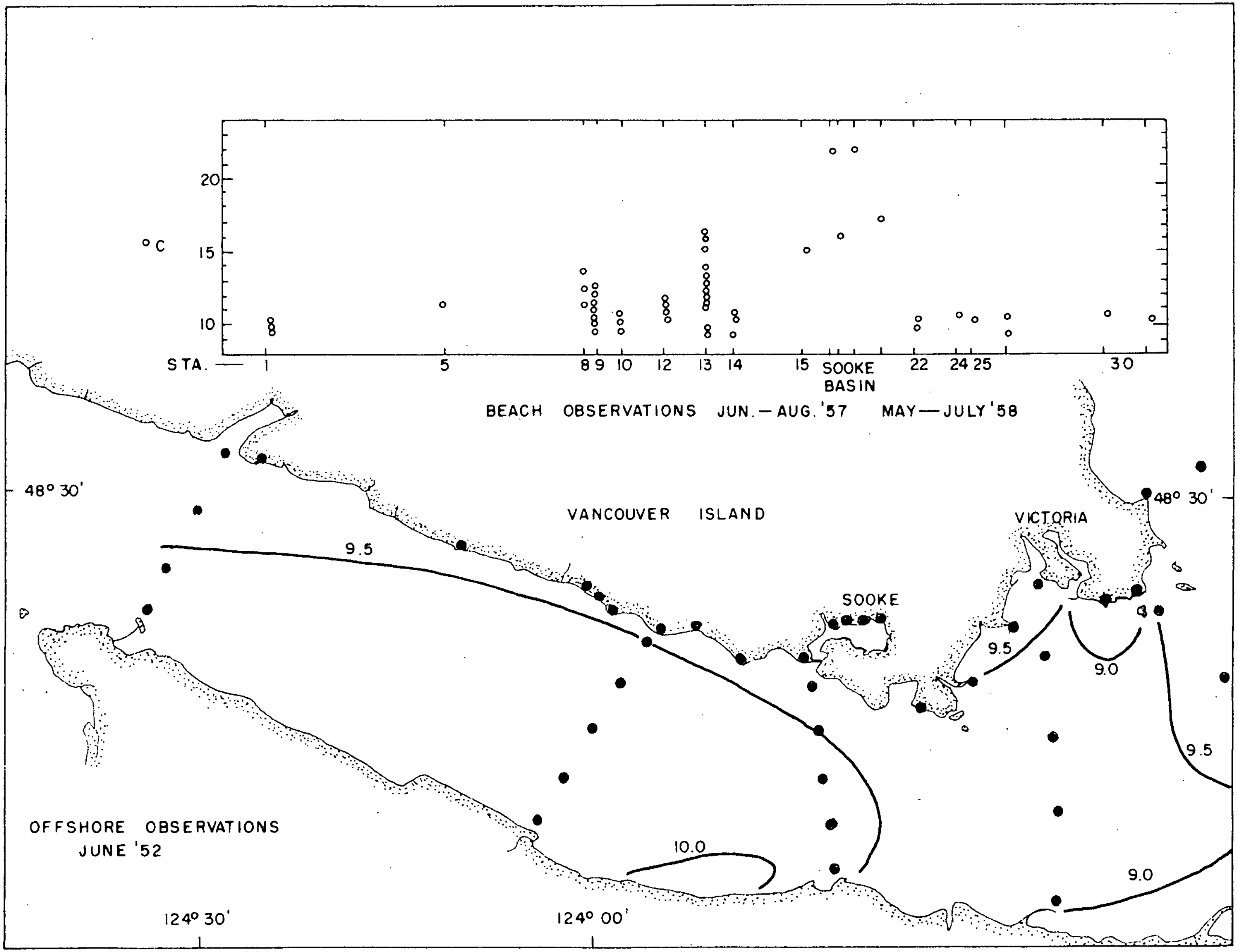

SWIFTSURE
RIVER JORDAN
SOOKE BAY
BECHER BAY
(INTERPOLATED)
SEPT. 28,'57
NOV. 23,'57
JUNE 18, '58
JUNE 17
JULY 13,'58
32.00
31.00
30.00
29.00
+ 1.00
SALINITY ‰
SIMULTANEOUS BEACH OBSERVATIONS
AVERAGE DEVIATIONS OF BEACH OBSERVATIONS FROM RACE ROCKS (1957)
STATION NO.
1
3
8 9 10
12
13
14
23
30

Figure 8. Winter surface temperature distribution of Juan de Fuca Strait.



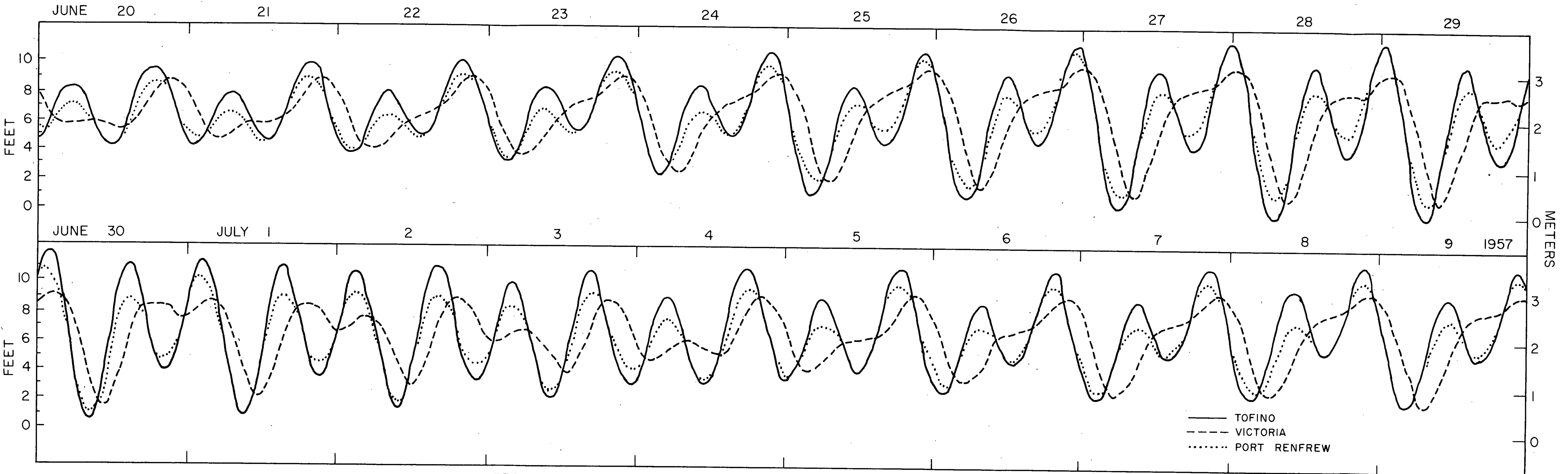
°C
15
10
5
STATION —
8 9 10 12 13 14 15
BEACH OBSERVATIONS SEPT '57 - APRIL '58
0 10 20 30 KILOMETERS
0 10 20 MILES
48° 30'
VANCOUVER ISLAND
VICTORIA
SOOKE
9.0
9.5
10.0
10.5
8.5
OFFSHORE OBSERVATIONS
NOV. 1951
124° 30'
124° 00'

Figure 9. Summer surface temperature distribution of Juan de Fuca Strait.



°C
20
15
10
STA.
1
5
8 9
10
12
13
14
15
SOOKE BASIN
22
24 25
30
BEACH OBSERVATIONS JUN.—AUG.'57 MAY—JULY'58
48° 30'
VANCOUVER ISLAND
VICTORIA
SOOKE
9.5
9.0
10.0
OFFSHORE OBSERVATIONS
JUNE '52
124° 30'
124° 00'

Figure 10. Records from tide gauges on southwest Vancouver Island.



RECORDS FROM TIDE GAUGES ON SOUTHWEST VANCOUVER ISLAND

Figure 11. Generalized diagram of tidal factors for mixed semi-diurnal tides.

Figure 12. Mean and extreme values of tidal factors on south-west Vancouver Island.

Figure 13. Higher values of tidal factors on south-west Vancouver Island. When these varied during the lunar month of the analysis, both values were plotted.

Figure 14. Lower values of tidal factors on south-west Vancouver Island. When these varied during the lunar month of the analysis, both values are plotted.

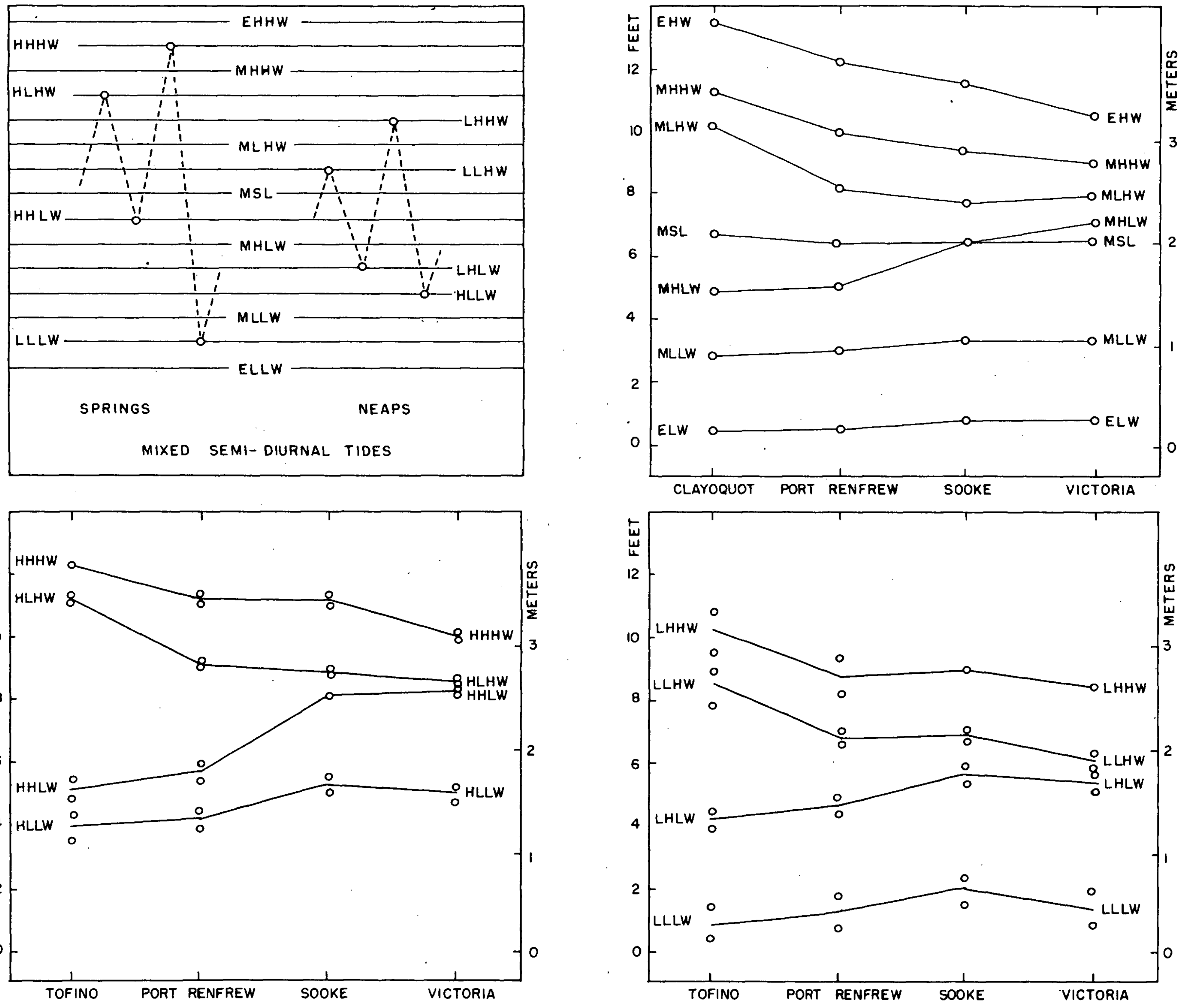
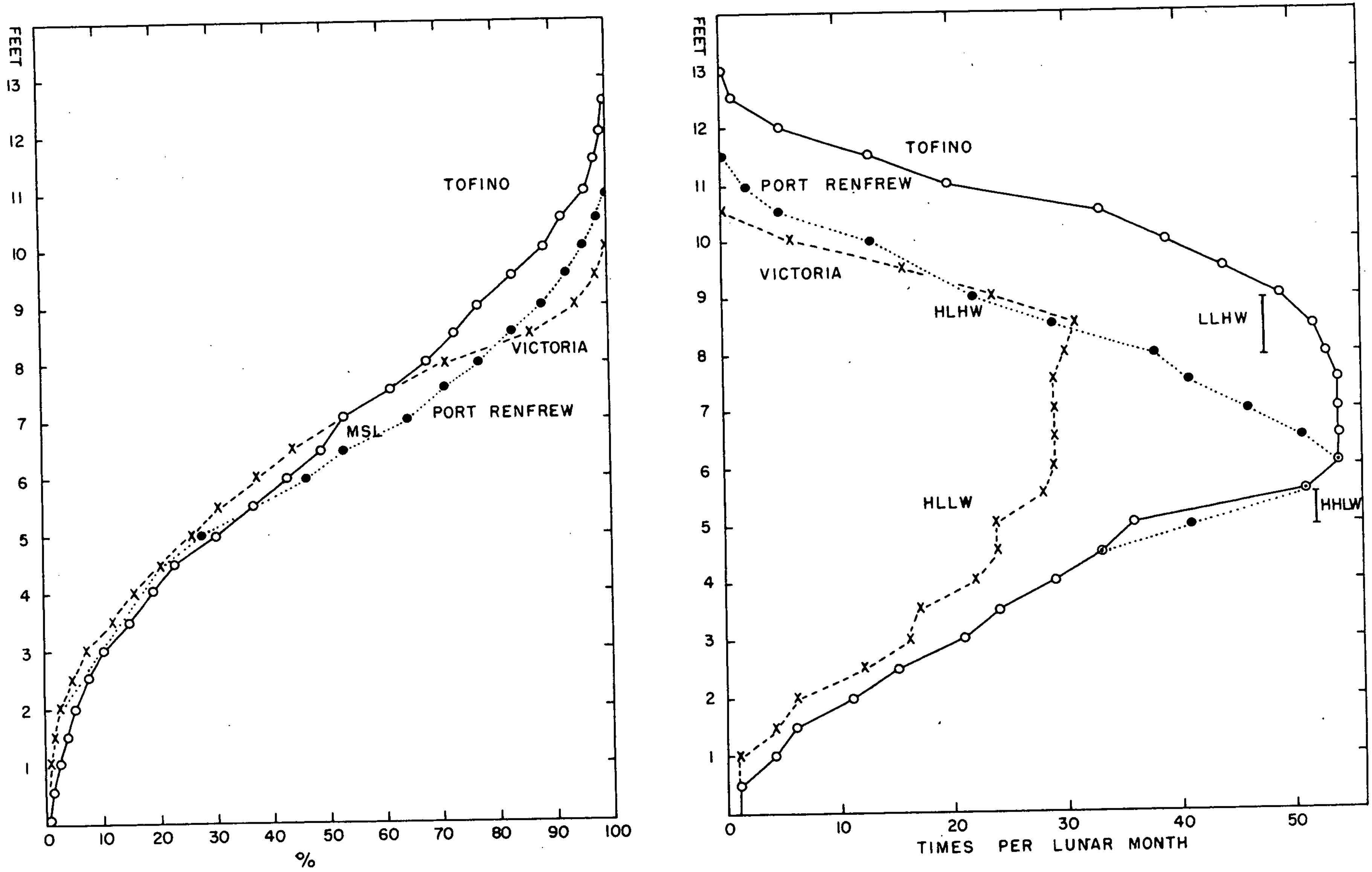

EHHW
HHHW
MHHW
HLHW
LHHW
MLHW
LLHW
MSL
HHLW
MHLW
LHLW
HLLW
MLLW
LLLW
ELLW
SPRINGS
NEAPS
MIXED SEMI-DIURNAL TIDES
FEET
METERS
EHW
MHHW
MLHW
MSL
MHLW
MLLW
ELW
CLAYOQUOT
PORT RENFREW
SOOKE
VICTORIA
HHHW
HLHW
HHLW
HLLW
TOFINO
LHHW
LLHW
LHLW
LLLW

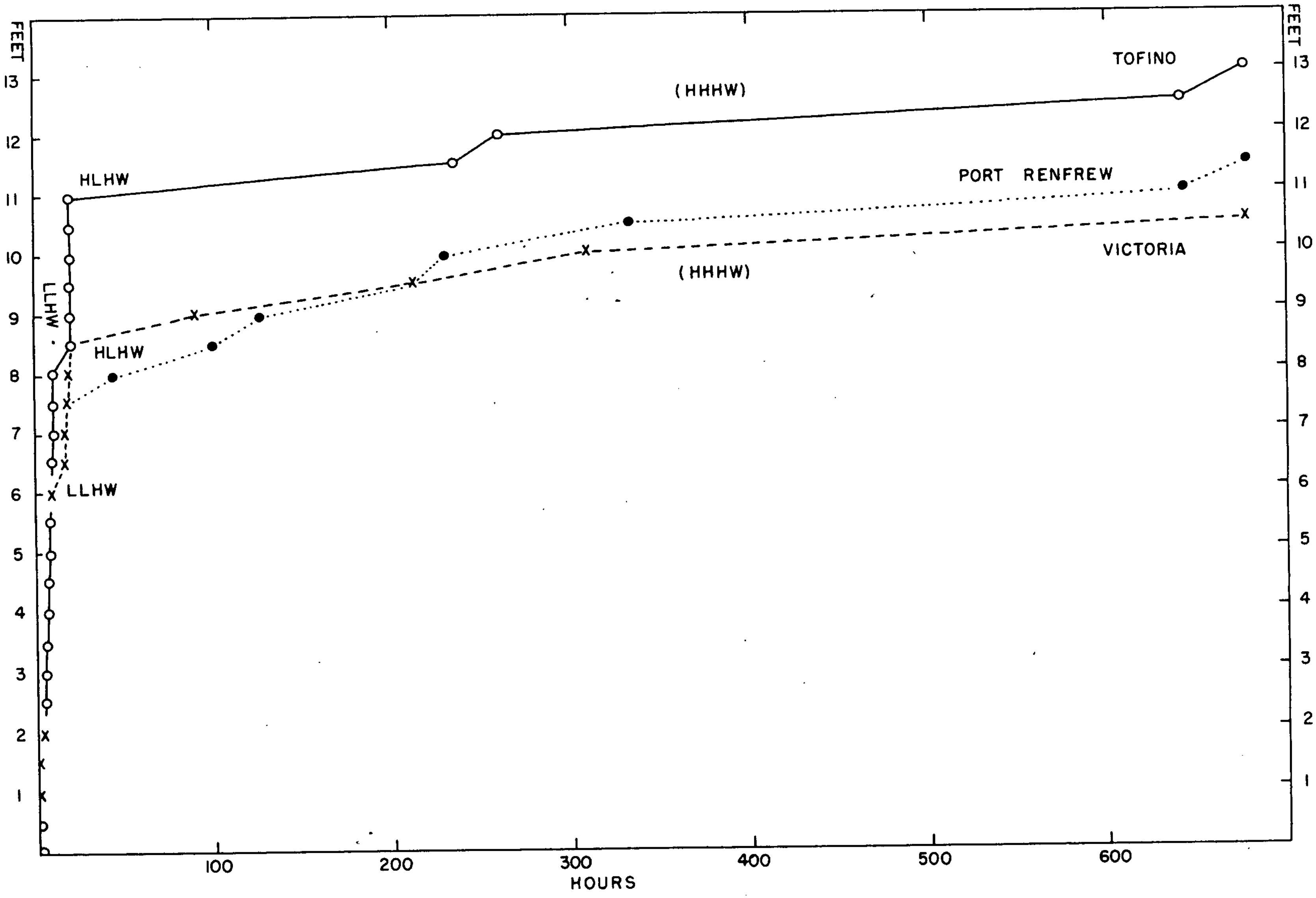
Figure 15. Percentage of time a level is exposed to air.

