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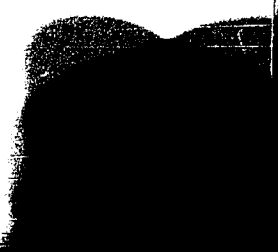
MARINE ALGAL FLORA OF BERMUDA

by
Albert J. Bernatowicz

A dissertation submitted in partial fulfillment
of the requirements for the degree of
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1952

Committee in charge:

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SEASONAL CHANGES IN THE MARINE ALGAL FLORA OF BERMUDA

by Albert J. Bernatowicz

Fluctuations in abundance and reproductive condition of marine algae were studied at all seasons in a variety of habitats at Bermuda. Four types of habitats, viz., fish ponds, well-protected coves with associated mangrove thickets, moderately exposed bays, and wave-swept shores, are described, some ecological features of each are discussed, and the most common species in each are listed.

One hundred and fifty-one species were examined for reproductive structures and the results, by month, are tabulated. Each month, reproductive structures were found among collections of about 50 per cent of the species examined. A considerable segment of the algal flora, including some of the most common species, was found in fruit only sparingly or not at all, either sexually or asexually. In three species evidence suggesting a seasonal alternation of generations was found.

The seasonal changes in the vegetation are described for each type of habitat and the histories of a few species are recounted to illustrate different types of growth cycles. Excluding Myxophyceae and coralline Rhodophyceae, there are about three times as many annuals as perennials. Thirty-five species, including most of the intertidal algae, are considered to be perennials. The annuals are listed according to the seasons during which they flourished, even though many were present in reduced quantity in other seasons. The largest number of annuals flourished in winter and in spring. The cycle of growth for most species started in autumn, rose to a maximum in spring, and declined during summer.

Comparison of the changes in the vegetation with meteorological records discloses that, although Bermuda has a warm-water flora, the cycle

of growth started before the lowest sea temperatures were reached and continued, apparently unaffected, through the coldest months, undergoing generalized decline during the season of maximum temperatures. However, it cannot be inferred that temperature was of special significance at the close of the growth cycle, since maximum insolation also occurred at this time. Furthermore, it is noted that the difference between the vegetation of autumn and that of spring was associated with changes in light conditions and not with a difference in temperature.

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INTRODUCTION

The Problem Defined and Delimited

In the terrestrial environment the seasonal succession of plant species and the cycles of growth and reproduction are familiar even to the most casual observer. According to the time of year, certain species appear, flourish for a lesser or a greater period, and disappear; other species leaf-out in one season and defoliate in another; still other species show little change from month to month except for differences in rates of growth. The time of flowering, setting of fruit, germination of the seed --all form a cycle of events which seems closely coordinated with the progression of the seasons. These rhythmic variations in abundance, whether of organisms or of various aspects of their life histories, have been given the name "aspection" by Nichols (1923, p. 14). Similar periodic behavior occurs in the marine environment, where algae rather than vascular plants are dominant, but aspection in these marine communities cannot be considered a familiar phenomenon, since the opportunities for observation are not so generally available as the opportunities for observation on land. It is this little-known subject, aspection in a marine algal flora, which is examined in the dissertation presented here.

To indicate the far-reaching scope of aspection, it is necessary to mention only a few of the implications of this topic.

From the point of view of the ecologist, the adaptations of an organism to its environment are of first-rank interest, and these adaptations often may be seen in the seasonality of the organism as clearly as in its habitat or geographical distribution (Bates 1949, p. 41). Among the several environmental influences said to be operating in aspection (Allee *et al.*

1949, p. 528), three are particularly prominent in marine situations: (1) direct action of one or more climatic factors such as temperature and insolation upon the algae; (2) indirect action of these basic physical factors on the organism--for example, desiccation produced by concurrent insolation and tidal exposure; and (3) direct action of the climatic agents on the medium surrounding the algae--for example, wave action caused by winds. It must be conceded that the limiting effects of these factors in controlling seasonal distribution may be as hard to determine as their role in areal distribution, but study of the seasonal responses offers an alternate approach to the solution of problems involving organism and environment. The ecologist is also concerned with the association of species into societies, and a lack of data on seasonality may preclude satisfactory descriptions of certain "transient societies" (Cotton 1912, p. 17). Aspection also affects the interrelationships of plants with animals, producing seasonal shifts in diet and shelter (Allee et al., p. 530).

To the student of evolution, seasonal fluctuations are significant, for the spreading of variants through a population will be strongly affected by changes in abundance (Bates 1949, p. 41). Also of interest to students of evolution is evidence drawn from data on periodicity that differing times of growth or reproduction may be operating as isolating mechanisms to strengthen the barriers which keep closely related forms distinct. Evidence of this nature in the genus Laurencia will be discussed in the section on reproduction.

Aspection impinges upon biochemical and physiological investigations from several directions. For example, the course of investigations must be based on the availability of experimental material, and availability may be as much a matter of seasonal occurrence as of areal distribution. Furthermore, the chemists' analyses must take into account possible variation of

chemical constituents from season to season--a phase of aspection which has been demonstrated in certain marine algae (Lapicque 1919, Black 1950). Studies of growth, the physiology of reproduction, pigmentation, photosynthesis, respiration, and nutritional requirements are intimately related to the problem of aspection, and, indeed, it is difficult or impossible to make a separation between this problem and any of the other fundamental biological questions.

Seasonal Studies in Various Parts of the World

Since seasonal succession is related to many different environmental influences, both climatic and local, our understanding of the mechanisms and significance of the cycles must be based on studies of many types of communities in all parts of the world. The first steps in such studies are the recognition and description of seasonal changes as they occur in nature. However, field observations which might serve to delineate these patterns of behavior have been performed on the algal vegetation of relatively few areas.

Europe

In Europe, contributions to this subject have come from only a few countries. The marine flora of the Gulf of Naples has been investigated with substantial attention to periodicity by Berthold (1882) and Funk (1927) and similar studies in the Gulf of Venice have been reported by Schiffner and Vatova (1938) and Vatova (1948). In France, Hariot (1912) has listed "for the convenience of collectors" the algae to be found at each season on a small portion of the Channel coast, and Feldmann (1937), with an interest in aspection per se, analyzes the marine vegetation of Alberes (on the Mediterranean coast) with respect to its seasonal components and times of reproduction. Various localities in the British Isles have also been

investigated from this point of view with different degrees of thoroughness. For the north of England and the Orkneys, Batters (1890) and Traill (1891), respectively, furnish taxonomic lists with comments on the seasonality of almost every species, and the Knight and Parke memoir (1931) on Manx algae provides valuable data and discussion, but Cotton's survey (1912) of the algae of Clare Island, Ireland, and Grubb's report (1936) on ecology at Dorset in the south of England only mention the fluctuations in a few communities.

Asia

Seasonal studies are almost completely unreported from Asia. Notable exceptions are the changes occurring during a monsoon period at Ceylon (Svedelius 1906b) and the brief but valuable summary of observations made near Madras, India, by Srinivasan (1946).

North America

The periodic changes which obtain along the Atlantic coast of North America have been very sparsely recorded. Collins (1900) calls attention to the topic but gives few data. Deliberate and careful notes on the changes occurring on a group of rocks at Woods Hole are reported by Davis (1913), but only a fragment of the flora is represented. Howe's list (1914) of algae found in winter in Long Island Sound is useful for purposes of comparison with the known summer flora. Investigations carried out by Bell (1927) and MacFarlane and Bell (1933) at Nova Scotia have been very fruitful and deserve to be repeated at other localities of the region. A considerable body of data is incorporated in the definitive systematic account of the algae of northeastern North America (Taylor 1937) but the subject of aspection is not treated as such. Our knowledge of the phenomenon further south does not extend below North Carolina but fortunately the two reports from this area

(Hoyt 1920, Williams 1948) give more than passing attention to the matter.