Figure 16. Times per lunar month a level is submerged.



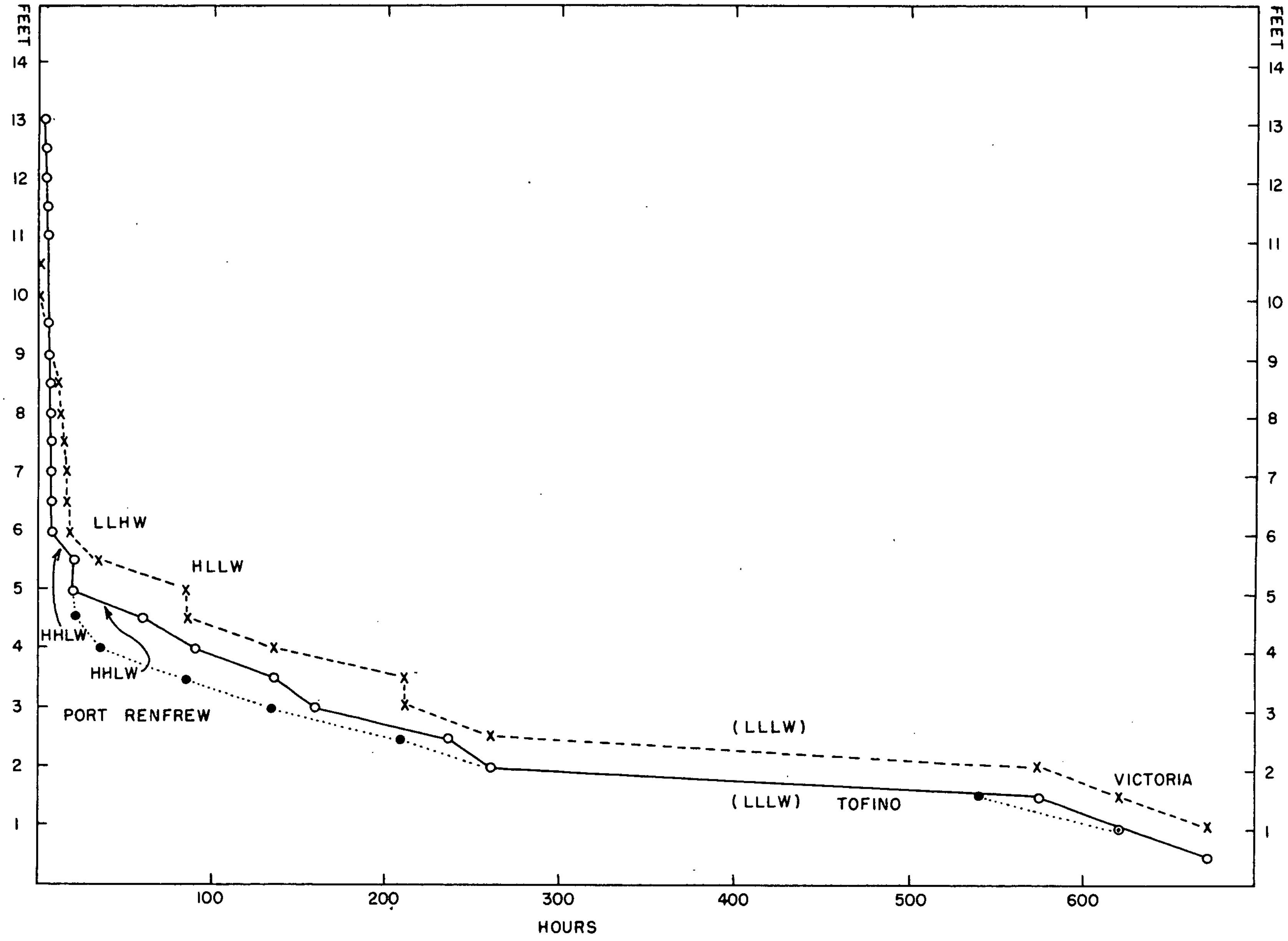
FEET
TOFINO
VICTORIA
PORT RENFREW
MSL
%
FEET
TOFINO
PORT RENFREW
VICTORIA
HLHW
LLHW
HLLW
HHLW
TIMES PER LUNAR MONTH

Figure 17. Hours duration of maximum emergence per lunar month.



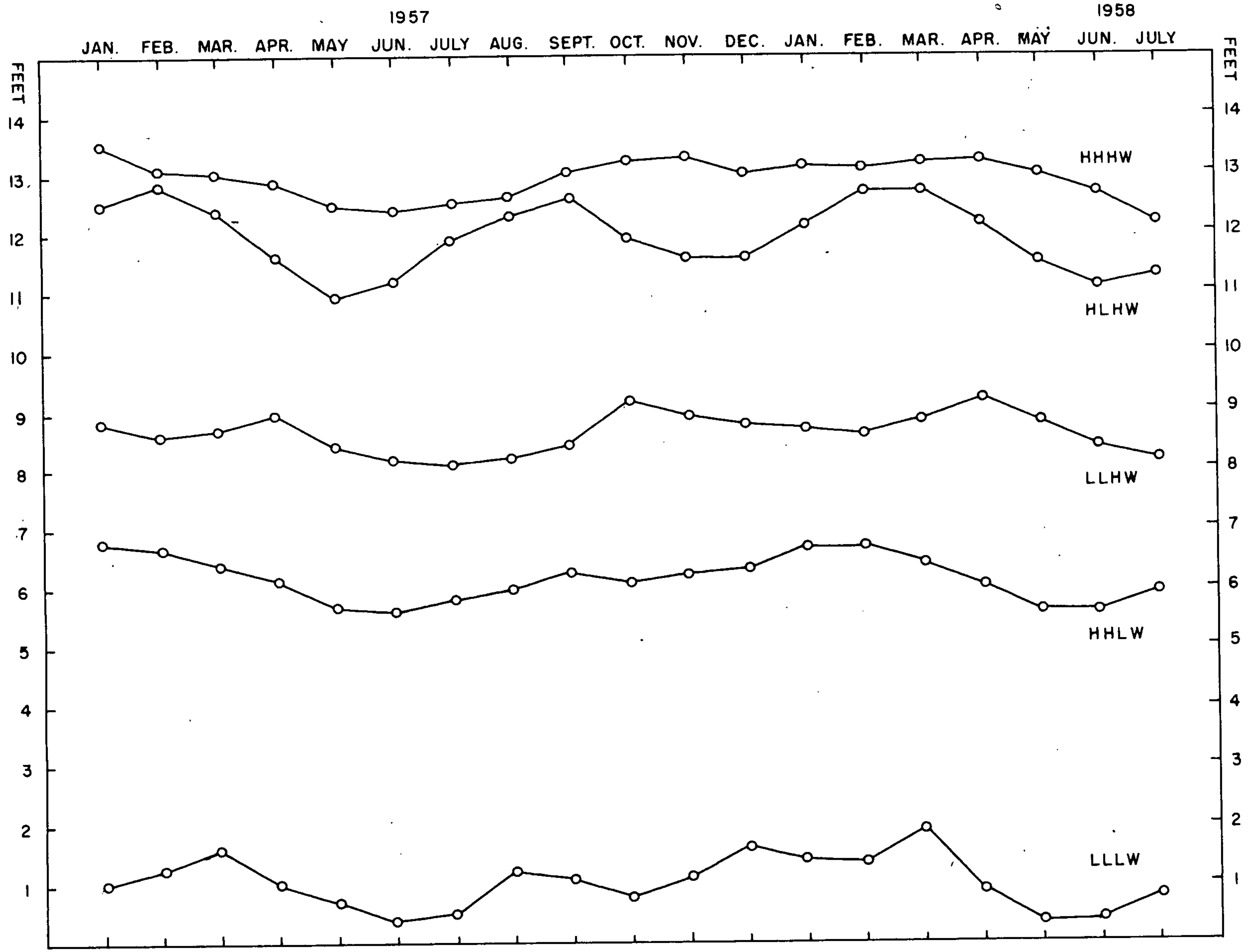
FEET
13
12
11
10
9
8
7
6
5
4
3
2
1
TOFINO
(HHHW)
HLHW
PORT RENFREW
VICTORIA
(HHHW)
LLHW
HLHW
LLHW
100
200
300
400
500
600
HOURS

Figure 18. Hours duration of maximum submergence per lunar month.



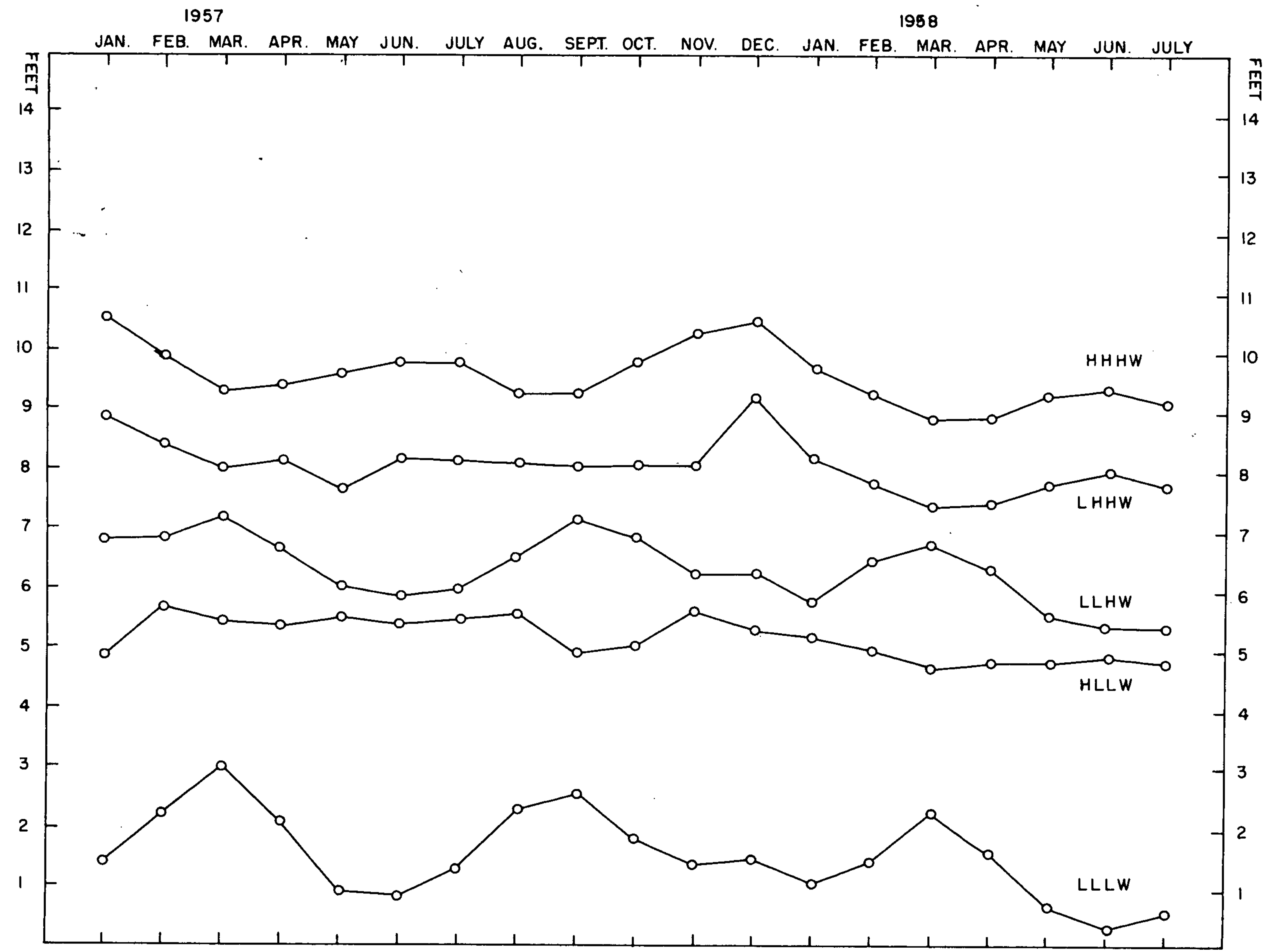
FEET
14
13
12
11
10
9
8
7
6
5
4
3
2
1
LLHW
HLLW
HHLW
HHLW
PORT RENFREW
(LLLW)
(LLLW)
TOFINO
VICTORIA
100
200
300
400
500
600
HOURS

Figure 19. Variations in some tidal factors at Clayoquot.



1957
1958
JAN.
FEB.
MAR.
APR.
MAY
JUN.
JULY
AUG.
SEPT.
OCT.
NOV.
DEC.
JAN.
FEB.
MAR.
APR.
MAY
JUN.
JULY
FEET
14
13
12
11
10
9
8
7
6
5
4
3
2
1
HHHW
HLHW
LLHW
HHLW
LLLW

Figure 20. Variations in some tidal factors at Victoria.

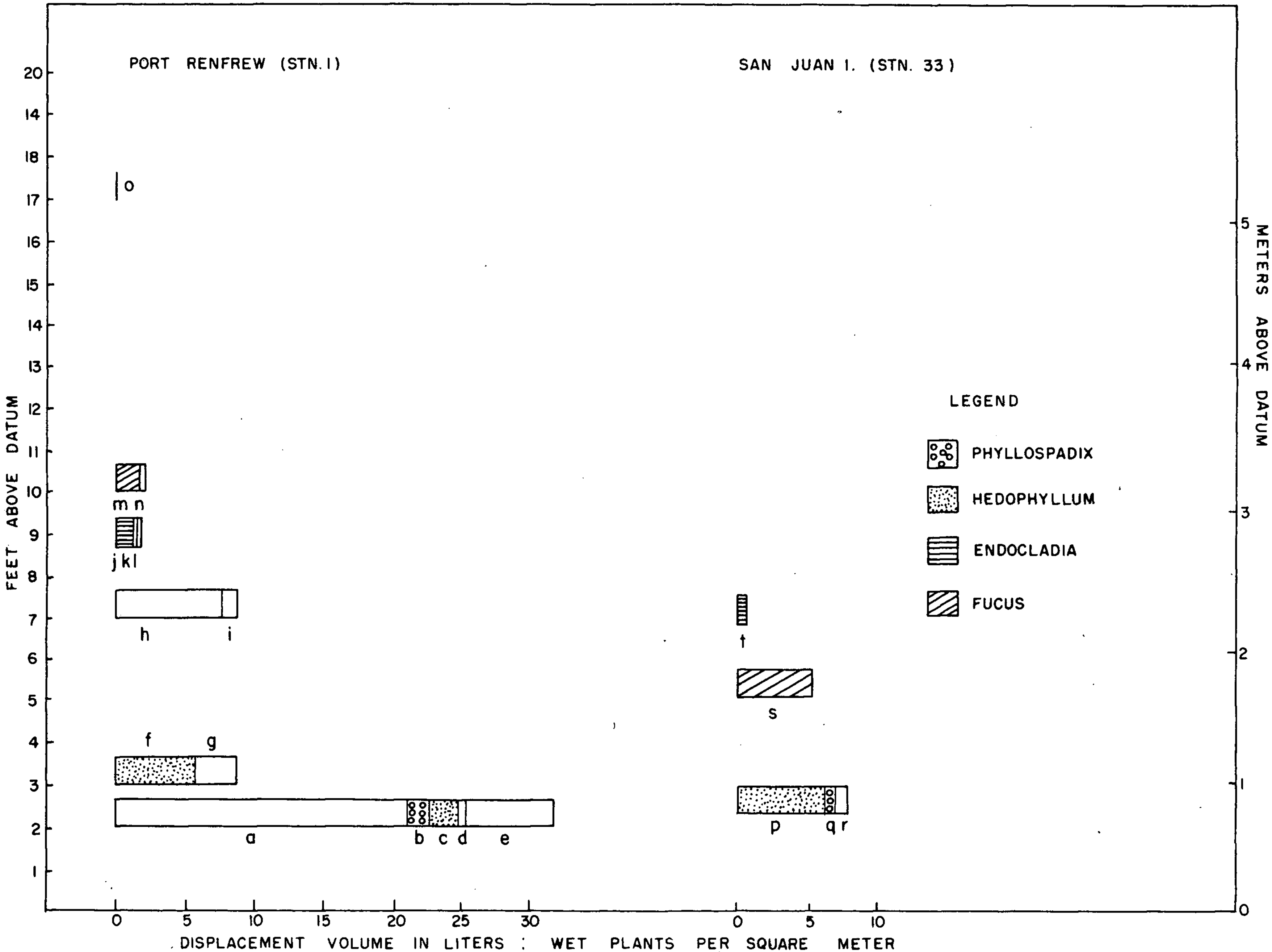


1957
1958
JAN.
FEB.
MAR.
APR.
MAY
JUN.
JULY
AUG.
SEPT.
OCT.
NOV.
DEC.
JAN.
FEB.
MAR.
APR.
MAY
JUN.
JULY
FEET
14
13
12
11
10
9
8
7
6
5
4
3
2
1
HHHW
LHHW
LLHW
HLLW
LLLW

Figure 21. Some quantitative measurements of the intertidal flora.