Seasonal cycles on the Pacific coast of North America are even less known than those on the Atlantic side. Some notes have been published on the winter flora at Puget Sound (Hurd 1917), but apparently no attempt has been made to follow the changes through a full sequence of seasons in this northern area. Our only information about aspection in the southern part of the Pacific range comes from Dawson's (1941, 1944) fragmentary descriptions of the changes seen during widely separated visits to Turners Island in the Gulf of California, and from whatever inferences may be culled from the taxonomic literature.

Research Aims

It is apparent from the preceding section that information concerning aspection among algal communities is very meager in all parts of the world and is completely lacking in many regions. Accordingly, the primary aim of the study here reported is to describe the seasonal changes in abundance and the trends of reproduction of the marine algae in an area from which we have no previous data.

Another observation which can be made from the extant literature is that some of our knowledge is based on the seasonal changes in only a small portion of the flora of an area, in some cases only on the few communities of a single tide pool, or of a small bay, or of a pile of rocks. Investigations of this type are valuable in that they permit very detailed observations and may aid in evaluating the significance of local influences; on the other hand, it becomes dangerous to consider them as typical of the region and to use them for purposes of comparison with other regions. It has been one of the aims of this investigation to include the communities of as many habitats as possible. In such a broad survey it is hoped that

local factors will fall into proper perspective without distorting the general pattern. This approach does not preclude future concentration of attention on small segments of the population. On the contrary, recognition of communities or species which will best repay detailed study should be facilitated by a knowledge of the over-all picture.

A third feature to be noted in the references to earlier work is the restriction of several investigations to only a part of the year. Although some valuable contributions have emerged from studies carried out during only one or two seasons, it cannot be denied that such studies were not indicative of the complete trend of successions. The present study has been planned to include all seasons, to the end that the full seasonal cycle may be described.

The Area Studied

When, in 1949, an opportunity arose to do field work on the algae of Bermuda, the combination of geographical and climatic features which I found there was so uniquely favorable to the study of seasonal successions that there was no hesitation in deciding on this research topic.

It has been mentioned that the primary aim of this investigation is to contribute information about an area from which we have no previous data. Not only is Bermuda in this category, but the whole warm Atlantic is unknown with respect to the seasonal changes in marine algal floras. Since the Bermuda flora has marked Caribbean affinities, the data collected at Bermuda have more than local significance.

The second aim, that of study in a variety of habitats, is easily satisfied at Bermuda. Within a radius of a few miles one finds reefs which are bathed by oceanic waters unaffected by continental influences, and harbors which are polluted by the refuse of civilization. The battered and

surf-swept shores of the periphery stand in sharp contrast to the undisturbed coves of the lagoons. Substrata include mud, mangrove peat, sand, and rock. Observations made in such a variety of habitats produce a fair representation of the complete vegetation of the region and insure that local pecularities will not be unduly magnified.

The third aim, to include all seasons of the year in the study with equal thoroughness, depends upon an equable climate, and from this point of view, Bermuda leaves little to be desired.

Other, very practical,advantages are associated with Bermuda. It is conveniently circumscribed and isolated, yet it is only three hours distant from New York by air. The presence of the Bermuda Biological Station insures the availability of laboratory facilities, guides, and transportation. The colony itself is small enough to permit thorough exploration but large enough to support a considerable flora. The taxonomic studies which are indispensable preliminaries to any ecological work have been extensively pursued and have resulted in very good catalogues of the algal flora (Collins and Hervey 1917, Howe 1918).

To make these points more concrete and to furnish a background for the report of the investigation, a brief description of the colony may be of assistance.

Description of Bermuda

The islands collectively known as Bermuda lie in the Atlantic Ocean almost due east of Charleston, South Carolina. The nearest point of land is Cape Hatteras, North Carolina, which is not quite 570 miles distant. Often confused with some of the West Indies, the Bermuda islands are actually slightly closer to New York City (about 675 miles) than to the nearest West Indian island, Abaco, in the Bahamas (about 700 miles). The Bermuda Biological Station is at approximately N. Lat. 32°22' and W. Long. 64°42'.

Complete details concerning the geology and origins of Bermuda are given in Sayles (1931) together with a very extensive bibliography on these topics. It hardly seems necessary, therefore, to give more than a brief sketch here. There seems to be no doubt that Bermuda was never part of the North American mainland. Rather, we are told that the islands are the visible remains of a volcano which rose from the floor of the ocean in Tertiary or pre-Tertiary times. Periods of submergence alternated with periods of emergence, and while the land mass was above water, dunes of calcareous material--shell fragments, remains of coral, algae--were built up by wind action. In the course of time these dunes became consolidated to form the so-called aeolian limestone which completely covers the surface of Bermuda and is a crust as much as 80 meters thick in some places.

Greater Bermuda includes the whole of this limestone cap covering the volcano and comprises an area of about 200 square miles, most of which is no more than 20 or 25 meters below sea level. The exposed portions, consisting of the five main islands and numerous small islets which we think of as Bermuda proper, are perched on the southeast rim of the volcanic platform and present only some 19 square miles of surface. They form a hook-shaped archipelago about 15 miles long and 5 miles wide. No spot in Bermuda is as much as a mile from the shore.

The various publications of W. A. Macky of the Bermuda Meteorological Office listed in the bibliography are the source for the following climatological data. The average yearly rainfall is 58.10 inches. July, with not quite 4 inches, is the month with the smallest average fall and October is the wettest month with an average of over 6 inches. The yearly average is roughly comparable to that of the wettest places on the Atlantic seaboard but it should be noted that there are no fresh water streams or naturally occurring standing bodies of fresh water in Bermuda, at least not on the

surface. This is due to the extreme porosity of the limestone. The frequent rains notwithstanding, there is no shortage of sunshine. Unpublished records of the Bermuda Meteorological Office show that July averages almost 10 hours of sunshine per day, or more than 300 hours for the month. The wettest month averages more than 6 hours of insolation daily, and even the darkest month (December) has almost 5 sunny hours a day.

Hurricanes are rare in Bermuda but gales are not uncommon. Winds blowing at a speed of 39 m.p.h. or more for at least 10 minutes are classified as gales and, on the average, 37 days a year are so affected. January and February are the worst months, with 6 to 8 days in which gales are to be expected.

Air temperatures show a range of only about 24°C. through the year. February is the coldest month with temperatures as low as 9.2°C. regularly expected, but its mean temperature is closer to 16°C. The warmest weather comes in August, although even then only a few days are likely to exceed 32°C. Measurements published by the U.S. Department of Commerce (1951) indicate that the sea temperature fluctuates through a range of about 15°C. through the year, from a February mean minimum of 15°C. to the mean maximum of nearly 30°C. in August. Setchell (1915) says that temperate regions have a sea temperature range of from 15 to 27°, subtropical regions show ranges of about 10°, and the tropical temperatures fluctuate through about 5°. In comparison with other regions, then, Bermuda may be considered to have moderately variable sea temperatures.

The tide at Bermuda is of the semidiurnal type. That is, there are two low waters and two high waters daily. The tidal range is relatively narrow. Neap tides have a range of only about 73 centimeters and the ranges predicted for the new moon and the full moon (springs) average 90 centimeters.