The displacement volumes of each of the major components of the flora are shown graphically, and designated by a letter. The letters are listed below, followed by the name of the plant. The number of individuals of the plant per square meter is indicated within the brackets.

a. *Lessoniopsis* (10), b. *Phyllospadix* (27), c. *Hedophyllum* (8), d. *Iridaea* (67), e. miscellaneous, f. *Hedophyllum* (45), g. miscellaneous, h. *Postelsia* (103), i. *Alaria nana* (82), j. *Endocladia* (100), k. *Rhodomela* (5), l. miscellaneous, m. *Fucus* (182), n. *Pelvetiopsis* (15), o. many *Prasiola*, p. *Hedophyllum* (15), q. *Phyllospadix* (5), r. miscellaneous, s. *Fucus* (130), t. *Endocladia* (320)

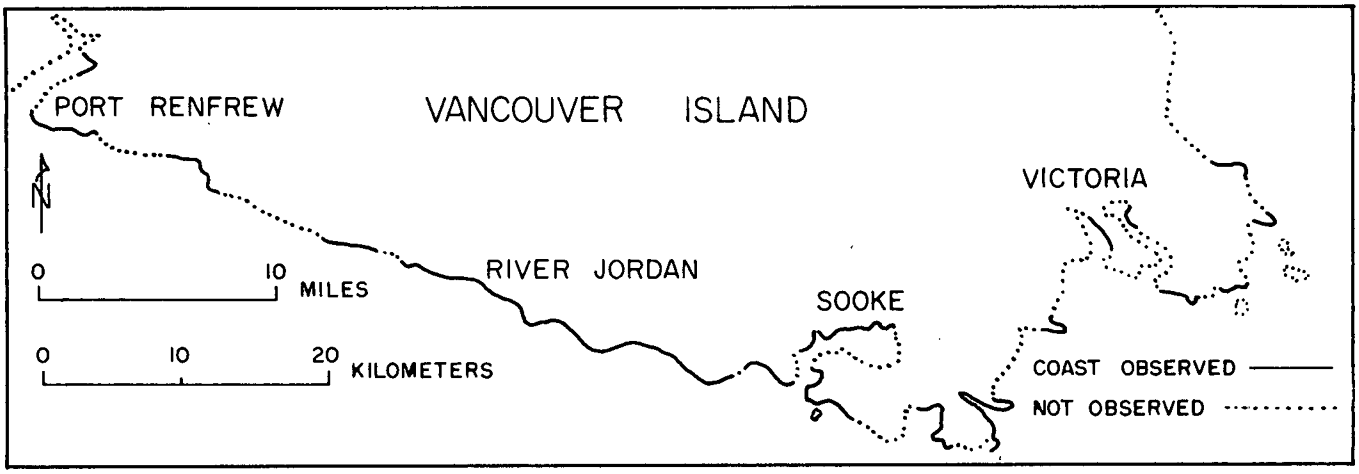


PORT RENFREW (STN. I)
SAN JUAN I. (STN. 33)
FEET ABOVE DATUM
METERS ABOVE DATUM
DISPLACEMENT VOLUME IN LITERS : WET PLANTS PER SQUARE METER
LEGEND
PHYLLOSPADIX
HEDOPHYLLUM
ENDOCLADIA
FUCUS
a b c d e f g h i j k l m n o p q r s t

Figure 22. Sections of coast observed at low tide.

Figure 23. Entrance to Sooke Basin.

L	--	limits of *Lessoniopsis*.
G	--	inner limit of *Gigartina*.
Eg	--	inner limit of *Egregia*.
S	--	outer limit of *Sargassum*.
C	--	inner limit of *Cymathere*.
H	--	inner limit of *Hedophyllum*.
P	--	inner limit of *Phyllospadix*.
Z	--	outer limit of *Zostera*.
En	--	inner limit of *Endocladia*.
Mi	--	inner limit of *Mitella*.
My	--	inner limit of *Mytilus californianus*.


PORT RENFREW
VANCOUVER ISLAND
VICTORIA
0 10 MILES
RIVER JORDAN
SOOKE
0 10 20 KILOMETERS
COAST OBSERVED
NOT OBSERVED
N

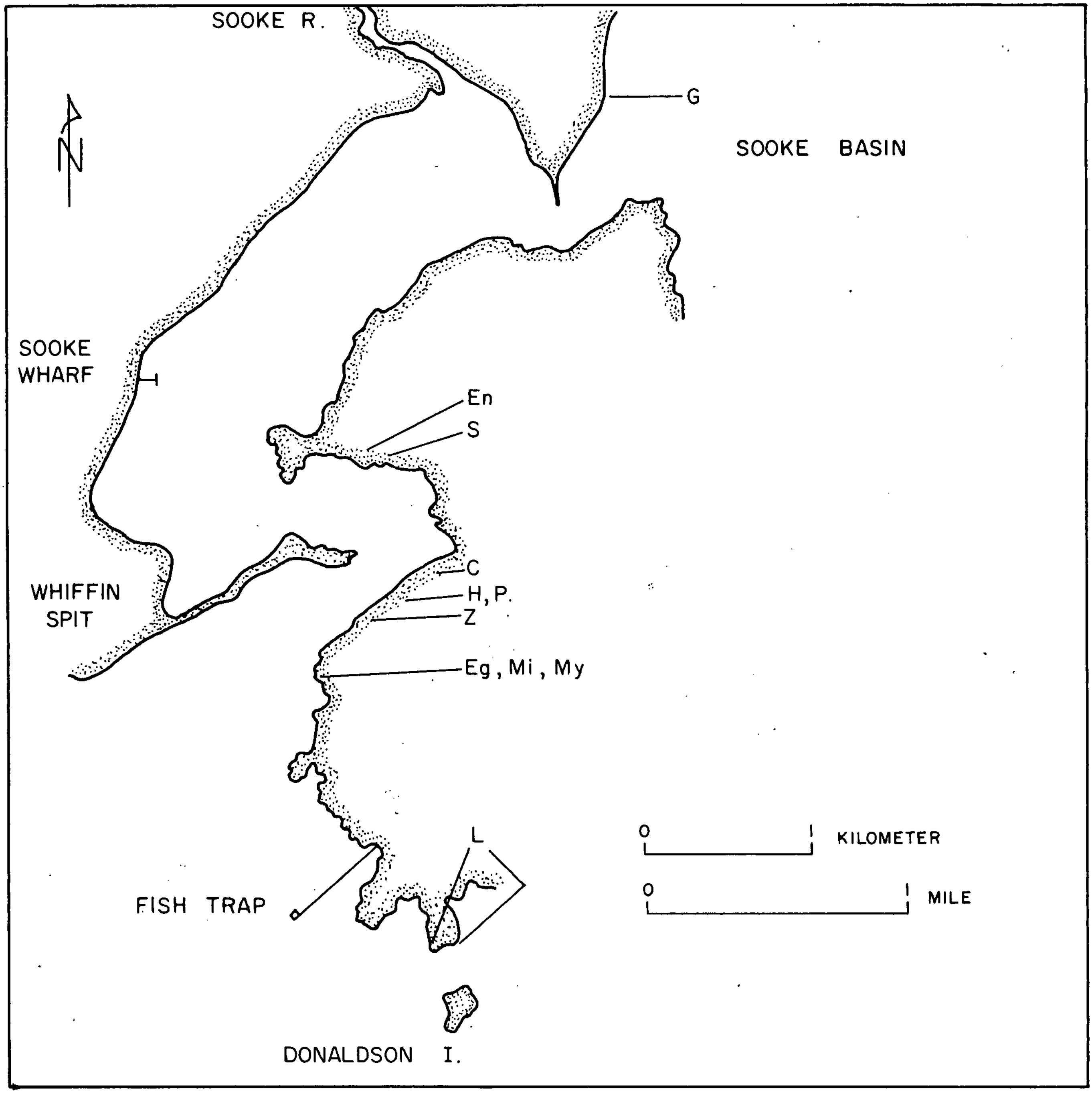
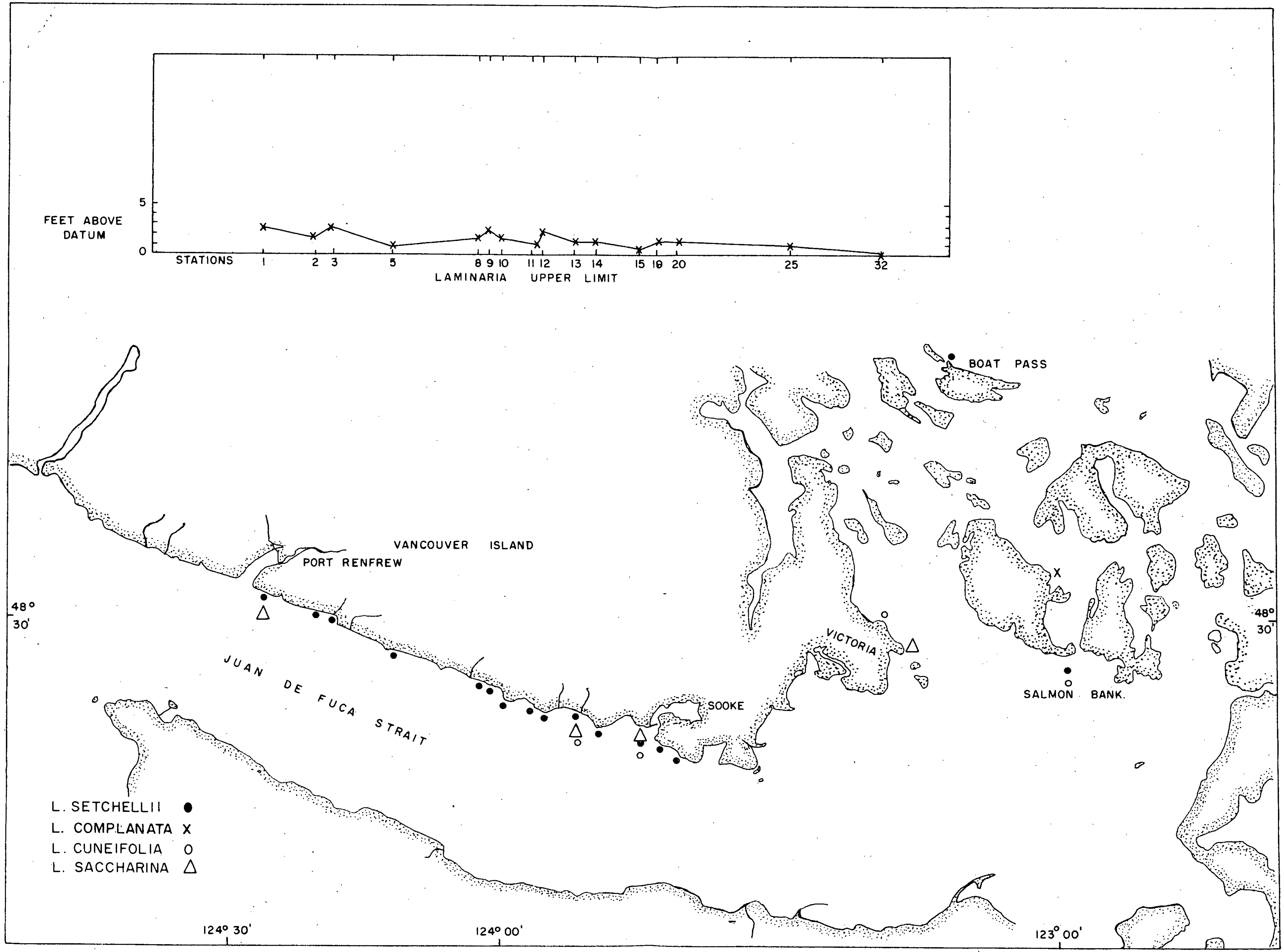
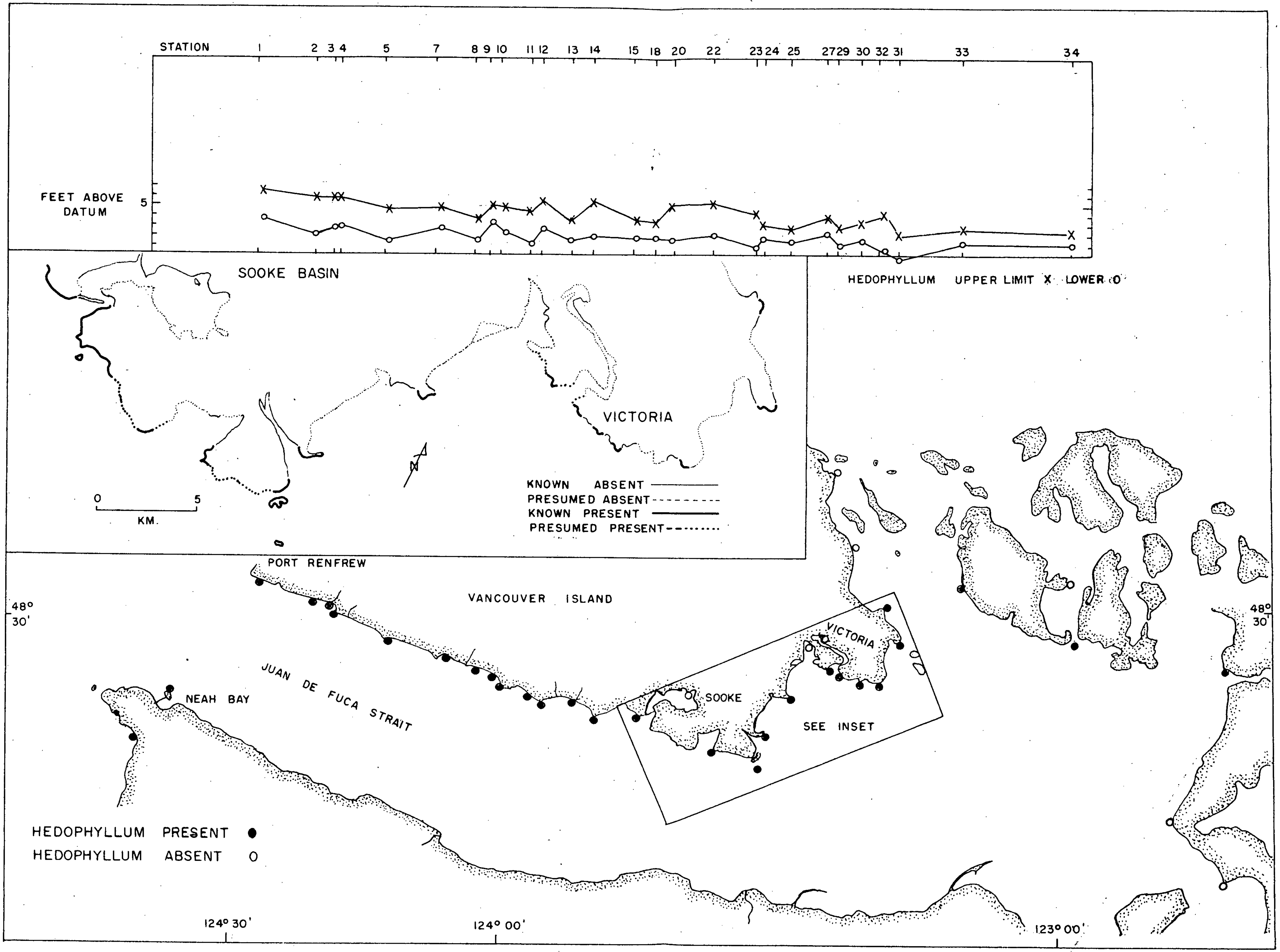

SOOKE R.
G
SOOKE BASIN
N
SOOKE WHARF
En
S
WHIFFIN SPIT
C
H, P.
Z
Eg, Mi, My
L
0 1 KILOMETER
0 1 MILE
FISH TRAP
DONALDSON I.

Figure 24. Distribution of *Laminaria*.



FEET ABOVE DATUM
5
0
STATIONS
1
2
3
5
8
9
10
11
12
13
14
15
19
20
25
32
LAMINARIA UPPER LIMIT
BOAT PASS
VANCOUVER ISLAND
PORT RENFREW
48°
30'
JUAN DE FUCA STRAIT
VICTORIA
SOOKE
SALMON BANK.
L. SETCHELLII ●
L. COMPLANATA X
L. CUNEIFOLIA O
L. SACCHARINA △
124° 30'
124° 00'
123° 00'

Figure 25. Distribution of <u>Hedophyllum</u>.



STATION
1 2 3 4 5 7 8 9 10 11 12 13 14 15 18 20 22 23 24 25 27 29 30 32 31 33 34
FEET ABOVE DATUM
5
HEDOPHYLLUM UPPER LIMIT X LOWER O
SOOKE BASIN
VICTORIA
KNOWN ABSENT
PRESUMED ABSENT
KNOWN PRESENT
PRESUMED PRESENT
0 5
KM.
PORT RENFREW
VANCOUVER ISLAND
48° 30'
JUAN DE FUCA STRAIT
NEAH BAY
SOOKE
SEE INSET
HEDOPHYLLUM PRESENT
HEDOPHYLLUM ABSENT
124° 30'
124° 00'
123° 00'

Figure 26. Composition of *Hedophyllum* populations observed.

1. -- all or mostly bullate.
2. -- mixed.
3. -- all or mostly smooth.

STN.	1a	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	[redacted]		18	19	20	21	22	23	24	25	[redacted]	27	[redacted]	29	30	31	32	33	34
MAY '57										2				2		1																			
JUNE												2	3	1	1																1				
JULY		3							3		3				1															1					
AUG.										3	3		3	3									2	2							1				
SEPT.																																			
OCT.																																			
NOV.										3																									
DEC.															3																				
JAN '58																3																			
FEB.																															3				
MAR.										3				1																					
APR.													1		1																				
MAY						1			2	2	3	2											1		1	1					1				
JUNE		2		3				2		2			3	1	1	1				2		2										1	1		
JULY		3	2		3														2		2			1				1						2	2
AUG.	3																																	2	

Figure 27. Variants of *Hedophyllum sessile*.


5 cm.
1. TW 138
5 cm.
2. TW 227
5 cm
4. TW 9
5 cm.
6. TW 2
5 cm
7. TW 115
5 cm.
3. TW 123
5 cm.
5. TW 42
5 cm
8. TW 212
9 TW 38
5 cm.

Figure 28. Growth in Hedophyllum sessile sporophyte.

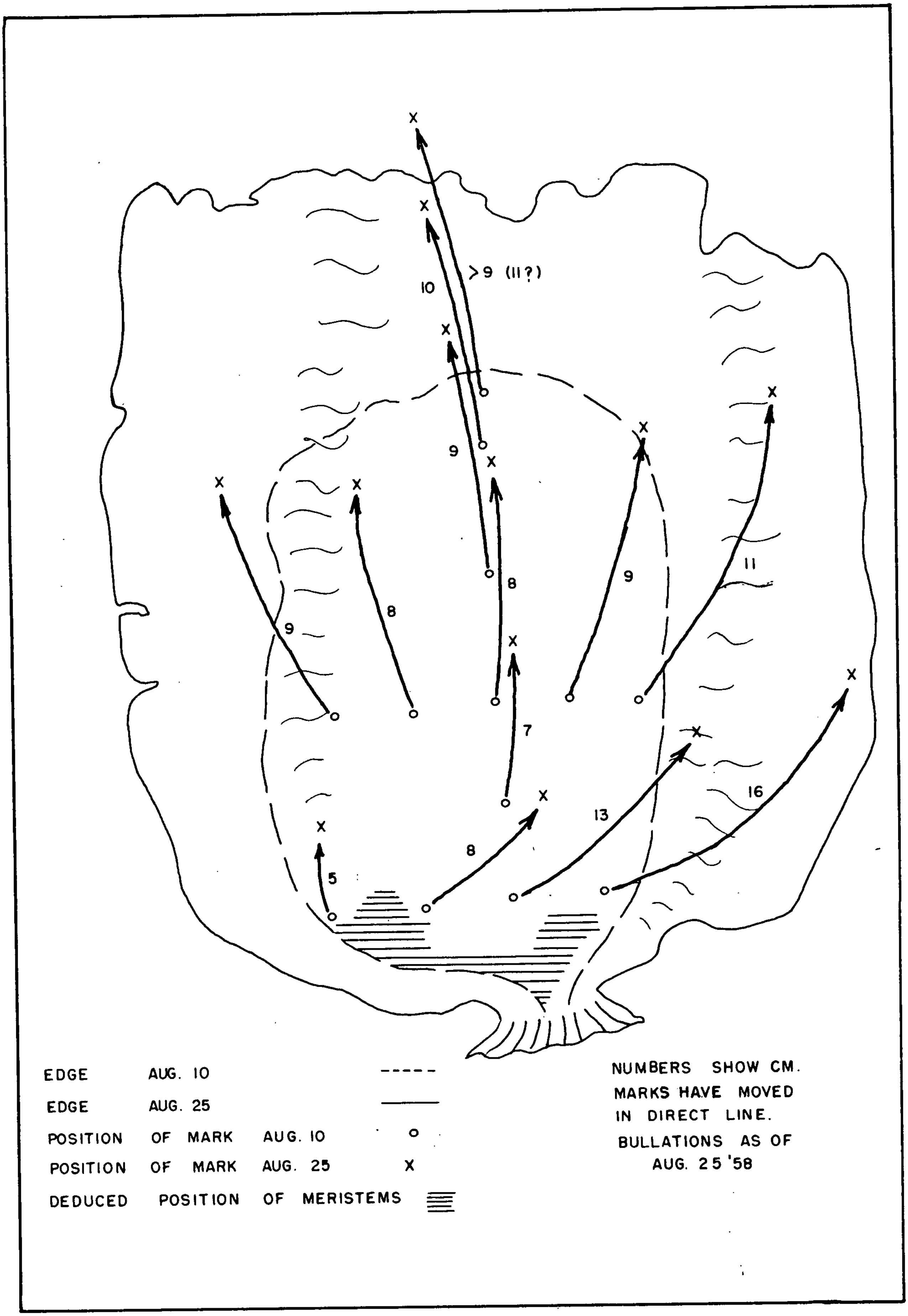
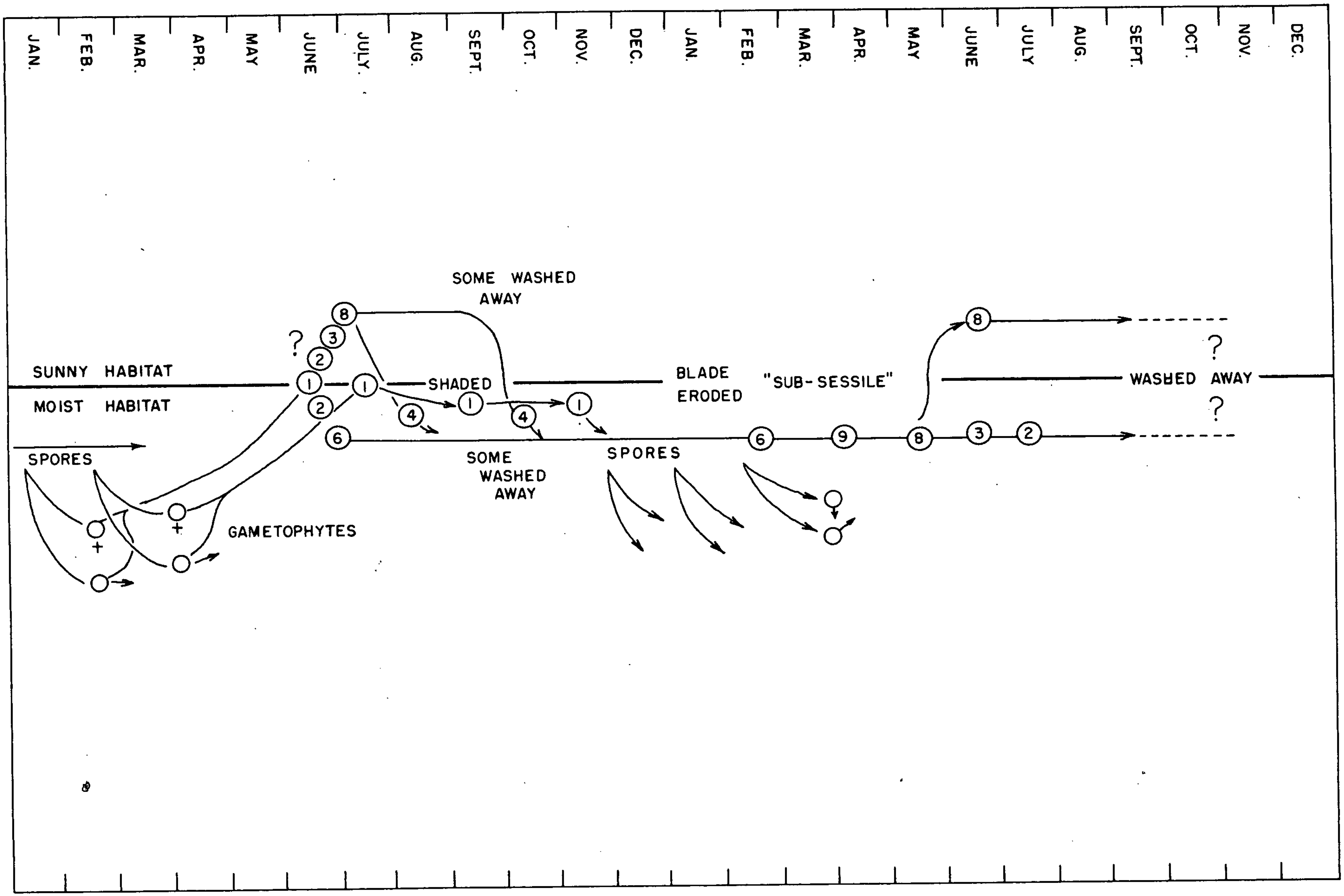

>9 (11?)
10
9
8
9
8
9
8
7
9
11
13
16
8
5
EDGE AUG. 10
EDGE AUG. 25
POSITION OF MARK AUG. 10
POSITION OF MARK AUG. 25 X
DEDUCED POSITION OF MERISTEMS
NUMBERS SHOW CM. MARKS HAVE MOVED IN DIRECT LINE.
BULLATIONS AS OF AUG. 25 '58

Figure 29. Presumed life cycle of *Hedophyllum sessile*. See text and Figure 27 for explanations of numbers.



JAN.
FEB.
MAR.
APR.
MAY
JUNE
JULY
AUG.
SEPT.
OCT.
NOV.
DEC.
JAN.
FEB.
MAR.
APR.
MAY
JUNE
JULY
AUG.
SEPT.
OCT.
NOV.
DEC.
SOME WASHED AWAY
SUNNY HABITAT
MOIST HABITAT
SHADED
BLADE ERODED
"SUB-SESSILE"
WASHED AWAY
SPORES
SOME WASHED AWAY
SPORES
GAMETOPHYTES

Figure 30. Distribution of Postelsia and Macrocystis.

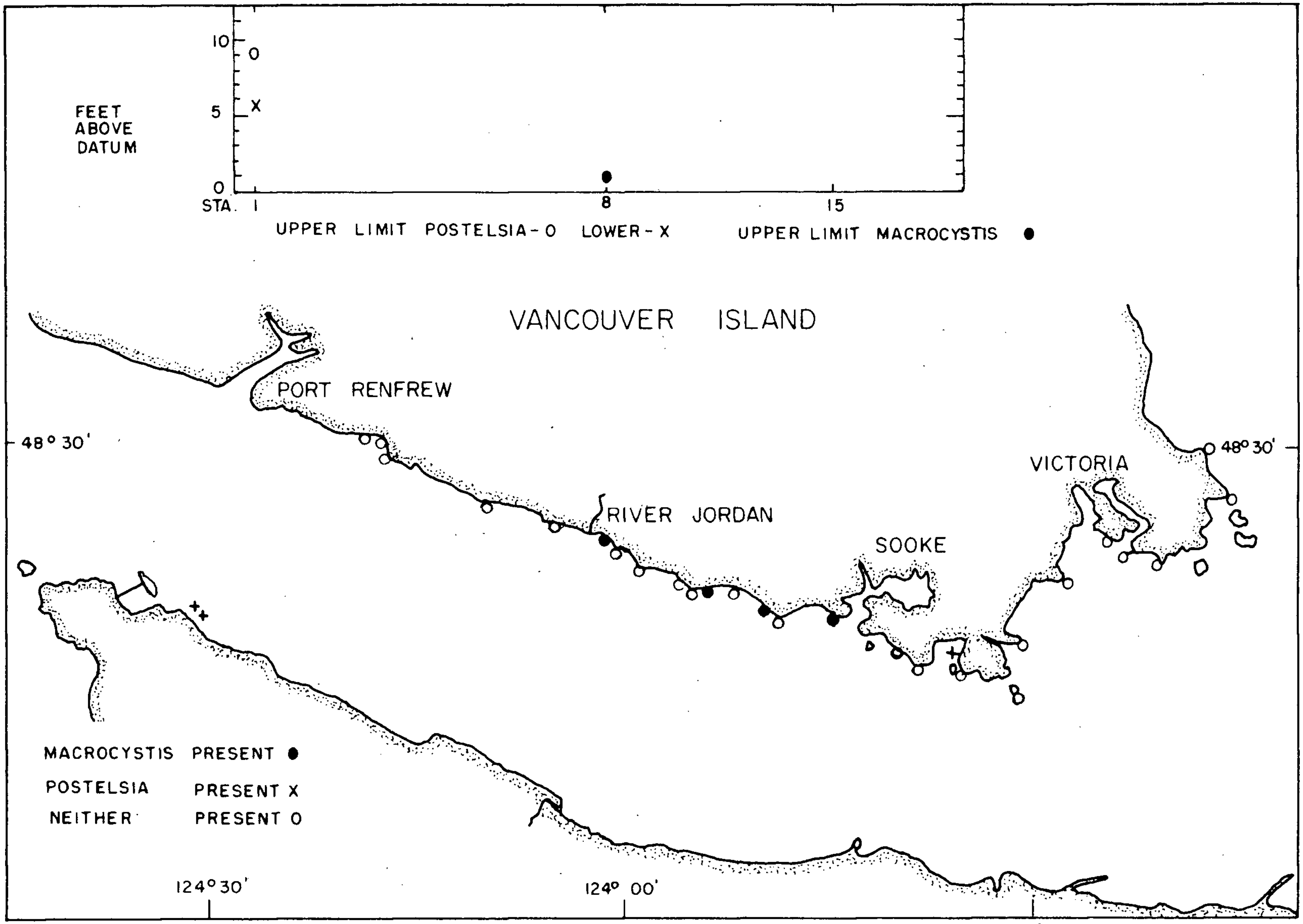

FEET
ABOVE
DATUM
10
5
0
STA. 1
8
15
UPPER LIMIT POSTELSIA - O LOWER - X
UPPER LIMIT MACROCYSTIS ●
VANCOUVER ISLAND
PORT RENFREW
48° 30'
RIVER JORDAN
SOOKE
VICTORIA
48° 30'
MACROCYSTIS PRESENT ●
POSTELSIA PRESENT X
NEITHER PRESENT O
124° 30'
124° 00'

Figure 31. Distribution of Lessoniopsis.

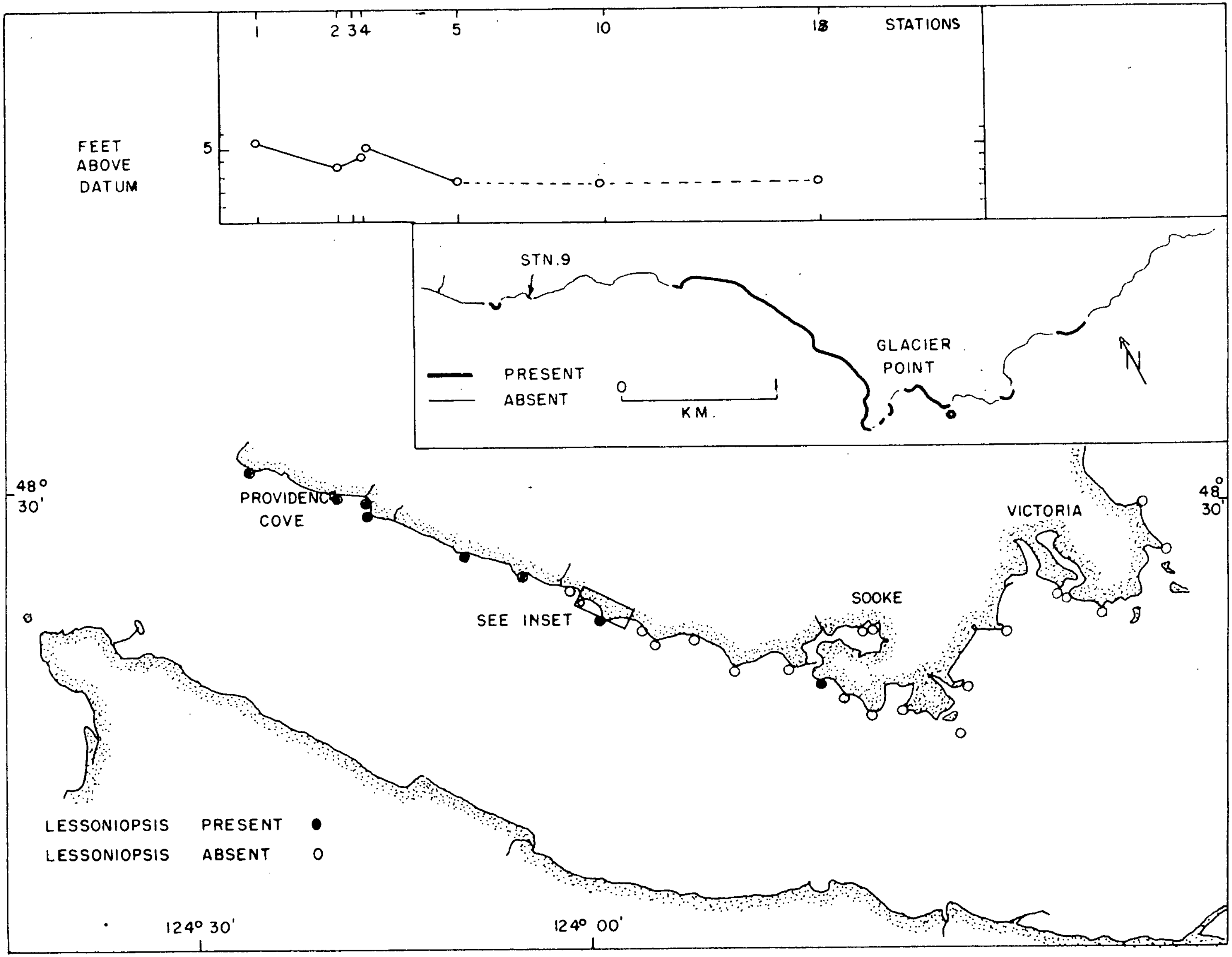

1
2 3 4
5
10
18
STATIONS
FEET
ABOVE
DATUM
5
STN.9
GLACIER
POINT
PRESENT
ABSENT
0
KM.
N
48°
30'
PROVIDENCE
COVE
SEE INSET
SOOKE
VICTORIA
48°
30'
LESSONIOPSIS PRESENT
LESSONIOPSIS ABSENT
124° 30'
124° 00'

Figure 32. Younger individual of *Alaria marginata* variant 1. After specimen TW78, from Glacier Point. Sori are stippled.