The vegetation of Bermuda resembles that of more southern climates. Britton (1918, p. vii) estimates that about 80 per cent of the native land plants are also found in the West Indies or southern Florida or in both, and that about 8.7 per cent of the species are endemic. Collins and Hervey (1917, p. 7) furnish a table which shows the percentage of Bermuda algae occurring in other floras. They conclude that the most striking inference to be drawn from their table is the distinctness of the Bermuda flora, inasmuch as only some 41 per cent of the species were also found in Jamaica and there was even less correspondence with the other areas. Since their table was published, more extensive catalogues of various Atlantic floras have appeared and it seems worthwhile to note how many of the Bermuda species are found in these lists. Expressed percentage-wise, the species common to Bermuda and to the Florida and West Indian region (Table 1) are a considerably larger part of the flora than Collins and Hervey were able to estimate from the information available to them. The intensity of collecting in the several regions has not even now become equalized, and no doubt these figures would require further adjustment if all algal reports for the areas concerned were tracked down and verified. Nevertheless, it seems clear

TABLE 1

PERCENTAGE OF BERMUDA ALGAE REPRESENTED IN OTHER FLORAS

	Danish West Indies (Børgesen 1913-1920)	Bahamas (Howe 1920)	Florida (Taylor 1928)	Northeast North America (Taylor 1937)
Chlorophyceae	60	52	65	17
Phaeophyceae	65	50	68	15
Rhodophyceae	50	62	71	14
All classes	56	57	68	15

that the Bermuda marine flora has marked affinities with the Caribbean flora and little relationship with the more northern flora.

Procedures

Observations were made during three visits to Bermuda, covering the periods 10 February 1949 to 13 June 1949, 17 August 1949 to 13 September 1949, and 6 November 1950 to 6 February 1951. The visits were so timed that no season was omitted from the observations. The conditions found at the beginning of each visit gave strong indication that the trends existing during the previous inspection were continuing. That is, the rich vegetation which had been seen in June was found to be diminishing but not absent upon my return in August; the moribund and depleted aspect of September foreshadowed the relatively barren situation prevalent in November; and the scene at the end of the last trip in February 1951 was strikingly similar to the original flora which had been present at the beginning of the study in February 1949.

The procedure followed entailed almost daily excursions to the algal habitats about the islands. The survey covered the greatest number of bays consistent with the limitations of time and transportation, and the necessity for broad sampling. Among the bays near the Biological Station, a few were selected for special attention because of the variety of species they supported, but in general the records for a species reflect the behavior of that species in Bermuda as a whole, and not merely in a local habitat.

The records of field observations were made as notes and by the collection of specimens. The approximately 2500 collections, consisting of some 11,000 herbarium specimens, which were brought back to Michigan represent a fair sampling of the distribution in time and space of the algae at Bermuda. They were a necessary means of confirming the determinations made in the field, and have been an invaluable aid in the study of fruiting periods.

HABITATS

General Considerations

The several types of algal habitats to be found in Bermuda differ in the kinds of substrata, degree of exposure to wave action, insolation, and other features, all of which exert an influence on the vegetation. The effect on the vegetation may be so conspicuous that the habitats are often as distinctively typified by the plant communities they support as by the factors of the environment. To illustrate with an extreme example, we have only to note the vegetational differences between sandy bays which are normally surf-swept and sandy bays which are rarely subject to surf. Even when the sea is becalmed, the normally surf-swept sandy bay can be distinguished by its complete lack of macroscopic plant life, while the bay of quiet waters displays a profuse growth of sea grasses and algae.

This extreme example may appear to be an exception if one has only lists of species to study, for some species seem to be ubiquitous. For example, Anadyomene stellata, Caulerpa racemosa, Colpomenia sinuosa, Bostrychia binderi, Centroceras clavulatum, and Polysiphonia howei are abundant everwhere about Bermuda and deserve prominent mention in a list of species of almost any kind of habitat. Comparison of such lists may suggest a similarity of habitats, but it must be borne in mind that species of apparently general distribution are associated into different communities and may show morphological adjustements or changes in level relative to the tides when they are found in different habitats. A similarity of lists does not reflect any uniformity of the vegetation, then, and the lack of uniformity requires consideration of several types of habitat.

There is, as yet, no generally useful system of classifying habitats. Historical and critical reviews of the many attempts to classify habitats have been published by Cotton (1912), Gislen (1930), Feldmann (1937, 1951), Davy de Virville (1940), and Chapman (1946). The most commonly suggested elements of these classifications are the levels, substrata, and degree of wave action. Following such a scheme, the marine vegetation of Bermuda may be ecologically described as a number of belts occupying superimposed levels, each level containing several types of substrata, and with the growth on any substratum, whether rocky or unconsolidated, being further affected by varying degrees of exposure to wave action.

The usefulness of such an arrangement is limited for several reasons. There has been a chaotic lack of unanimity both in the names applied to many of the categories and in the degree to which any category has been subdivided. For example, the vertical divisions have been called regions (Cotton 1912, Funk 1927), zones (Orbigny 1820, Johnson and Skutch 1928, Stephenson 1949), fringes (Stephenson 1949), stories (Fr., étages, Feldmann 1937), belts (Chapman 1946, Doty transl. of Feldmann 1951), and so forth, while the modifications due to substratum have been labelled formations (Cotton 1912) or facies (Feldmann 1937). The last two words have been used in various other senses. Further, the terminology has been confused by the use of biological features in some instances and topographical or environmental features in others. Thus, Johnson and Skutch (1928, p. 191) state that the "Submersible Zone" is occupied by "Vegetational Belts", examples of which are "The Sublittoral Belt", "The Lower Littoral Belt", etc. Later (p. 192), they mention the "Sublittoral or Alaria-Halosaccion-Melobesia Belt". Apparently their concept is that the coast can be described as consisting of zones (physiographic), and that each zone can be subdivided vertically into belts of vegetation (biological), but that the belts may be given names according to

their position (physiographic) or their biota (biological). Cotton (1912, p. 14) differs. His "regions" bear physiographic names ("littoral, sublittoral, elittoral") and are defined partly on the basis of tides and partly on the basis of algal growth. He does not list vegetational belts for his regions, but at any level he has one or more "Formations" of plants. These formations are not at all comparable to the belts of Johnson and Skutch, for more than one formation may exist at any level, depending on the nature of the substratum. Thus, although Cotton's formations are assemblages of plant associations (biological), they carry such names as "Rocky-shore formation" (physiographic). These inconsistencies are very easy to criticize academically, but it is more realistic to concede that they are the inevitable result of attempts to describe local situations. Unfortunately, this confusing lack of agreement in terms has made comparisons of the published ecological descriptions excessively difficult. A synthesis will probably have to be furnished by someone who has a first-hand knowledge of the conditions at many localities. At least for intertidal ecology, such a synthesis has been attempted (Stephenson and Stephenson 1950).

Even if we accept a system which is based on environmental characters consistently, or some system which might be based on biological characters consistently, there remains a special hindrance to its usefulness. The difficulty lies in that the descriptions will be to a greater or lesser degree obscure to anyone who is not actually familiar with the topography of the locality. For example, one of these consistent systems (Feldmann 1951) would speak of the vegetation of the infralittoral belt, rocky facies, sheltered mode; of the infralittoral belt, muddy facies, sheltered mode; and would give similar breakdowns of the littoral and supralittoral belts without making the reader aware that all these conditions are characteristic of most quiet water bays at Bermuda--bays which are often only

100 meters in diameter. Faced with descriptions of this type, the reader is often forced to sort through a confusing number of abstract situations which are not easily related to any specific field conditions within his experience. On the other hand, a description of a bay as a habitat is more easily visualized and retained, because it combines a number of belts, facies, and modes into a larger unit.

Accordingly, I shall discuss the several types of habitat to be found in Bermuda as exemplified by specific bays, coves, or lengths of shoreline. The descriptions of these localities will be summarized by the application of terms recommended by Feldmann (1951). In his system belt is the most inclusive term and the vegetation of a region is to be considered as occurring in four belts--the supralittoral belt, the littoral belt, the upper infralittoral belt, and the lower infralittoral belt. Next in order of rank is the facies, which refers to the character of the substratum. Thus, in any belt there may be rocky, sandy, and muddy facies side by side. Finally, Feldmann takes into consideration the water conditions, such as degree of wave action and salinity, and uses the term mode for these.

Fish Ponds and Landlocked Salt Water Pools

Description

Here and there at Bermuda portions of bays have been walled off to make small pens in which lobsters or fish are kept until needed for table use. These so-called "fish ponds" and a few somewhat similar pools of natural occurrence are the most easily studied of Bermuda algal habitats, and it seems feasible to describe them first. Near the Biological Station such a pond exists at the head of Richardsons Cove, which is on the south side of St. Georges Island. It is about 4 meters long and 3 meters wide, with

its bottom nearly 1.7 meters below the surrounding land. However, at low tide it contains only some 0.4 or 0.5 meter of water and at high tide less than 1.2 meters. The bottom is of very soft mud over limestone, but a few small rocks have been thrown in and these, with the rock substratum furnished by the wall, support the major portion of the vegetation. In general, such fish ponds have access to the sea through one or more small holes deliberately left in the outer wall, but the pond at Richardsons Cove has, in addition, connection with a subterranean cave at its landward side. Consequently, with the rising tide water passes through the fish pond to fill the cave and a similar flushing action takes place as the tide falls.

The naturally occurring landlocked pools show some differences from the fish ponds. Their access to the sea is either by percolation through the porous limestone, or by a subterranean channel, and they may be more than 2 meters deep even at low water. Furthermore, the tidal range, some 0.4 meter, is about half that of the fish ponds.

Ecological Factors

Since the fish ponds and landlocked pools have little or no surface connection with the sea, only under extraordinary circumstances are they disturbed by waves. This extreme protection from wave action is their most prominent ecological characteristic.

Another factor to be considered is the diminished light reaching these protected places. Almost invariably the fish ponds and their natural analogs are located in the shade of trees or ledges, and their vertical sides afford further shade except when the sun is directly overhead. As a result, the algae of these habitats grow under conditions of greatly reduced illumination.

A less obvious factor is the temporary dilution or at least stratification of the water which occurs during rains. Because of the reduced

tidal exchange of water in the landlocked pools and the lack of turbulence from waves, rain water is not readily mixed with the salt water, nor is it flushed away rapidly. Consequently, we may expect that species with narrow tolerance to changes in salinity will be at a disadvantage in these almost enclosed bodies of water.

Feldmann's Classification

In terms of belts, facies, and modes, the fish ponds and landlocked pools consist of a littoral belt with rocky facies and quiet mode, and an upper infralittoral belt with both rocky and muddy facies, again of quiet mode.

Vegetation

The vegetation of the fish ponds and pools consists of relatively few species. According to the season, members of the following lists are especially prominent:

Chlorophyceae

Bryopsis plumosa
Bryopsis hypnoides
Caulerpa crassifolia
Caulerpa racemosa
Caulerpa sertularioides
Ulva lactuca

Rhodophyceae

Amphiroa fragilissima
Halymenia bermudensis

Phaeophyceae are rarely found in these places. As is often the case under conditions of deep shade, the Rhodophyceae and Chlorophyceae here show unusually rich coloration, and the lack of mechanical stresses from waves permits the development of more species with broad membranous thalli here than in any other type of habitat in Bermuda. As a result, the flora of the fish ponds and pools appears much more luxuriant than the brief list of species would suggest.

Examples

The fish ponds included in this study are in Dollys Bay and Emilys Bay on St. Davids Island, in Richardsons Cove on St. Georges Island, in a cove on Hamilton Island looking out on Ferry Reach, in Tuckerstown Bay on Hamilton Island, and in Shark Hole, Harrington Sound. The landlocked pools are almost restricted to the Walsingham area of Hamilton Island, but a somewhat similar situation exists at Gravelly Bay on the south shore of Hamilton Island. The "Cliff Pool" near the southwest corner of Harrington Sound, from which Collins and Hervey (1917, p. 64) collected floating forms of Caulerpa, is also of the landlocked-pool type, but it was inaccessible for periodic observation.

Quiet, Sand-Bottomed Coves

Description

Whereas the fish ponds are small and easily inspected, the coves with which they are usually connected are more complex from the point of view of the observer. This is due partly to their larger size and partly to the more numerous species inhabiting them, but there are further variables introduced in the types of substrata, the degree of wave action, and the amount of insolation which necessitate detailed study.

Size.--Richardsons Cove, on the south side of St. Georges Island, is typical of a quiet, sand-bottomed cove. It is about 125 meters long and is almost 100 meters wide at the mouth, tapering gradually for about two-thirds of its length and narrowing abruptly in the final third, where mangroves encroach from the head of the cove.

The head.--Mangroves are almost invariably present around the heads of quiet water coves and, at least in Bermuda, are never found in areas exposed to any considerable wave action, so that they serve as one of the

most obvious indicators of the type of locality we are considering. The species involved are Rhizophora mangle and Avicennia nitida. In general it appears that firm sand and shallow water are more favorable than soft mud and deeper water to Avicennia. Accordingly, it is usually found on the landward side of the thicket and may even spready sparsely along the sides of the cove if there is adequate protection from waves. Rhizophora may be found on mud as well as on sand and is usually more abundant when both species form a thicket. Occasionally, as at Mullet Bay and Coot Pond, Avicennia forms stands alone, but these are hardly dense enough to be called thickets. Salicornia is usually present in the thickets, and often extends beyond the shade of the mangroves until it is replaced by the fully terrestrial flora.

The shore.--Where there are no mangroves at Richardsons Cove, the shore consists of limestone, essentially of smooth contours but with occasional undercut niches and eroded sharp edges. Coves which have no mangrove thicket at all commonly have at least a beach of sand or gritty mud near the head, but the sides are nevertheless of continuous rock, just as at Richardsons Cove.

The shores of the Florida Keys, which support an algal flora similar to that of Bermuda, have been described by the Stephensons (1950) as consisting of an "upper platform", a "lower platform", and a "reef flat". A step-like arrangement of the shore region also exists at Bermuda, and in quiet water bays it seems to be comparable with that of the Florida Keys. The upper platform is, at its landward edge, a gently sloping mass of almost bare rock, often knobby or spiky. A fringe of the land vegetation reaches the highest portions of the upper platform, the more common species being Stenotaphrum secundatum, Limonium carolinianum, Sesuvium portulacastrum, Borrichia arborescens, and Conocarpus erecta. Just above the

reach of ordinary high tides the upper platform changes its slope abruptly and drops almost vertically for 0.6 to 0.8 meter very nearly to the level of ordinary low tides. It is this steep portion of the shore rock which I have described as essentially of smooth contours and it resembles a smooth wall along the sides of the cove. In quiet water coves the width of the upper platform is usually less than 2 meters except where the shoreline has been changed by construction, whereas the Stephensons' account of the Florida Keys lists a minimum width of the order of 5 meters and a maximum of about 23 meters. The difference is probably a result of different contours of the land for the most part, but may also be due to different degrees of wave action. With even moderate wave action, the higher portions of the upper platform might be washed by salt water for some distance landward sufficiently often to prevent any growth of land plants. On the other hand, in very sheltered spots terrestrial plants can come almost to the water's edge, and the consequent formation of humus would cover that which was originally bare limestone, leaving only a narrow "upper platform" visible. In Bermuda bays with moderate wave action, the upper platform more closely resembles that of the Florida Keys, although even here it may be narrow if the shore slopes steeply.

At the foot of the upper platform the shore rock forms a shelf which extends, with a gentle slope, outward for 1 to 3 meters and usually ends some 0.1 to 0.3 meter above the sand bottom of the bay. This shelf is probably what the Stephensons call the "lower platform" in Florida, in which case the sandy bottom corresponds to their "reef flat".