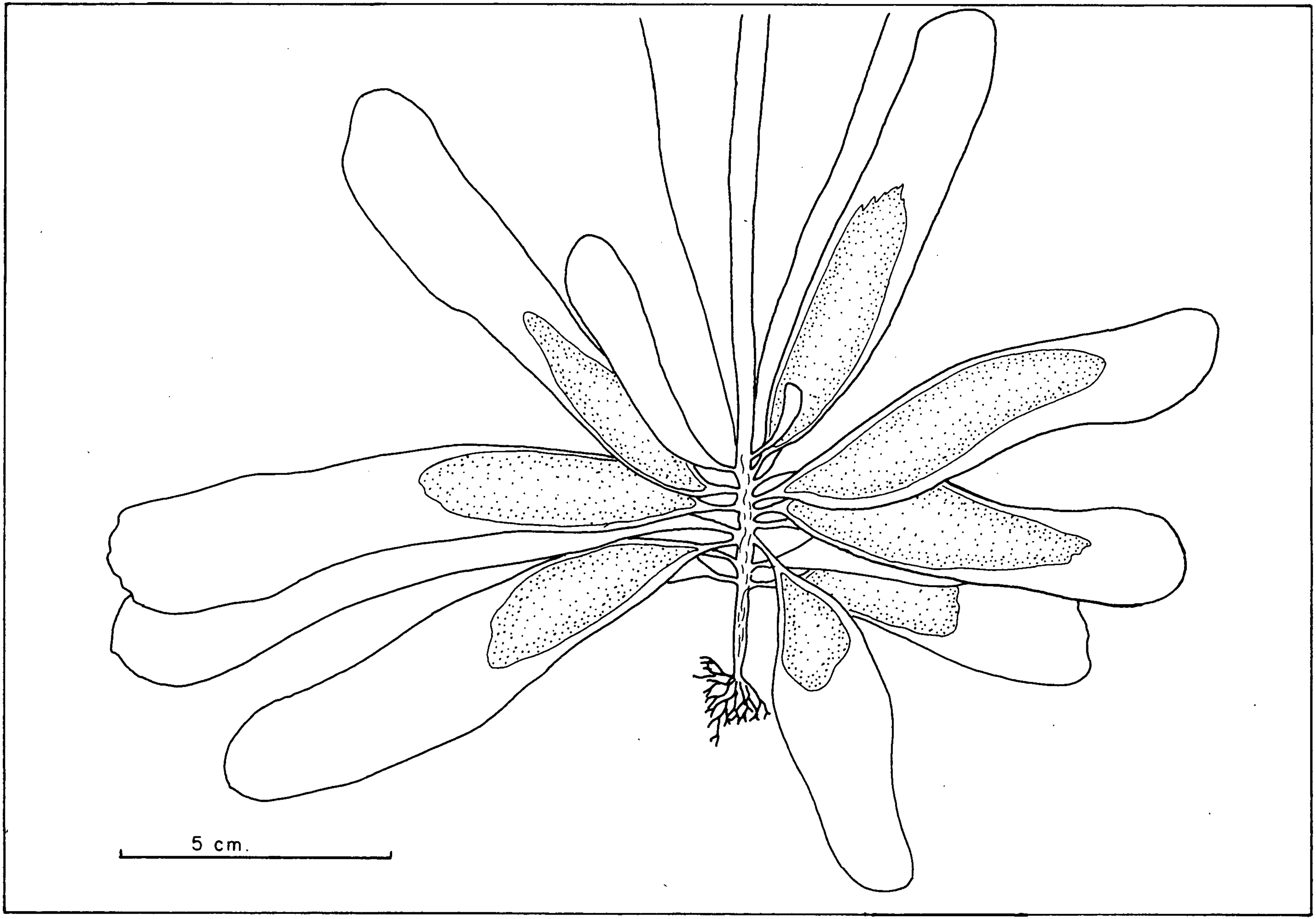

5 cm.

Figure 33. Older individual of *Alaria marginata* variant 1. After specimen TW 155, from Magdalena Point.

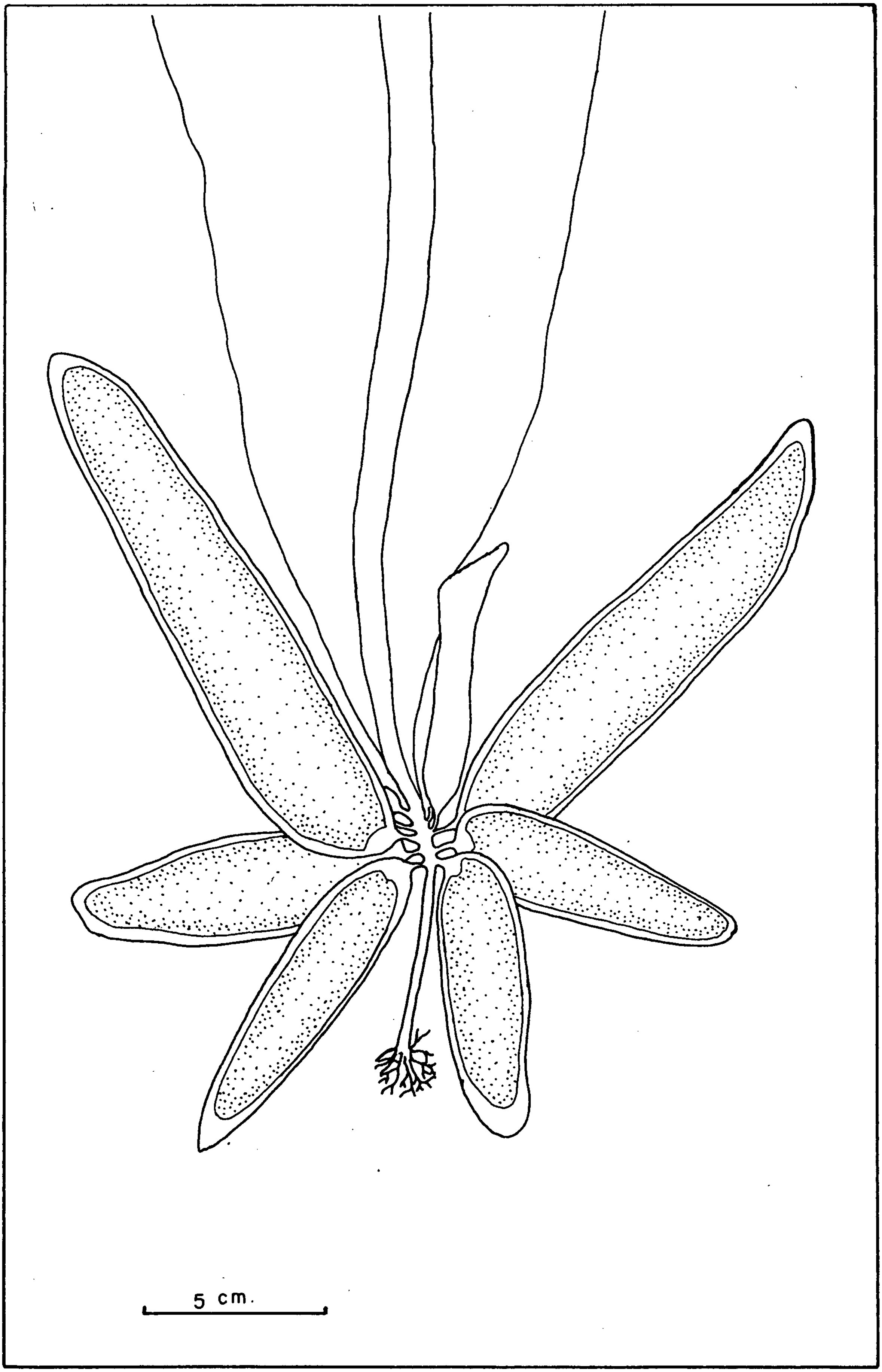

5 cm.

Figure 34. Younger individual of _Alaria marginata_ variant 2. After specimen TW 6, from Otter Point.

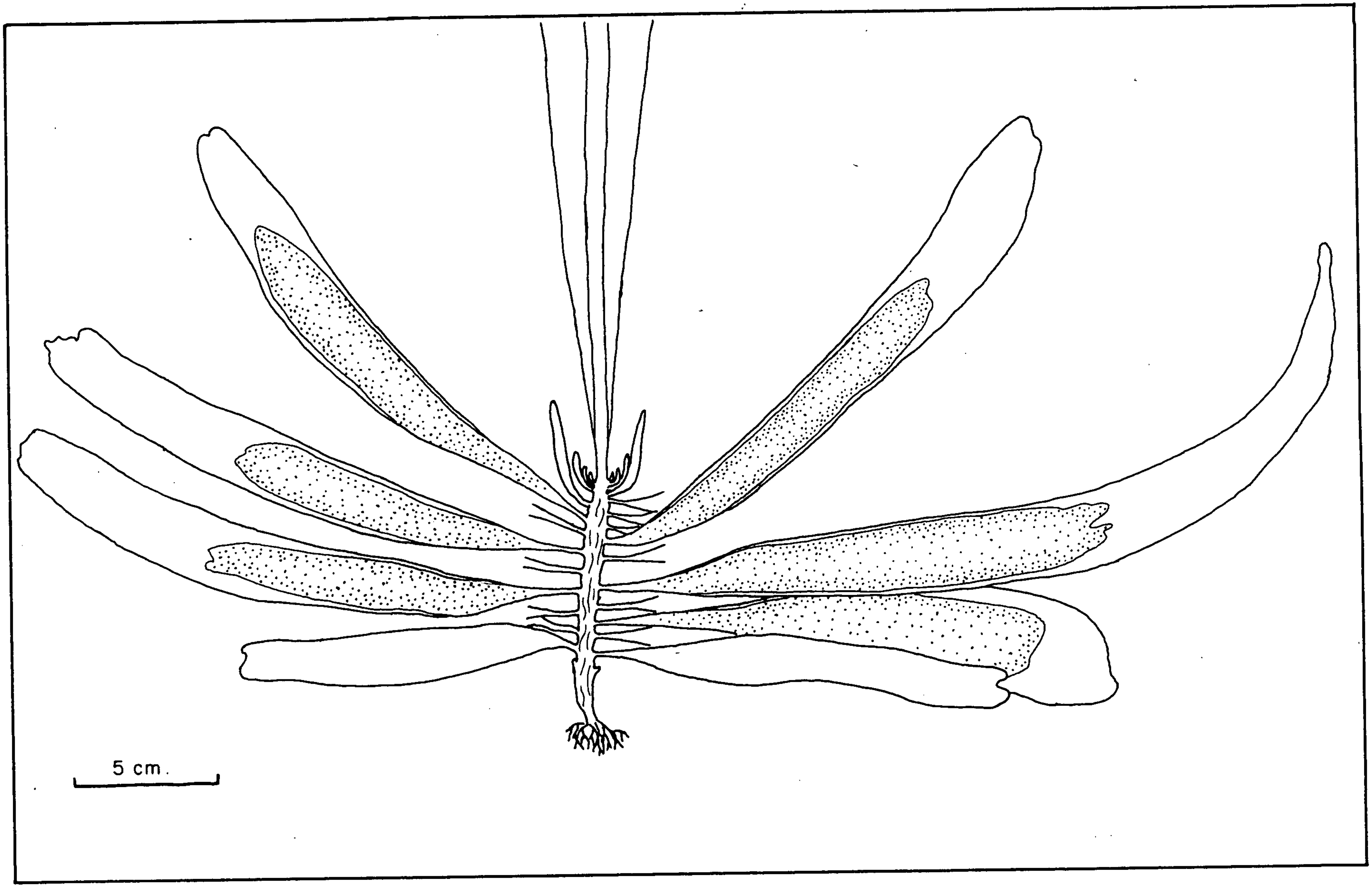

5 cm.

Figure 35. Older individual of *Alaria marginata* variant 2. After specimen TW 137, from Otter Point.

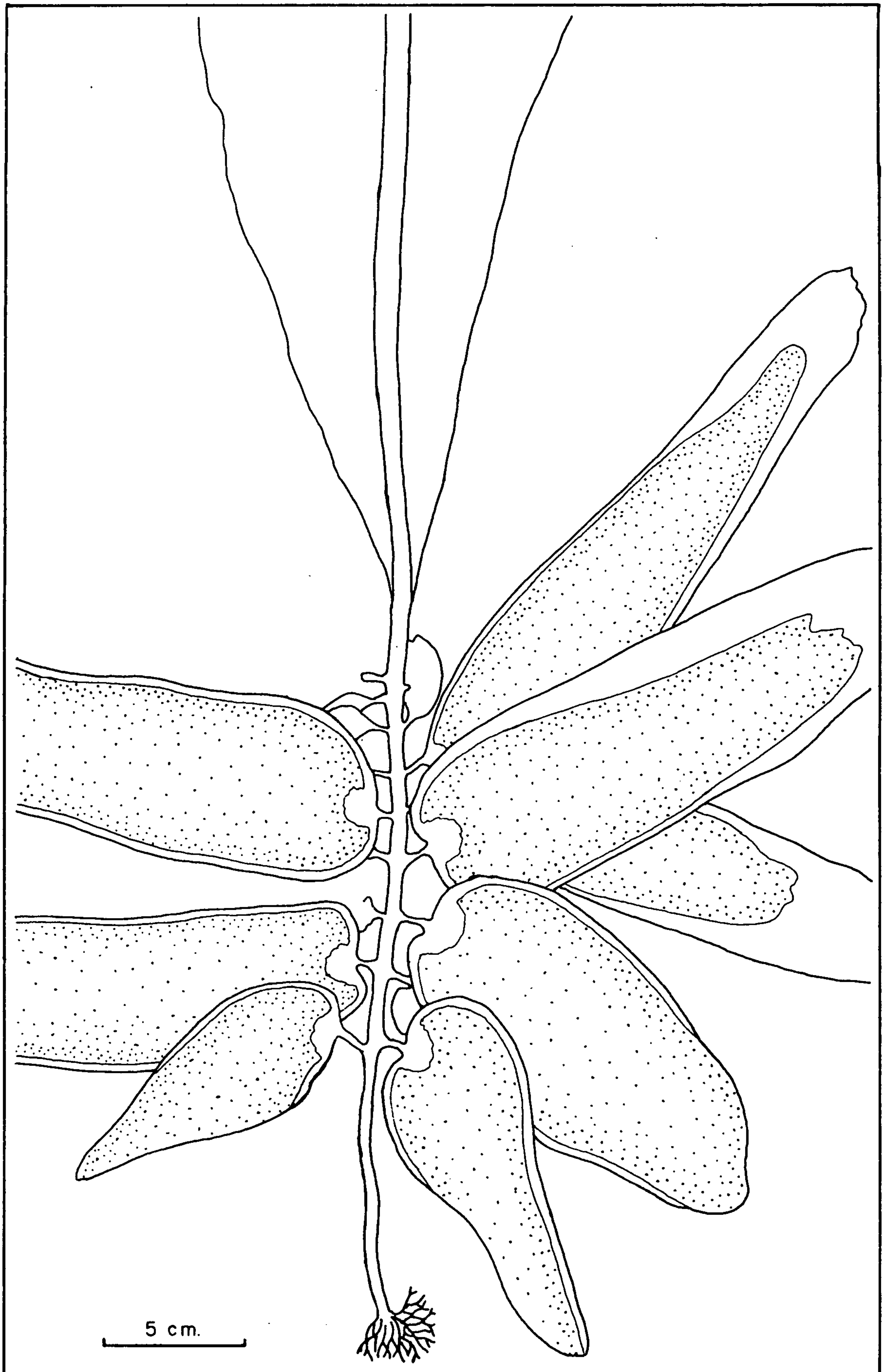

5 cm.

Figure 36. A typical specimen of *Alaria nana* from its type locality.
After specimen TW 168, from Port Renfrew. Only a few of the sporophylls are shown.

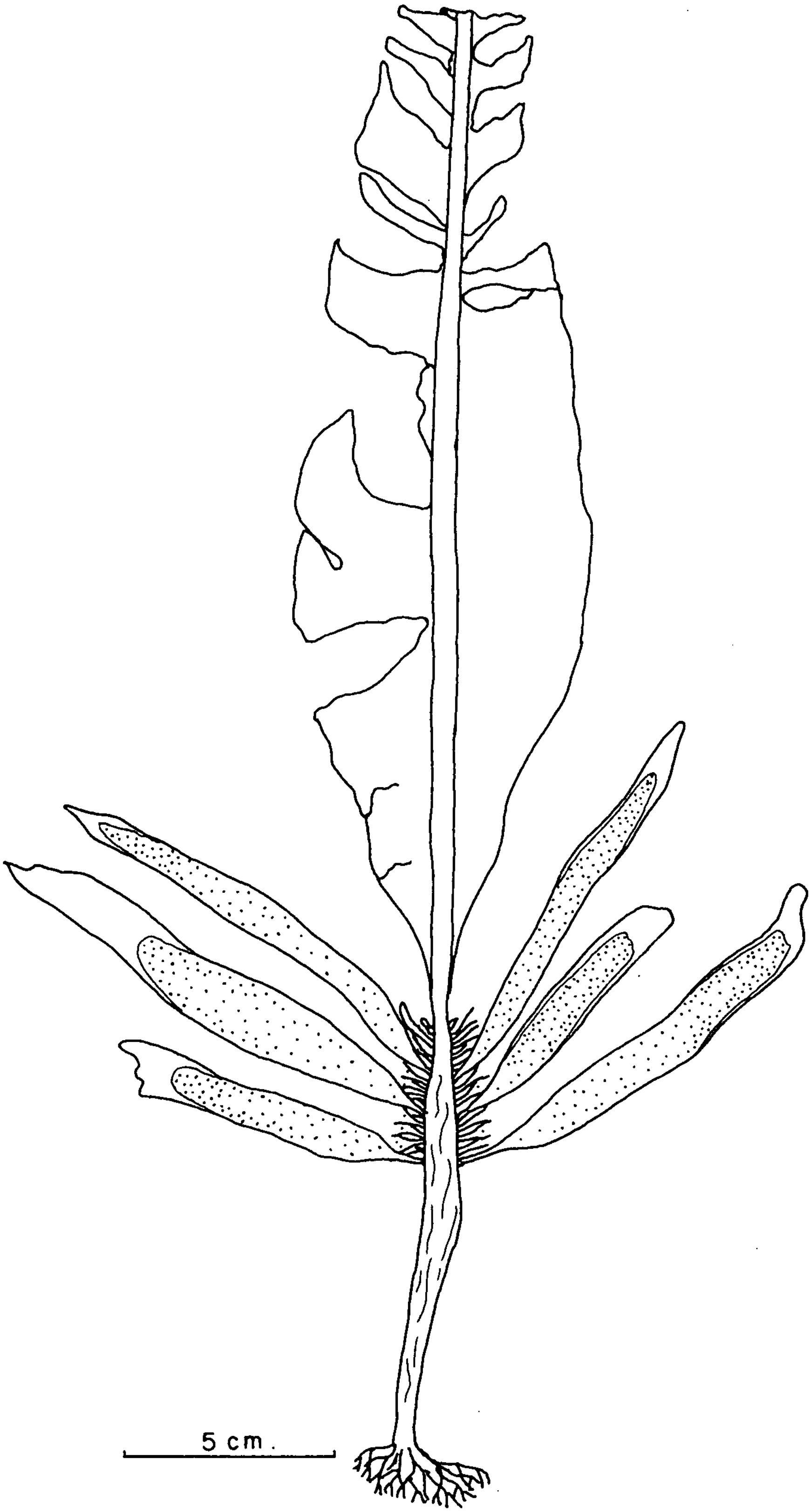

5 cm.

Figure 37. _Alaria_ _nana_

a. young individual, after TW244, from Glacier Point.
b. old individual, after TW15, from Otter Point.

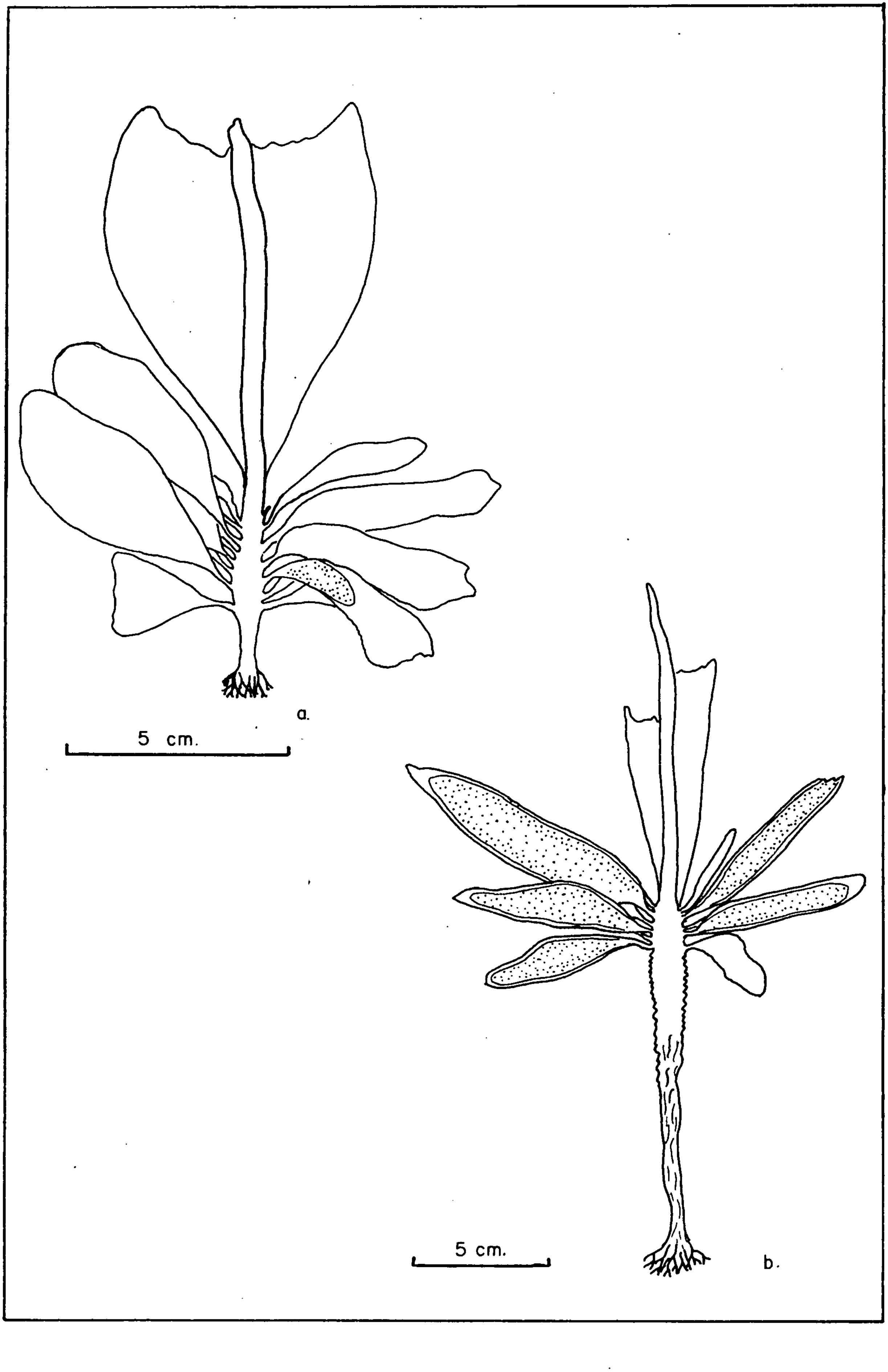

a.
5 cm.
5 cm.
b.

Figure 38. *Alaria tenuifolia* f. *tenuifolia*
After specimen TW 208, from Albert Head.

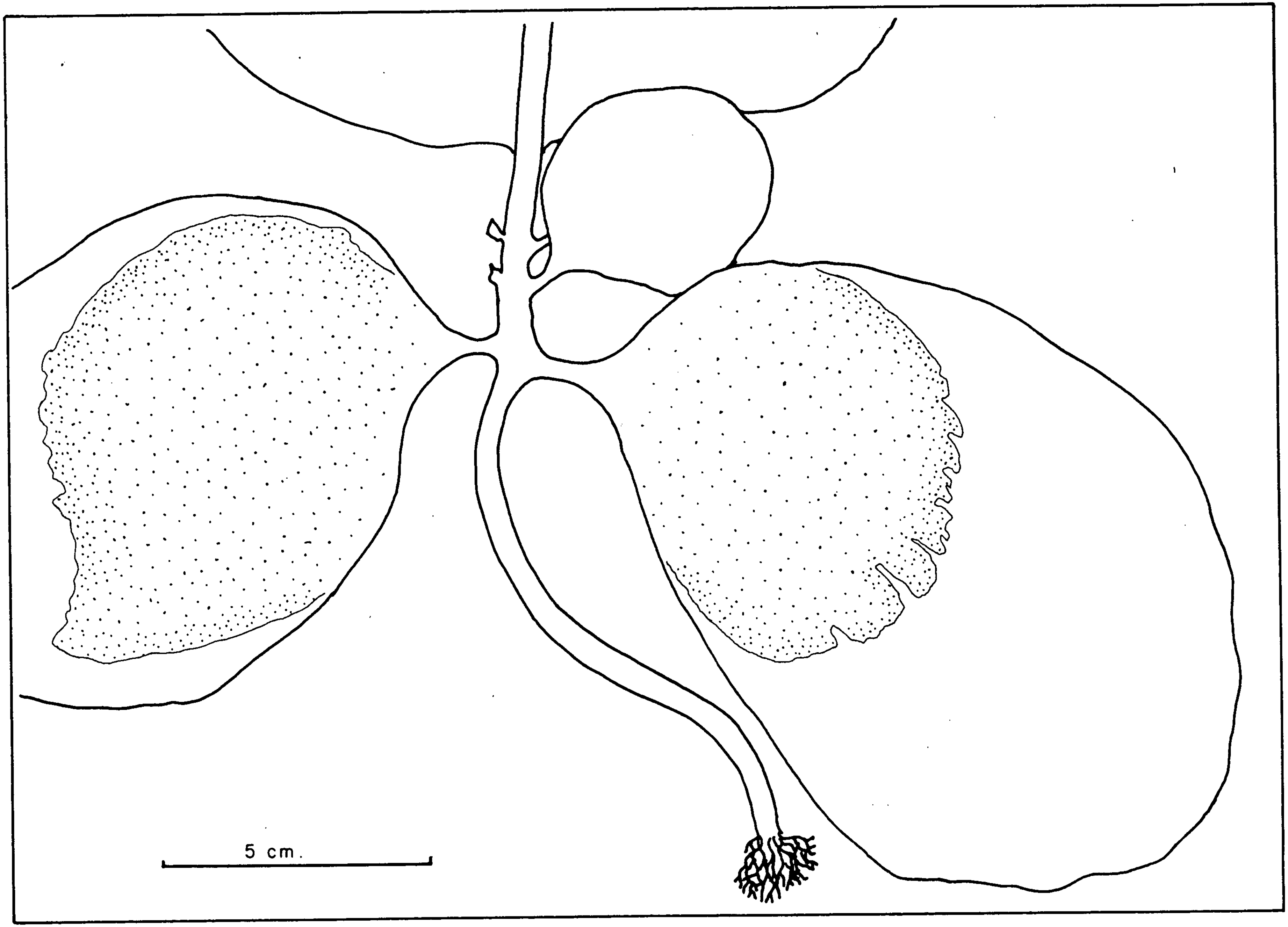

5 cm.

Figure 39. Alaria tenuifolia f. amplior
After specimen TW 232, from Station 33.

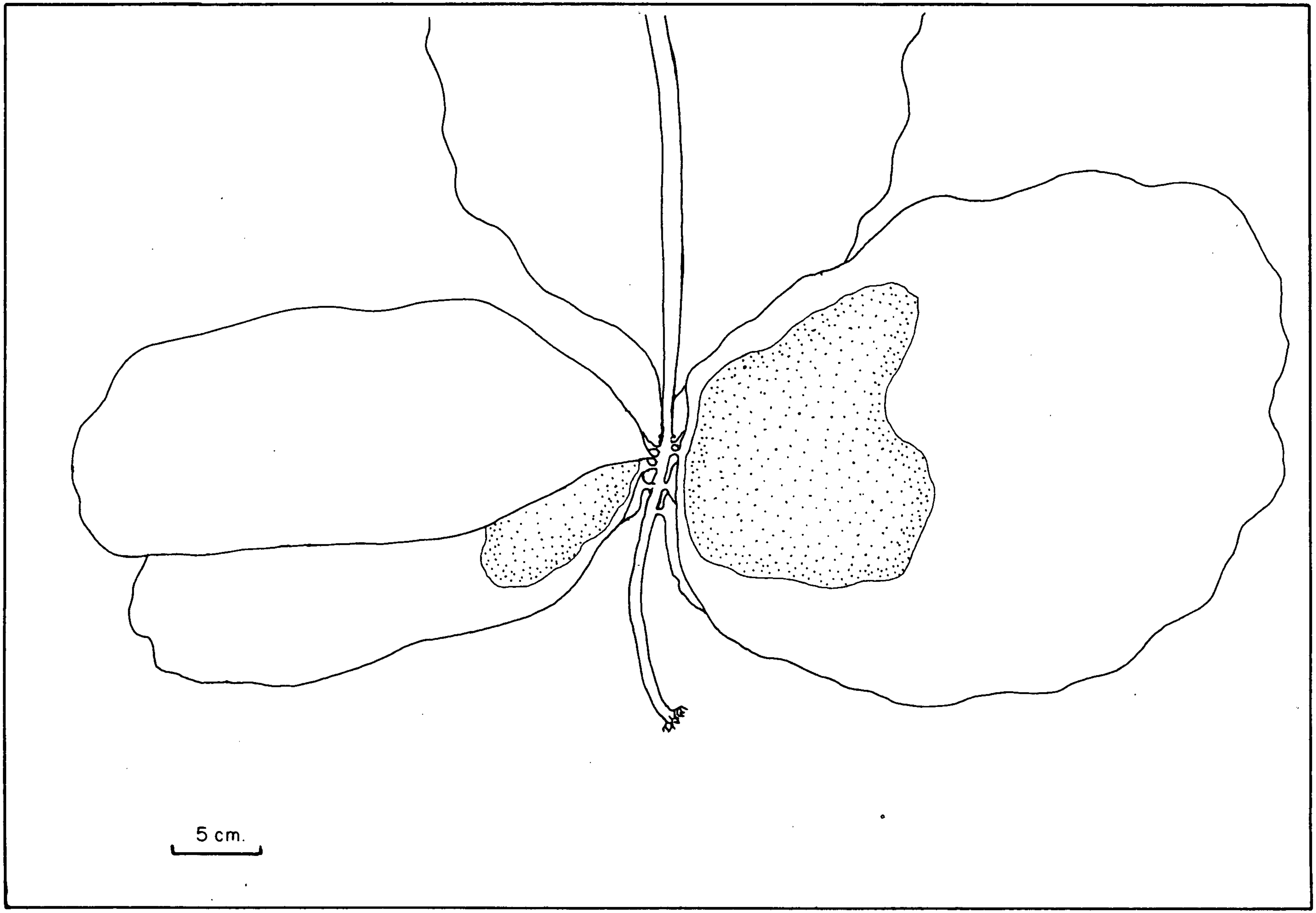

5 cm.

Figure 40. *Alaria valida* f. *longipes*.
After specimen TW 279, from Keystone, Whidbey Island.

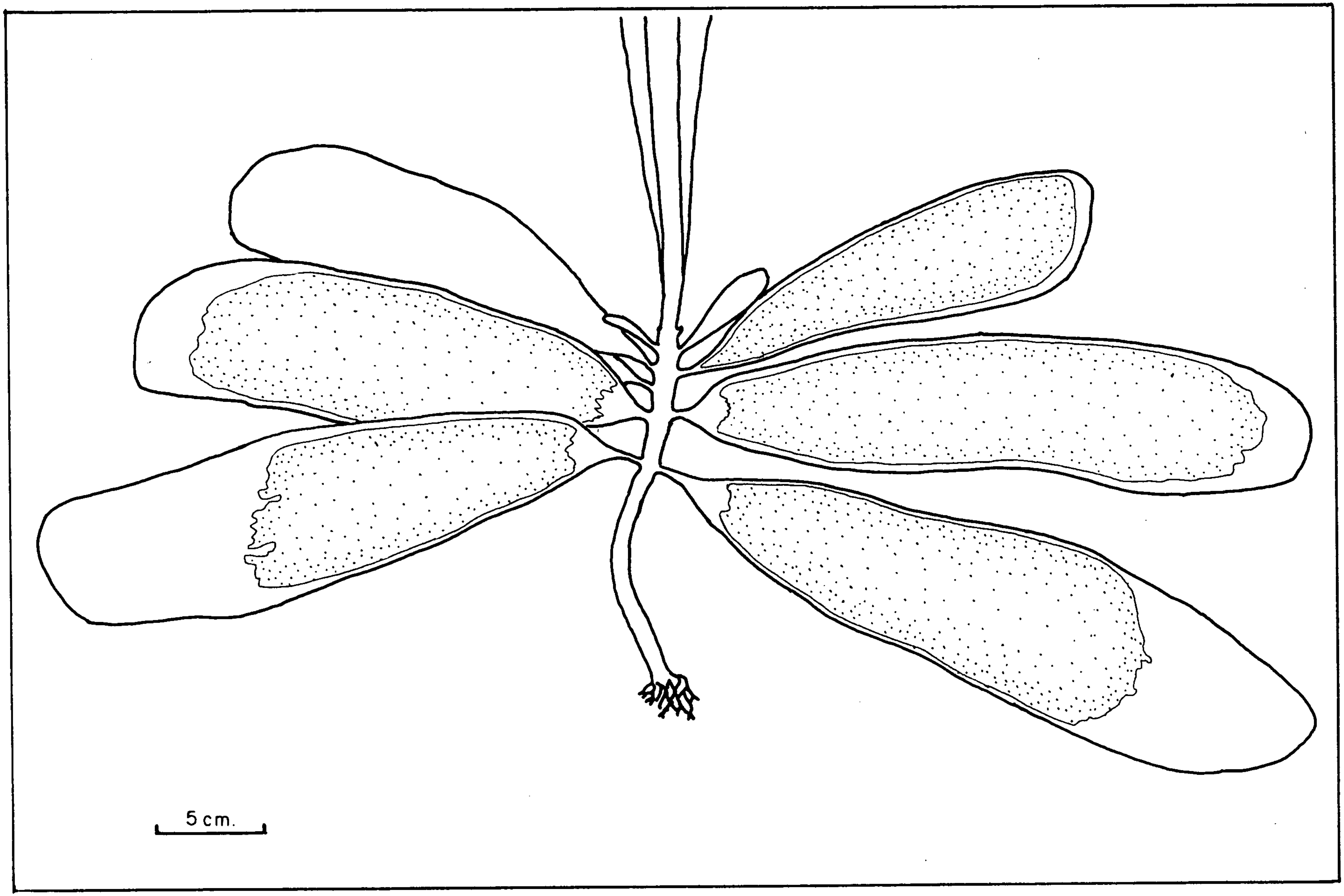
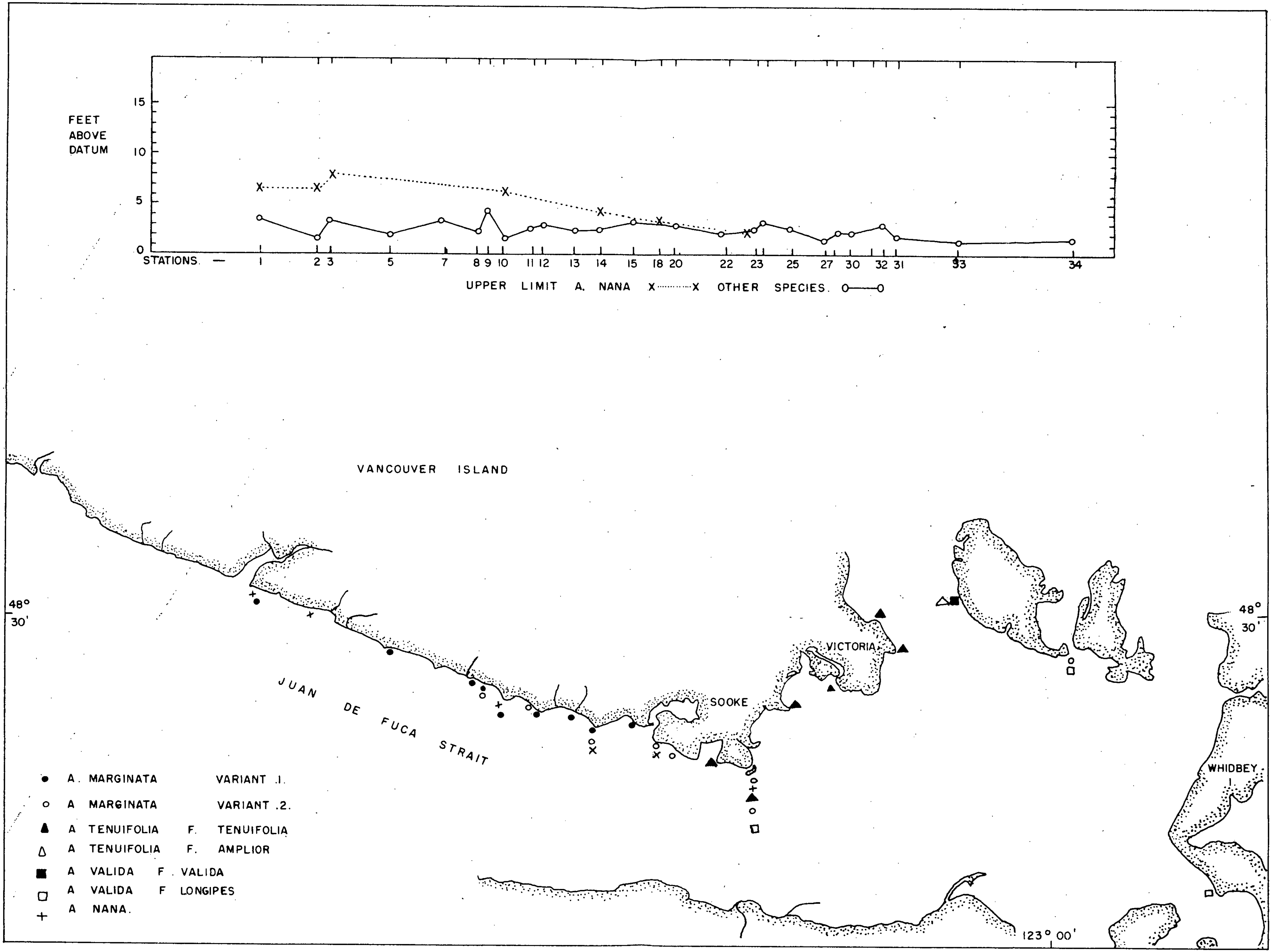
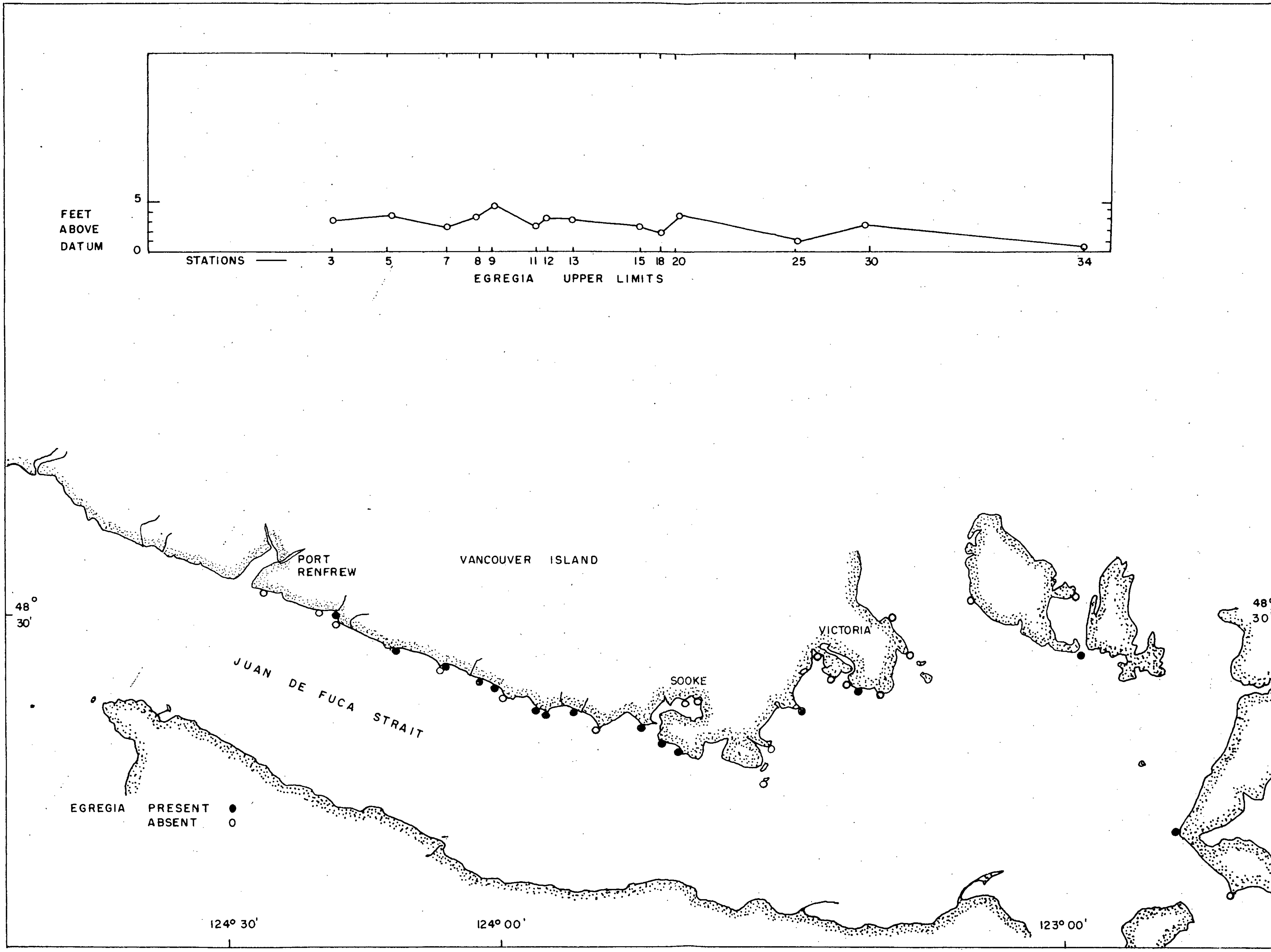