The causes of the step-like configuration of shore rocks are unknown. The Stephensons' account does not relate the platforms to any definite tidal levels, and, especially in the case of the step between the lower platform and the floor of the bay, I have not been able to detect

any coincidence with tidal phenomena. Terraced shores are also found on the Isle of Man (Knight and Parke 1931, p. 3), on Kangaroo Island, Australia (Womersley 1948, p. 149), at Bikini (Taylor 1950, p. 9), and, no doubt, elsewhere. Kuenen (1950, p. 434) describes "beach sandstone" and "cay sandstone" which are also terraced, rather differently from ours, it is true, but also of unknown causation. It is difficult to believe that the step-like arrangement of the shore rock is not somehow related to the action of the sea water, whether by erosion or by solution. To the marine ecologist the lack of agreement with any recognized tidal level suggests that some agency or complex of agencies, hitherto unrecognized, may be effecting this configuration. Such an agency could conceivably affect biological zonation also, and its discovery would be very interesting.

The bottom.--The bottom of the typical quiet cove consists of sand or gritty mud. This is neither the pink sand nor the golden sand of which tropical beaches are said to be composed, but is gray or buff-colored at the surface and has considerable amounts of black nongraunular matter dispersed below the surface. In the vicinity of mangroves the bottom is more mud than sand, sooty and soft in color and texture and smelling strongly of hydrogen sulphide. Within the mangrove thicket there is usually a peaty substratum, but some portions of the great mangrove colony at Hungry Bay are growing on sand (Plate I) and even on mixtures of sand and stones (Plate II).

Depth.--The coves are shallow, rarely exceeding 2 or 3 meters in depth. In the vicinity of mangroves, the bottom may be exposed from shore to shore during some of the extremely low tides (Plate III), and the contour of the bottom slopes gently downward toward the mouth of the cove without any abrupt declivity except where channels have been dredged for boat passage.

Ecological Factors

Emersion.--The shallowness of the coves and the gentle slope of their floors is undoubtedly very important ecologically. Plates IV and V show, respectively, the situation at low water of neap tides and at low water springs. The difference in water level was hardly 0.2 meter, yet a large expanse of ordinarily submerged growth was laid bare during the extreme low tide. Obviously, a large proportion of the vegetation of such areas must be composed of plants which are able to withstand unusual fluctuations in duration of emersion and submergence.

Sunlight.--The strong insolation to which the algae of quiet coves are exposed is another ecological factor which cannot be ignored. Except among the mangroves, there is very little overhead shade in these coves, and the calm waters do not shield the algae from the sun as much as waves would. This increase of light penetration where there is minimum wave action was observed by Poole and Atkins (1926). They measured the meter-candles of illumination falling at the same instant on two photometers, one of which was held above the water while the other was lowered to various depths. Limitations of apparatus prevented measurements within the first meter of depth, but graphs of the results were extrapolated to include the uppermost layers of water. The graphs seem to show that from 5 per cent to 31 per cent of the vertical light registered by the air photometer did not enter the sea. The loss, which the authors attribute to surface reflection, was least when the sea was extremely calm and was greatest when there was considerable wave action. Clarke (1936) has shown that the major part of this loss is not due to surface reflection or to back radiation but that it is caused by an "opaque layer" which exists within the first meter below the surface when the sea is not glassy

calm. He suggests that bubbles are responsible for the opacity of this layer. Whatever the explanation, the increased penetration of light under conditions of calm water seems to be adequately demonstrated.

Some ecological implications of the effect of wave action on light were disclosed by Tschudy's (1934) experiments. He enclosed fragments of several red algae and of a brown alga in stoppered containers and submerged them at various depths. For any given duration of time, usually 8 to 10 hours, maximum evolution of oxygen took place in the containers at the surface of the sea if the day was cloudy or the water was "choppy", whereas it took place at about 5 meters depth if the day was clear and the water calm. Tschudy concludes that the intensity of light at the surface was too great for maximum photosynthesis during calm and clear days. This is probably not true for all algae, but it suggests that species which find optimum light conditions near the surface in wave-swept habitats would be at a disadvantage near the surface in quiet coves, and, of course, vice versa.

Substrata.--The sides and bottom of a quiet cove generally consist of rock and sand or gritty mud which serve as substrata for the attachment of algae, and the mangrove thickets furnish a substratum of peaty mud. With few exceptions, species whose attachment organs are adapted to one substratum are not to be found on another. The species which grow on rocks, for example, are those with a disc-like holdfast, and such a holdfast is ineffective on unconsolidated material like sand or mud. Conversely, many algae of the sandy bottom are held in place by a structure resembling a rootstock, and the interwoven rhizoids forming this "rootstock" are unable to penetrate any substratum which is more compact than sand or soft mud. Finally, on the tough, peaty mud of the mangrove thickets we find a short velvety turf whose lower parts penetrate only a few millimeters into the substratum--a means of anchorage intermediate between the surface attachme

of the algae growing on rocks and the penetrating rhizoids of those growing in sand.

All three types of substrata with their characteristic algal growths are found only in the quiet coves. In less sheltered habitats, one or more of the substrata are lacking and there is a consequent limitation of the vegetation.

Bacterial activity.--There is no direct evidence that bacteria are especially important in the ecology of quiet coves at Bermuda. However, inferences from the literature combined with observations in the field suggest that bacterial activity may have uncommon potential in quiet coves, and, since the role of bacteria has generally been ignored by phycologists, it seems worthwhile to call attention to some of the indirect evidence and its implications with respect to nutrient cycles.

The bacteria which are of immediate interest are those whose presence is visibly manifested by a calcareous precipitate. Sand, rock surfaces, debris, and algae in Richardsons Cove and similar habitats at Bermuda are covered by a thin layer of chalky mud which effervesces when it is treated with dilute acid. The origin of this calcareous deposit has not been investigated at Bermuda, and it may be merely silt which has been churned up by dredging operations and boat traffic. However, a large volume of work in other areas, reviewed by ZoBell (1946, p. 100), has disclosed that the precipitation of calcium carbonate ooze in tropical seas is primarily a microbiological process, the principal organisms concerned being the ammonifying, denitrifying, and sulphate-reducing bacteria. Hatch, Rastall, and Black (1938, p. 173) point out that ammonifying and sulphate-reducing bacteria are strongly represented in mangrove swamps and are responsible for deposition of calcareous ooze in these localities. This may be the explanation for the chalky sediment found in Bermudian quiet coves, and,

for correlative evidence, we may remember that the bottom deposits near mangroves at Bermuda smell strongly of hydrogen sulphide.

The implications of calcium carbonate precipitation by marine bacteria were recognized soon after Drew (1911, 1914) discovered that denitrifying bacteria have this power. When Vaughan (1914) pointed out the magnitude of the precipitation effected by Drew's bacteria in the Tortugas area, McClendon (1918) proposed that such a process would require appreciable amounts of nitrates or nitrites. Since he found very low concentrations of nitrogen compounds in Tortugas waters, McClendon suggested that Drew's bacteria might be responsible for the diminution of fixed nitrogen. Since it is now known that denitrifiers are not the only bacteria involved in calcium carbonate precipitation, McClendon's inference cannot be applied to all habitats. It would be most interesting to know how the bacterial flora differs in the various types of algal habitats, and what relation obtains between the bacteria and the nitrogen cycle in a given cove.

Feldmann's Classification

Following the scheme advanced by Feldmann (1951), it is possible to recognize in quiet coves a supralittoral belt, a littoral belt, and an upper infralittoral belt, but there is no lower infralittoral belt because of the shallowness of the coves. The uppermost belt, the supralittoral, supports almost no algal growth and may be ignored for practical considerations. The littoral and upper infralittoral belts contain two types of facies--a rocky facies provided by the limestone at the sides of the coves, and an unconsolidated facies consisting of peaty mud near the mangroves and of sand on the bottom. In all the belts and their facies we are concerned with quiet water modes exclusively.

Vegetation

Mangrove algae.--Botanically, the quiet sandy coves are distinguished by their mangrove thickets, by a profuse growth of bottom-dwelling marine phanerogams and algae, and by patches of small and inconspicuous algae on the intertidal rock surfaces. Beneath the mangroves, relatively few species of algae grow, as can be seen from the following list:

Myxophyceae

Calothrix pilosa

Chlorophyceae

Cladophoropsis membranacea
Dichotomosiphon pusillus
Monostroma oxycoccum
Rhizoclonium hookeri
Vaucheria nasuta

Rhodophyceae

Bostrychia binderi
Bostrychia montagnei
Bostrychia tenella
Caloglossa leprieurii
Catanella repens
Polysiphonia howei

These few species grow very abundantly on the prop roots and pneumatophores of the mangroves and on the soil surrounding them. Bostrychia montagnei is dominant but is almost invariably associated with the other Rhodophyceae as thick, beard-like growths on the mangroves (Plate II). On muddy or peaty soil, Dichotomosiphon is especially prominent and makes extensive velvety patches, interrupted here and there by smaller patches of Cladophoropsis and Vaucheria. Cladophoropsis becomes more important than Dichotomosiphon in sandy areas, where it forms pads or cushions several centimeters in diameter (Plate I). It is interesting to note that Caulerpa verticillata is the dominant alga of the mangrove vegetation at Guadeloupe (Feldman and Lami 1936, p. 884), and is commonly on mongrove roots in the Danish West Indies (Børgesen 1907, p. 344), but at Bermuda this species was found only once among mangroves, although it is prominent in other habitats. In their ecological studies

of Caulerpa, Børgesen (loc. cit., p. 345) and Svedelius (1906a, p. 108) report that Caulerpa verticillata does not grow above low water level, and this is true of the species at Bermuda also. Since much the greater part of a Bermuda mangrove thicket is regularly laid bare at low tide, emersion is undoubtedly one of the reasons why Caulerpa verticillata is not the dominant alga among mangroves here. However, its rarity even on the submerged roots at Bermuda demonstrates that more than the single factor of emersion is involved.

Marine phanerogams.--Apart from the mangroves, the phanerogams of quiet bays are Diplanthera wrightii, Cymodocea manatorum, and Thalassia testudinum. Diplanthera is the least abundant of the three and seems to be restricted to the softer portions of the bottom, often at levels which are exposed at low tide. Cymodocea and Thalassia are able to grow on firm sand as well as on shifting sand or mud, and may be found at all depths of a bay. Thalassia is by far the most abundant of these marine phanerogams (Plate III) and parallels, in abundance and ecological relationship, the Zostera marina of cooler temperate waters. Britton (1918, p. 6) and Prat (1935, p. 168; 1936, p. 10) report Zostera from Bermuda, but I was not able to find the species. If it is present at all, it is not a characteristic member of the flora of quiet bays.

Infralittoral algae.--The bottom-dwelling and epiphytic algae which are common in quiet coves during all or part of the year comprise a very respectable list:

Myxophyceae

Lyngbya majuscula
Symploca hydnoides

Phaeophyceae

Aegira zosterae
Colpomenia sinuosa
Dictyota indica
Ectocarpus mitchellae
Hydroclathrus clathratus
Padina vickersiae
Sargassum polyceratium
Scytosiphon lomentaria

Chlorophyceae

Acetabularia crenulata
Anadyomene stellata
Avrainvillea longicaulis
Avrainvillea nigricans
Caulerpa racemosa
Cladophoropsis membranacea
Codium pilgeri
Cympolia barbata
Enteromorpha plumosa
Halimeda monile
Halimeda tridens
Neomeris annulata
Penicillus capitatus
Penicillus pyriformis
Udotea flabellum
Valonia macrophysa
Vaucheria bermudensis
Vaucheria dichotoma
Vaucheria piloboloides

Rhodophyceae

Acanthophora spicifera
Amphiroa fragilissima
Callithamnion byssoideum
Centroceras clavulatum
Ceramium subtile
Coelothrix irregularis
Fosliella farinosa
Galaxaura obtusata
Herposiphonia secunda
Herposiphonia tenella
Laurencia gemmifera
Laurencia obtusa
Polysiphonia havanensis
Polysiphonia opaca
Spyridia filamentosa

The Sargassum is the dominant alga wherever the rock of the shore extends downward below low tide level or where scattered fragments of rocks may be available. It does not usually grow in depths greater than about a meter, even though appropriate opportunities for attaching itself may be available. Rather, it tends to form a girdle near the shore. Of the remaining algae, there is a curious frequency of brittle types. Not only in the truly calcareous algae, represented by several Chlorophyceae and one or two Rhodophyceae and Phaeophyceae, but also in certain noncalcified genera of fairly general distribution, the specimens found in quiet water coves present a stiff or friable texture. Penicillus, Halimeda, Udotea, Acetabularia, Neomeris, and Cymopolia are the Chlorophycean genera which are encrusted with lime, and Amphiroa and Padina are, respectively, the Rhodophycean and Phaeophycean examples of chalky plants. Laurencia, Spyridia, and Dictyota are very common noncalcified genera whose representatives in sheltered places occur as loose masses which are impossible to disentangle without reducing them to a handful of nondescript fragments.

It is easy to see that such thalli could not long exist under conditions of violent surf, but whether there is associated with this brittleness some advantage which selects for brittle types and against leathery types in quiet water coves is not so clear.

Another general characteristic of the submerged vegetation of quiet coves is its drab appearance, which is in sharp contrast to the richly colorful vegetation of the fish ponds. In the coves the normal grass-green tone of the most abundant Chlorophycean genera is masked by their covering of lime. The usual red and brown hues associated with Rhodophyceae and Phaeophyceae are replaced by a dingy buff color, partly because of a weakly developed pigmentation which seems to be related to the strong sunlight (Strain 1951, p. 246)--the antithesis of the cases in the shaded fish ponds --and partly because of the calcareous sediment which covers the algae with a tan bloom.

Littoral algae.--The commonest algae to be found between the tide marks on the shore rock of quiet coves are:

Rhodophyceae

Bostrychia binderi
Bostrychia tenella
Catenella repens
Caloglossa leprieurii
Polysiphonia howei

In addition to these diminutive red algae, a few intertidal species of Chlorophyceae and Myxophyceae are often present in small quantity, but Phaeophyceae are essentially absent except where there is no danger of dessication. Several reports (Svedelius 1906b, p. 197; MacCaughey 1918, p. 46; Isaac 1938, p. 19; Taylor 1950a, p. 11) make it evident that this dominance of Rhodophyceae over Phaeophyceae in the littoral belt is characteristic of warm climates. It is in striking contrast to the bulky fucoid vegetation of the shore in cooler regions.

Examples of Quiet Coves

It now remains to specify a few bays, coves, or lengths of shoreline at Bermuda which I have classified as quiet, sand-bottomed coves. On the south shore of St. Georges Island the shore line from Mullet Bay westward to the end of the island is almost uniformly of this type and includes Mullet Bay, Richardsons Cove, Soldiers Bay, and several unnamed coves. The north side of St. Davids Island is similarly sheltered. Here are Whites Bay, Great Bay, Dollys Bay, and Emilys Bay. The south shore of Coney Island and the northeast shore of Hamilton Island may be placed in this category in toto. Elsewhere on Hamilton Island, quiet conditions may be found at Walsingham Bay and Tuckers Town Bay, which look out on Castle Harbor, the inner portions of Hungry Bay on the south shore, and Stovel Bay and Fairylands Creek in the Spanish Point area of Hamilton Island. Other examples exist, but these were most often visited.

Moderately Exposed Bays

A number of localities along the north shore of the islands show similarities which make it possible to group them as a type of habitat intermediate between the quiet coves and the wave-swept shores and reefs. The more protected portions of these places, for example, the head of a bay, differ only slightly from the quiet coves, but other portions show constant and rapid exchange of water. During storms, true waves are expected in such places, but the more usual activity is choppiness or a restless swell.

Description

Size.--A specific example of this type of habitat is Whalebone Bay, on the north side of St. Georges Island. Roughly 200 meters long and 150

meters across the mouth, it is a conspicuous indentation in an otherwise smooth shoreline, but it is by no means comparable to the great bights of the sea which are called bays in other parts of the world.