5 cm.

Figure 41. Distribution of *Alaria*. The geographical distribution is based on collected material only.



FEET
ABOVE
DATUM
15
10
5
0
STATIONS —
1
2 3
5
7
8 9 10
11 12
13
14
15
18 20
22
23
25
27
30
32 31
33
34
UPPER LIMIT A. NANA X·········X OTHER SPECIES. O——O
VANCOUVER ISLAND
JUAN DE FUCA STRAIT
SOOKE
VICTORIA
WHIDBEY I.
48° 30'
123° 00'
A. MARGINATA VARIANT .1.
A MARGINATA VARIANT .2.
A TENUIFOLIA F. TENUIFOLIA
A TENUIFOLIA F. AMPLIOR
A VALIDA F. VALIDA
A VALIDA F LONGIPES
A NANA.

Figure 42. Distribution of *Egregia*



FEET
ABOVE
DATUM
5
0
STATIONS
3
5
7
8
9
11
12
13
15
18
20
25
30
34
EGREGIA UPPER LIMITS
PORT
RENFREW
VANCOUVER ISLAND
VICTORIA
SOOKE
JUAN DE FUCA STRAIT
48°
30'
48°
30'
EGREGIA PRESENT ●
ABSENT O
124° 30'
124° 00'
123° 00'

Figure 43. Vertical distribution of various Phaeophyta.

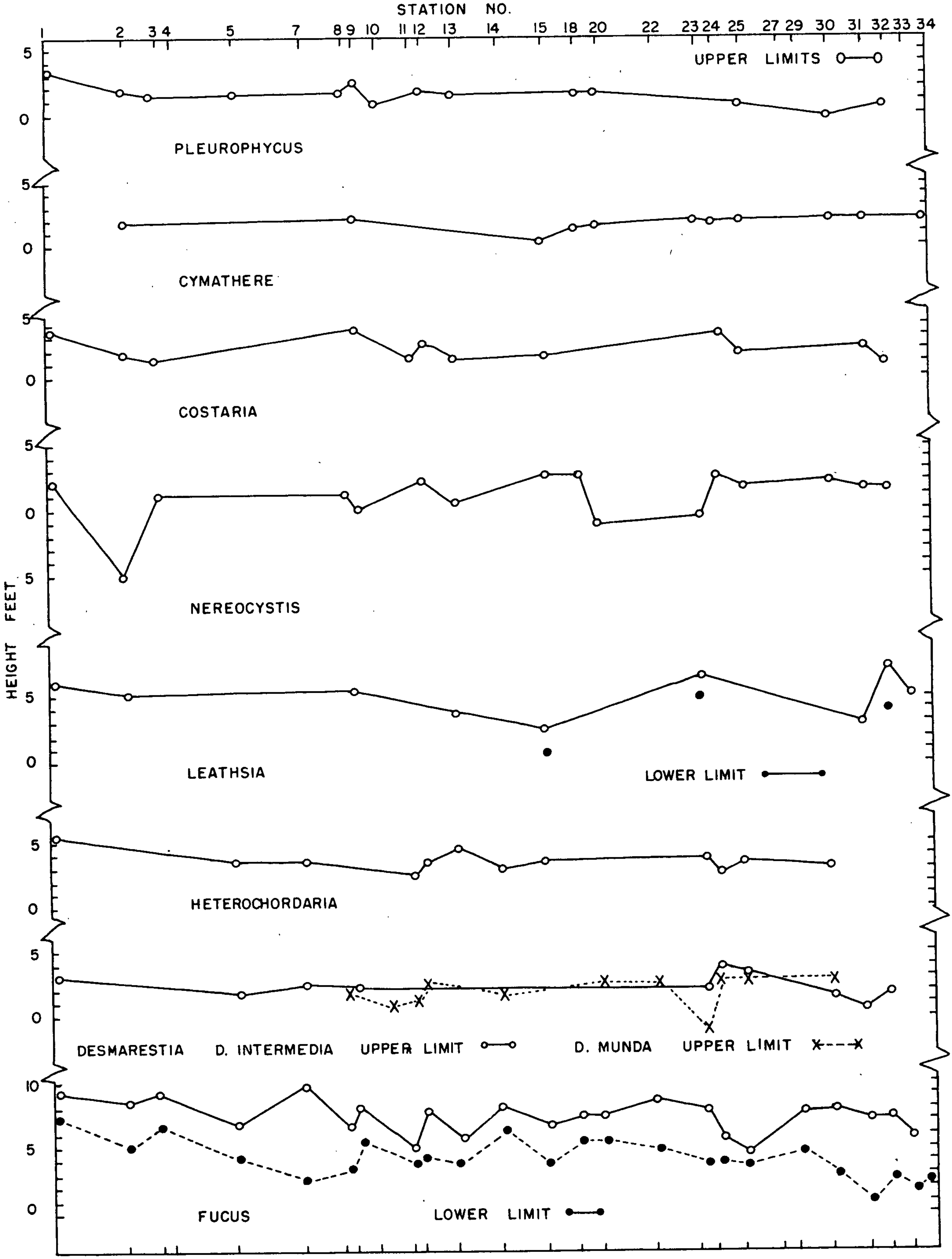

STATION NO.
1 2 3 4 5 7 8 9 10 11 12 13 14 15 18 20 22 23 24 25 27 29 30 31 32 33 34
UPPER LIMITS
PLEUROPHYCUS
CYMATHERE
COSTARIA
NEREOCYSTIS
HEIGHT FEET
LEATHSIA
LOWER LIMIT
HETEROCHORDARIA
DESMARESTIA
D. INTERMEDIA
UPPER LIMIT
D. MUNDA
UPPER LIMIT
FUCUS
LOWER LIMIT

Figure 44. Distribution of Cystoseira and Sargassum.

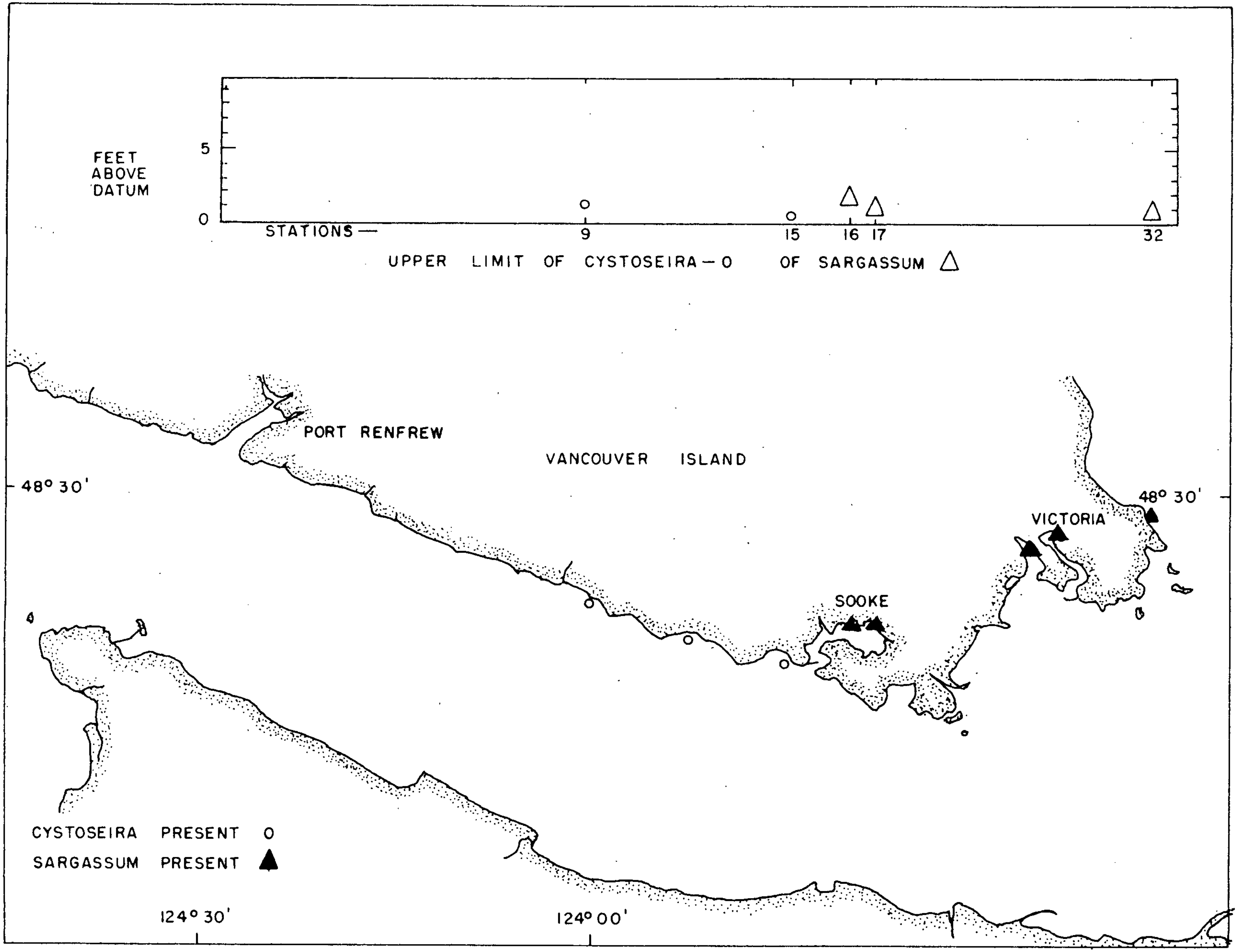
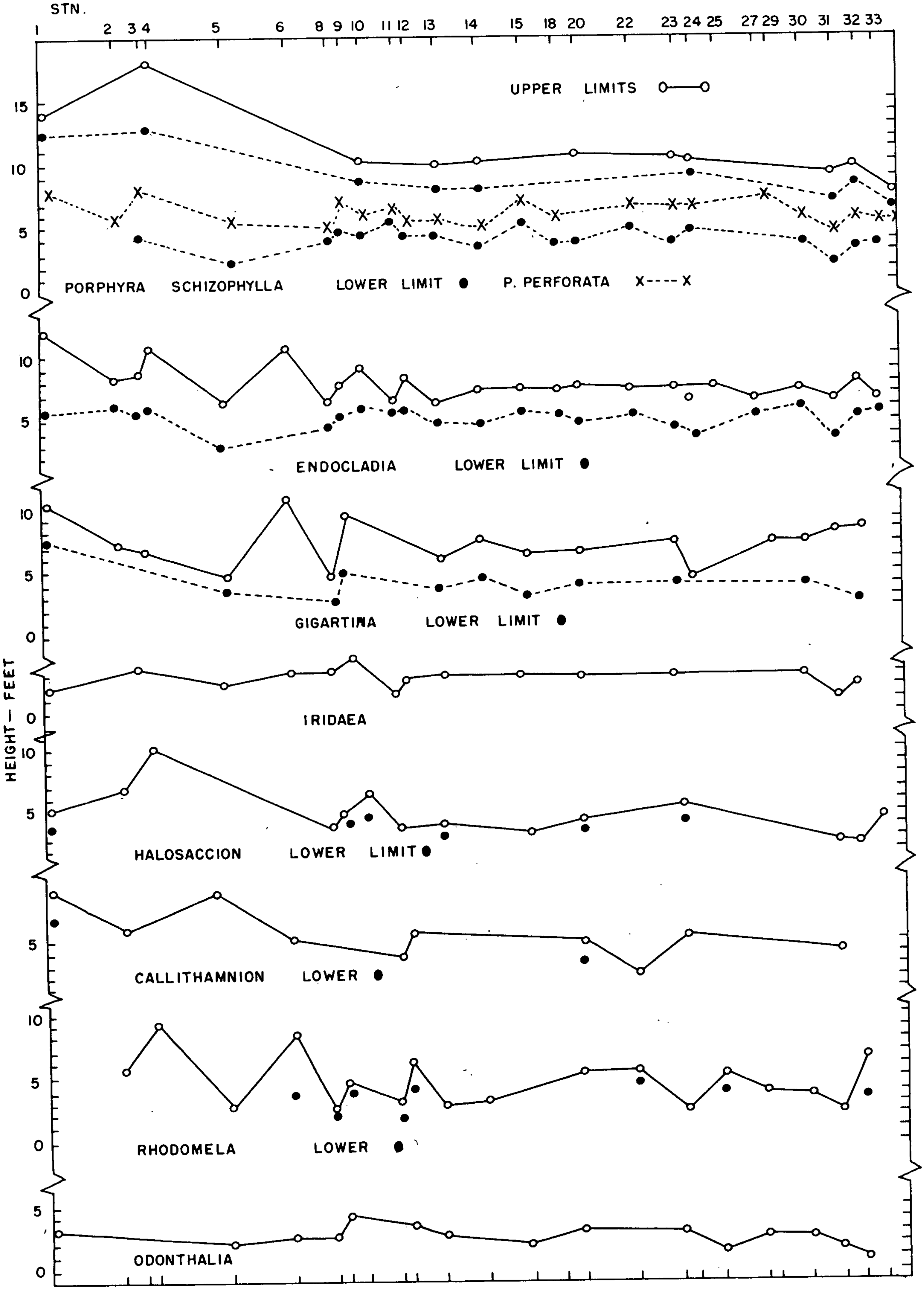
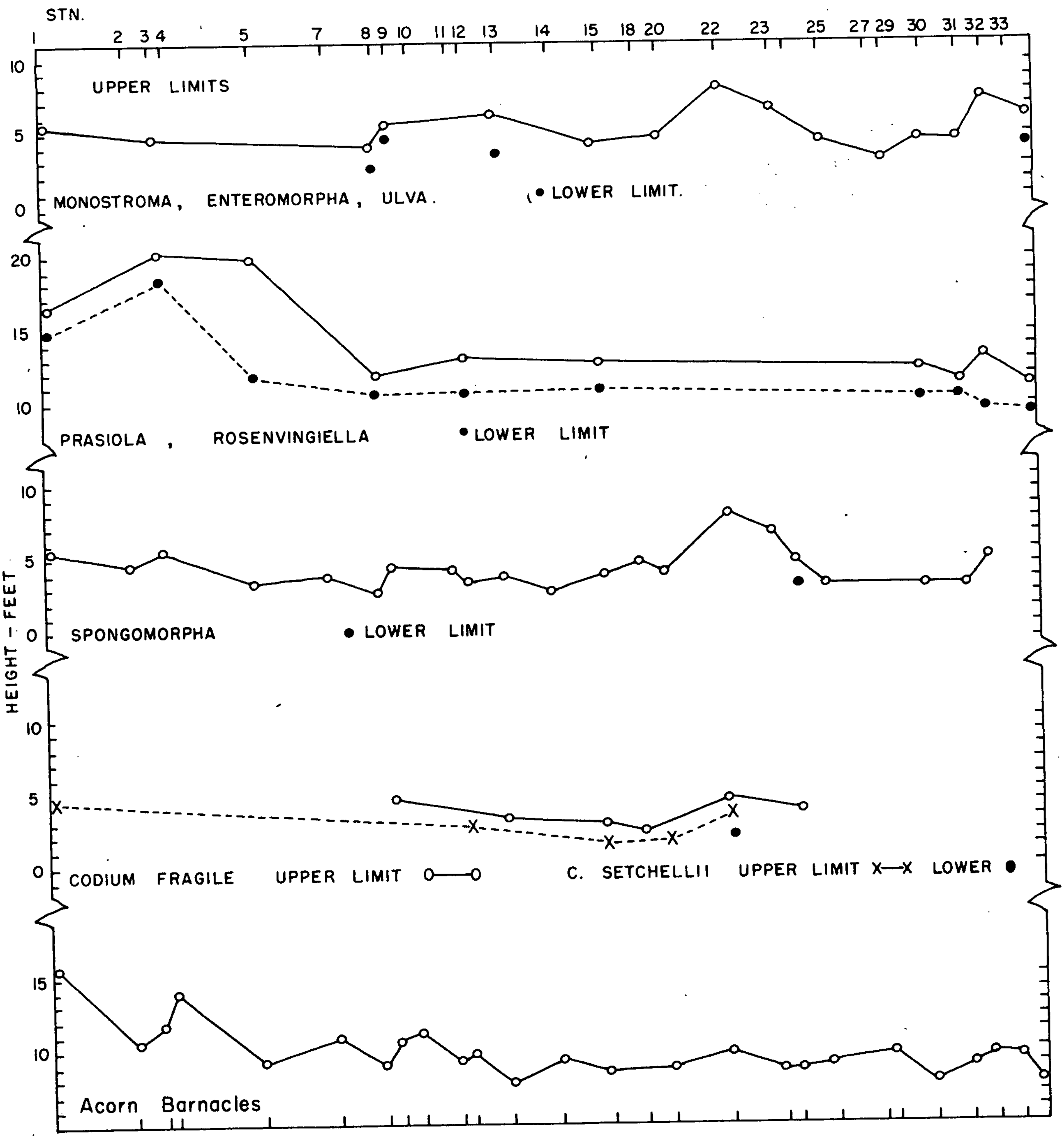