The head.--The head of Whalebone Bay is a sandy beach and, unlike the condition in quiet coves, neither this nor the other bays of this category have mangrove thickets in place of the beach.

The shore.--Inner portions of the bay have a low limestone bed at the shore, but at the mouth the shore is more steeply inclined, even to the point of resembling cliffs. The three "platforms" or levels discussed in connection with the quiet coves are more difficult to delimit here. The upper platform is replaced by the almost vertical faces of the steep rocks of the mouth and so is nonexistent as a topographic feature in many spots. The lower platform in the same places is well below the mean low tide level, as much as 0.6 meter, and varies in width from a meter or more to a few centimeters. Where the shore is most nearly perpendicular, no step-like arrangement of platforms is discernible at all, and the shore rock plunges down to the sandy bottom. Nearer the head, the gentle slope of the shore makes for wider upper and lower platforms than one finds in quiet water, although sometimes the declivity is so even that the two platforms merge and extend seaward as a single rocky flat. Whether composed of one or two platforms, the shore rock ends abruptly with a drop of a few centimeters to the last level, which is the sandy bottom of the bay.

The character of the shore rock of moderately exposed bays differs in several particulars from that of the quiet coves. First, with increasing wave action we find many more crevices, undercut surfaces, and even occasional boulder-like sentinels where waves have cut through the isthmus of a small point of the mainland. Second, below low tide level the rock is usually vertical or steeply sloped where waves are common, whereas the

submerged parts of quiet areas are generally flat or gently sloping. Third, from high tide level and upward as high as waves reach, the moderately exposed shore is eroded into a mass of knife edges. The difference here is a matter of degree, for almost any Bermuda limestone which is not covered by soil shows considerable dissectionddue to weathering. Fourth, the irregularities of exposed shores include occasional small basins of water in which, depending on the level, the water may be constantly replaced or may be stagnant. A stunted flora grows in such basins, usually of species which normally grow at some lower level.

The bottom.--At Whalebone Bay and other bays of moderate exposure the bottom is of sand, with frequent flat rock surfaces along the sides and a scattering of massive corals toward the mouth. The sand is firm, there seems to be no admixture of black, muddy particles, at least not in the top few centimeters, and there is no release of hydrogen sulphide. In all these respects the bottom differs from that found in a typical quiet cove.

Depth.--As in the more sheltered examples, the bottom in moderately exposed coves is almost flat, the gentle grade leading down to a depth of only 3 to 5 meters near the mouth.

Ecological Factors

Substrata.--Whereas the quiet coves contain three types of substrata, moderately exposed coves have only two--sand and rock. The peaty mud is absent, and the algae which normally grow on this mud are also absent. This does not mean that fewer species grow if there is a decrease in the variety of substrata, for other factors also affect the picture. Rather, the differences in substrata seem related to the types of communities present in any situation.

Microtopography.--The configuration of the rock surfaces along the sides affects the vegetation in several ways. The slope of the surface is well known to affect the size of the population (Børgesen 1908, p. 705; Bell and MacFarlane 1933, p. 290; Kitching, Macan, and Cary 1934, p. 682). Presumably, the more nearly horizontal surfaces are more thickly populated because spore settlement is easier. Another consequence of the irregularities of the rocks in exposed places is the shelter afforded against sun and waves. Shade is perhaps the more common result of these irregularities, for undercut surfaces, crevices, and vertical surfaces are all likely to be shaded at some part of the day, but many of them are the result of wave action and so do not constitute protection from wave action.

Wave action.--The significance of wave action is also manifold. I have mentioned that quiet coves are sunny coves, and the reverse conditions obtain where wave action is found. Since the waves are probably responsible for most of the unevenness of the rock and for Clarke's opaque subsurface layer, they are of singular importance in providing shade. This is probably one of the reasons for the colorful flora in exposed areas in place of the bleached and drab flora of quiet areas.

The mechanical force of the waves undoubtedly inflicts stresses on the algae. Certain species apparently could not withstand even the difference in exposure between the relatively calm head of Whalebone Bay and the moderately churned waters of the mouth, and the difference between the general conditions at Whalebone Bay and those in quiet coves is even more pronounced.

Other consequences of wave action have been variously interpreted. An increase in aeration may be expected (Adeney 1926), but its importance requires investigation. Feldmann (1937, p. 36, 96) is of the opinion that

the effect of waves on oxygen content has been overstated, but Dawson (1944, p. 197) present evidence, albeit inconclusive, that the oxygen content of active waters is higher than that of quiet waters. The latter author believes oxygen has ecological importance second only to temperature, whereas Womersley (1947, p. 235) expresses doubt that the oxygen content, whether increased by wave action or by photosynthesis, is of importance in algal ecology "for the most part". Feldmann feels that the importance of waves is essentially due to the mechanical stresses inflicted on the algae and to the temperature regulation afforded by constant mixing of offshore waters with lagoon waters. This supposition seems reasonable, for at Bermuda I have rarely found the portions of an exposed bay to differ in temperature, whereas in sheltered waters a distinct change of temperature may be noticed as one wades from shallow water to deeper water, or from the shade of mangroves into the sunny portions of the cove.

Despite the great amount of investigation devoted to intertidal ecology, the ecological mechanisms associated with wave action in the littoral region are no less obscure than in the infralittoral. Stephenson (1943) feels that waves are an agency second to none in importance between tide marks, contributing coolness, dampness, shade, and some other factors which he is unable to specify. He describes as beneficial the "turmoil" of the waves, but it is difficult to see how "turmoil" operates ecologically except as a mechanical stress.

Feldmann's Classification

If the description of the moderately exposed coves be reduced to the terminology employed by Feldmann, we find that the essential difference from the previously described habitats is in the so-called "mode".

As before, we are concerned with the littoral and upper intralittoral belts, each of which contains both rocky and unconsolidated facies, but the mode is now somewhat less sheltered. The difference is quantitative rather than qualitative, but this slightly increased exposure to wave action with the resultant erosion of the rock surfaces exerts a marked influence on the flora.

Vegetation

Infralittoral algae.--Apparently the sum total of the ecological conditions in moderately exposed bays is favorable to algal growth, for a diverse and abundant vegetation develops there, of which the following species are the most common:

Chlorophyceae

Anadyomene stellata
Bryopsis pennata leprieurii
Caulerpa cupressoides
Caulerpa racemosa
Caulerpa verticillata
Cladophora fuliginosa
Codium isthmocladum
Dasycladus clavaeformis
Halimeda monile
Halimeda tridens
Halimeda tuna
Penicillus capitatus
Penicillus pyriformis

Phaeophyceae

Aegira zosterae
Colpomenia sinuosa
Dictyopteris delicatula
Dictyopteris justii
Dictyota bartayresii
Dictyota cervicornis
Dictyota dentata
Dictyota dichotoma
Dictyota divaricata
Dictyota linearis
Ectocarpus duchassaingianus
Padina pavonia
Padina sanctae-crucis
Padina vickersiae
Pocockiella variegata
Sargassum bermudense
Sphacelaria tribuloides
Zonaria zonalis

Rhodophyceae

Antithamnion cruciatum
Botryocladia occidentalis
Centroceras clavulatum
Ceramium subtile
Crouania attenuata
Dasya collinsiana
Dasya rigidula
Dudresnaya crassa
Falkenbergia hillebrandi
Galaxaura squalida
Helminthocladia calvadosii
Heterosiphonia gibbesii
Heterosiphonia wurdemanni
Jania rubens
Laurencia microcladia
Laurencia obtusa
Laurencia papillosa
Liagora ceranoides
Liagora farinosa
Liagora valida
Lophocladia trichoclados
Seirospora purpurea
Spyridia aculeata
Trichogloea herveyi
Wurdemannia miniata

Sargassum is again the dominant alga below low tide level, but during certain seasons Dictyopteris justii becomes very abundant and may show local dominance. Very rich growths of Caulerpa racemosa, Codium intertextum, and Padina vickersiae make prominent belts about low tide level in spring and early summer.