FEET ABOVE DATUM
5
0
STATIONS —
9
15
16
17
32
UPPER LIMIT OF CYSTOSEIRA — O OF SARGASSUM △
PORT RENFREW
VANCOUVER ISLAND
48° 30'
48° 30'
VICTORIA
SOOKE
CYSTOSEIRA PRESENT O
SARGASSUM PRESENT ▲
124° 30'
124° 00'

Figure 45. Vertical distribution of various Rhodophyta.



STN.
1 2 3 4 5 6 8 9 10 11 12 13 14 15 18 20 22 23 24 25 27 29 30 31 32 33
UPPER LIMITS O——O
PORPHYRA SCHIZOPHYLLA LOWER LIMIT ●
P. PERFORATA X----X
ENDOCLADIA LOWER LIMIT ●
GIGARTINA LOWER LIMIT ●
IRIDAEA
HALOSACCION LOWER LIMIT ●
CALLITHAMNION LOWER ●
RHODOMELA LOWER ●
ODONTHALIA
HEIGHT – FEET

Figure 46. Vertical limits of various Chlorophyta and of Acorn barnacles.



STN.
1 2 3 4 5 7 8 9 10 11 12 13 14 15 18 20 22 23 25 27 29 30 31 32 33
UPPER LIMITS
MONOSTROMA, ENTEROMORPHA, ULVA.
● LOWER LIMIT.
PRASIOLA, ROSENVINGIELLA
● LOWER LIMIT
SPONGOMORPHA
● LOWER LIMIT
HEIGHT - FEET
CODIUM FRAGILE UPPER LIMIT O—O
C. SETCHELLII UPPER LIMIT X—X LOWER ●
Acorn Barnacles

Figure 47. Distribution of *Phyllospadix* and *Zostera*.

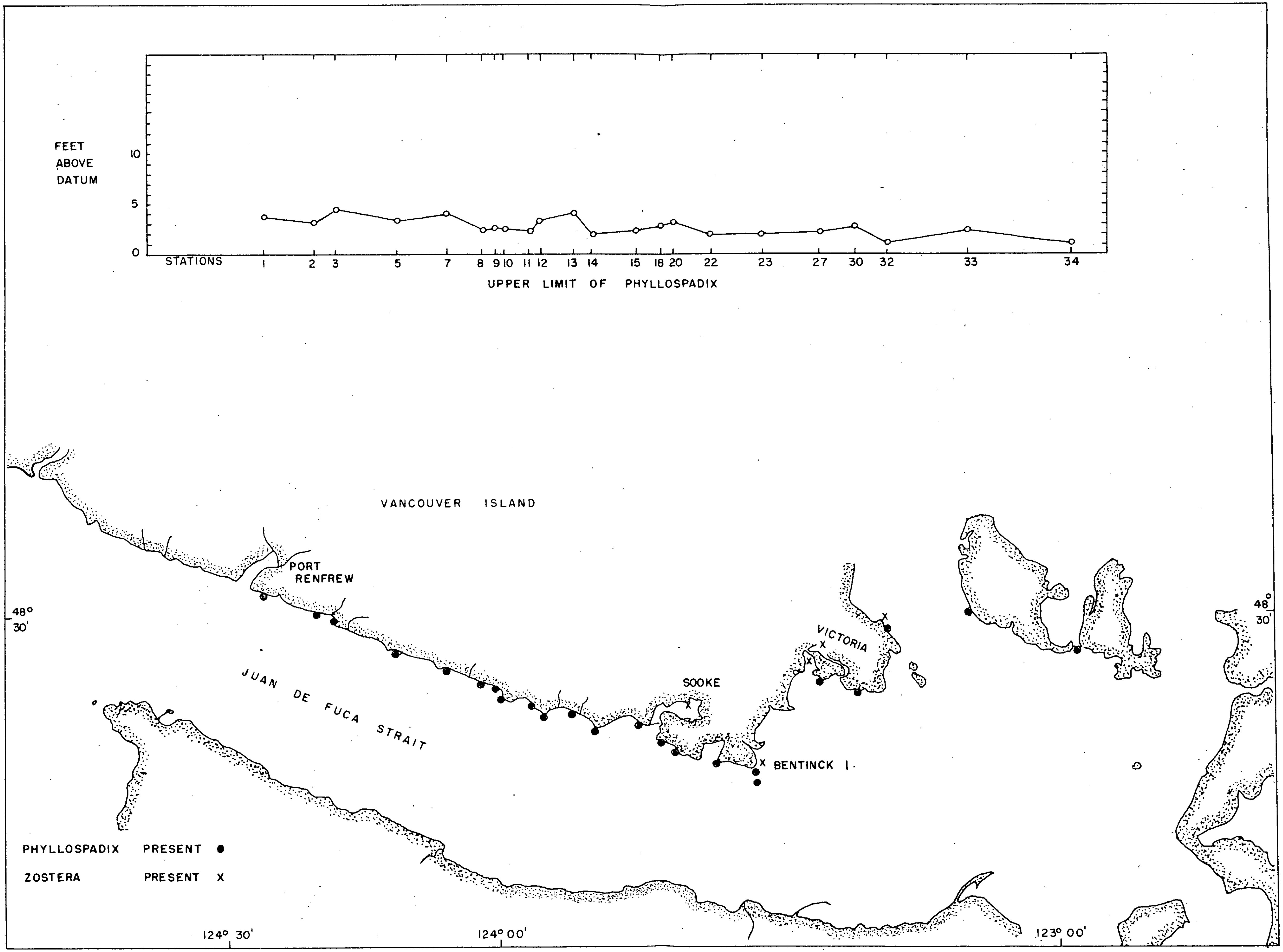
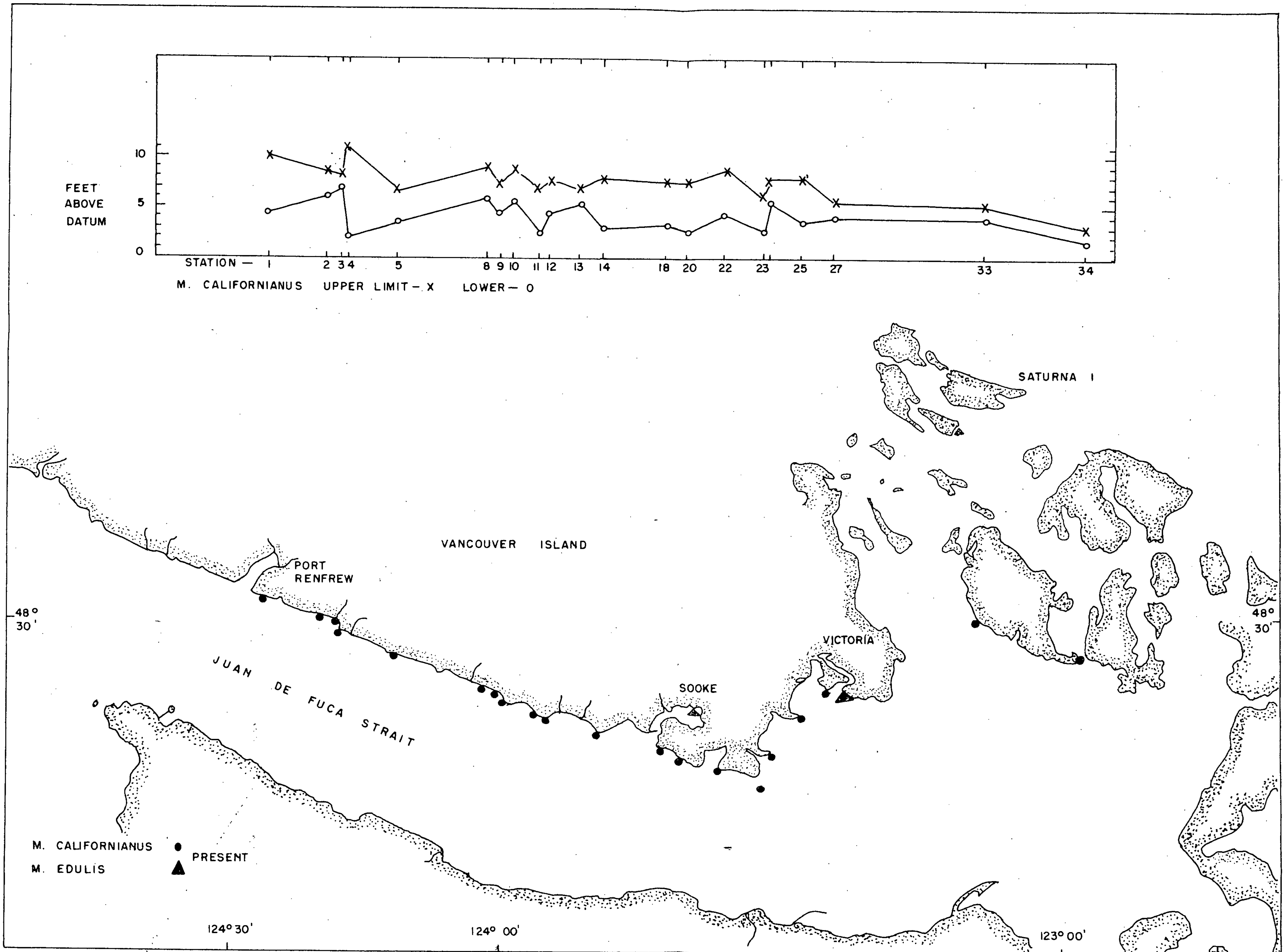
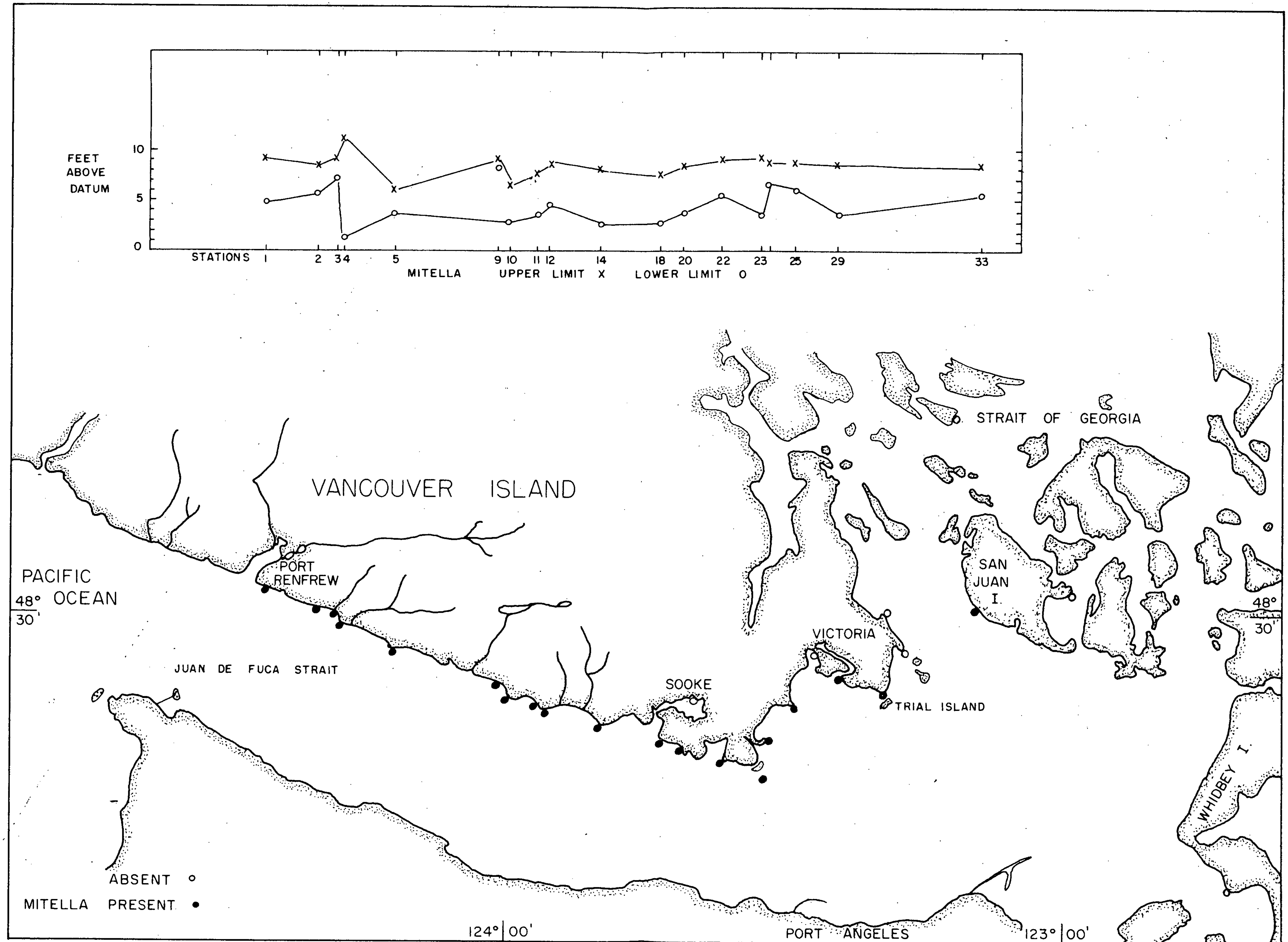

FEET
ABOVE
DATUM
10
5
0
STATIONS
1 2 3 5 7 8 9 10 11 12 13 14 15 18 20 22 23 27 30 32 33 34
UPPER LIMIT OF PHYLLOSPADIX
VANCOUVER ISLAND
PORT RENFREW
JUAN DE FUCA STRAIT
SOOKE
VICTORIA
BENTINCK I.
48° 30'
48° 30'
PHYLLOSPADIX PRESENT ●
ZOSTERA PRESENT X
124° 30'
124° 00'
123° 00'

Figure 48. Distribution of *Mytilus*.



FEET
ABOVE
DATUM
10
5
0
STATION — 1 2 3 4 5 8 9 10 11 12 13 14 18 20 22 23 25 27 33 34
M. CALIFORNIANUS UPPER LIMIT - X LOWER — O
SATURNA I
VANCOUVER ISLAND
PORT RENFREW
48° 30'
JUAN DE FUCA STRAIT
SOOKE
VICTORIA
M. CALIFORNIANUS
M. EDULIS
PRESENT
124° 30'
124° 00'
123° 00'

Figure 49. Distribution of *Mitella*.


FEET
ABOVE
DATUM
10
5
0
STATIONS 1 2 3 4 5 9 10 11 12 14 18 20 22 23 25 29 33
MITELLA UPPER LIMIT X LOWER LIMIT O
STRAIT OF GEORGIA
VANCOUVER ISLAND
PACIFIC OCEAN
PORT RENFREW
48° 30'
SAN JUAN I.
VICTORIA
JUAN DE FUCA STRAIT
SOOKE
TRIAL ISLAND
WHIDBEY I.
ABSENT
MITELLA PRESENT
124° 00'
PORT ANGELES
123° 00'