The vegetation on the sandy portions of the bottom strongly resembles that of quiet coves. It is dominated by Thalassia, and Cymodocea and calcareous green algae are common, but Diplanthera is absent. It is very interesting that Thalassia forms continuous meadows on the soft bottoms of sheltered areas, but on firm sand the colonies may exist as discrete patches, conspicuously elevated above the surrounding bottom. At Whalebone Bay one such patch covered more than 100 square meters. The elevation results from an accumulation of pebbles, shells, and fragments of calcareous algae among the rhizomes. Along its seaward edge a patch does not taper down to the original floor of the bay but ends abruptly, and here the thickness of the mat is about 15 centimeters. Growth of such a mat probably takes place in two ways. Debris washed in by waves lodges against the seaward face of the mat and is caught among the exposed roots of Thalassia, whereupon the plant is able to advance from the shore. At the same time, Halimeda and the other calcareous algae which are abundant in Thalassia beds furnish their skeletons upon death to add to the thickness of the mat. Where such a mat extends from shore, as it does at Whalebone Bay, portions of the bay are very possibly being reclaimed from the sea in the same manner that mangroves tend to fill in the bays where they grow. If this be the case, a very different end-product would result. That is, under mangroves a peaty substratum is formed which grades off in a short distance to mud and soil, whereas land built up as a result of Thalassia mats would resemble an unconsolidated relative of the aeolian

limestone of which Bermuda is composed.

Littoral algae.--The species growing intertidally make a much shorter list than the foregoing:

Chlorophyceae

Codium intertextum

Rhodophyceae

Bostrychia binderi	Gelidium pusillum
Bostrychia tenella	Polysiphonia howei

Codium and Gelidium form girdles low in the littoral belt and undergo only brief emersion, whereas the other species occur as scattered patches in eroded niches near high tide level, where they find protection from the waves.

Examples of Moderately Exposed Coves

As has been mentioned, this is a habitat found especially on the north shores of Bermuda. In addition to Whalebone Bay, which is on St. Georges Island, localities within this category are Baileys Bay, Crawl Point, Shelly Bay, Burton Bay and its environs, and Spanish Point, all on the north shore of Hamilton Island.

Wave-Swept Shores

Oceanic waves which reach Bermuda crash against the outlying reefs and lose a great part of their force, but some of the energy is conducted through the passages in the reefs or remains in the water which hurdles the reefs. On the north side of Bermuda this residual energy is apparently dissipated by the long journey over the several miles of shoals which separate the islands from the reefs, but on the south side and at the east end the reefs are very close to the main land mass and much of the force of the waves reaches the shore. Indeed, several coves on the south and east shores of Bermuda are so similar to the reefs in botanical

features that one may suspect they are ecologically similar. Since the reefs are too heavily battered by waves to permit regular inspections, the exposed portions of the south and east shores will be treated as the last in a series of habitats graded according to the severity of wave action.

Description

Red Hole, at the east end of St. Davids Island, represents such a habitat. It is a small embayment oriented in such a way that one side is more exposed to surf than the other, and since other places of the same degree of exposure are almost invariably open stretches of shoreline rather than bays, we shall discuss mainly the exposed side of Red Hole and not the embayment as a whole. The length of the exposed shore is about 200 meters.

The shore.--The limestone of the shore is much more eroded here than in either of the habitats described previously. Above high tide level there is the same mass of knife edges that was described for the higher parts of Whalebone Bay. Lower, the shore becomes pitted and pinnacled, and channels meander irregularly downward. Near low tide level, the rock is also much dissected, but because of the dense growth of algae it is impossible to determine whether the dissection resembles that of the higher rock surfaces. The terracing of the shore rock is more pronounced on wave-swept shores than at either of the more protected situations, but locally may become too involved to be identified with the three levels described by the Stephensons in Florida. Plate VI shows a relatively simple configuration of part of the shore at Red Hole. The deeply eroded upper platform gives way to a neatly delimited lower platform which is continually awash. The surf hides the abrupt descent from the lower platform to the floor of the bay. A more complicated stratification occurs

in the most exposed parts of this and other bays. For example, at Gravelly Bay (Plate VII) several terraces, not just one, are continually awash and are populated by the same plant communities seen in the single lower platform of Plate VI. A further complexity is added by a miniature rampart which rises to about low tide level and is separated from these terraces by a small lagoon approximately a meter in width and rather less in depth.

The bottom.--The bottom near the more protected parts of Red Hole is of coarse sand with frequent rock fragments, corals, and enough bare rock surface to suggest that the bottom is essentially rock with merely a thin cover of sand. Where the waves are strongest, the bottom could not be checked, but along other exposed shorelines it is generally of rock and corals until depths of 4 meters or more are reached.

Ecological Factors

Emersion.--Extreme differences in duration of emersion obtain at localities where wave action is strong, just as they do in the quiet water coves, but the causes of these extremes are not the same. In quiet coves it is shallowness which results in the emersion of large segments of ordinarily immersed bottom during the low water of spring tides at approximately fortnightly intervals. In more boisterous waters the differences in emersion take place on the rocks of the shore, where the continual surge and subsidence of swells and waves alternately wash and expose a band almost a meter high. Under such conditions the band is effectively immersed even during low tide, for it is constantly covered or dripping with water. However, following several days without wind, the sea is becalmed, and then much of the shore vegetation is liable to desiccation, extremes of air temperature, and the other concomitants of emersion. Unlike the tidally induced situation at quiet coves, the emersion of ordinarily submerged vegetation on wave-swept shores is not periodic, and the prerequisite succession

of calm days is apparently uncommon, for only three or four periods of such emergence were seen during this investigation. Stephenson (1943) and Williams (1949) report that many algae are killed by unusual fluctuations in emersion, but no evidence of wide-spread mortality was seen at Bermuda.

Substrata.--Most of the surface available for attachment of algae in habitats subjected to strong wave action consists of rock, and this represents a further restriction in the types of growth-forms which compose the communities of these places. This means that algae adapted to sand or mud are scarce in these habitats. It should be noted that lack of sand is not necessarily the reason for absence of sand-rooted species, since even those surfy bays which have only sand for a substratum are invariably destitute of algae. Clearly, there must be a balance between the moving power of the waves and the permanence of the substratum before plants can be established.

Microtopography.--The ecological significance of the configuration of the shore rock is the same in heavily exposed localities as in the moderately exposed bays. Local protection from sun and waves is afforded, and spore lodgement is facilitated wherever we find very irregular surfaces.

Wave action.--Some of the effects of wave action have been mentioned in the discussion of the ecology of moderately exposed bays, and the discussion applies to wave-swept shores also. In addition, we may mention that the upper limits of vegetation may be raised a meter or more where splash wets the shore.

Feldmann's Classification

Reduced to the terminology of Feldmann, the wave-swept shores are difficult to distinguish from the moderately exposed bays. The belts are the same--littoral and upper infralittoral. The facies are essentially the same--consolidated and unconsolidated facies in each belt. There is

no unconsolidated facies (sand) in the littoral belt of our specific example, Red Hole, but it can be found intertidally along some exposed shorelines of Bermuda (the bathing beaches). The mode is one of active waters in the wave-swept habitats, but as has been pointed out in comparing the moderately exposed bays with the quiet coves, the difference is only in degree.

Until we know more precisely how the various ecological agencies operate in producing markedly different floras in each of our habitat types, we are forced to depend on lengthy descriptions for the characteristics of habitats.

Vegetation

Infralittoral algae.--A list of the major elements of the flora of Red Hole and similar bays shows some resemblance to that of moderately exposed bays but has little in common with quiet coves:

Chlorophyceae

Bryopsis pennata
Caulerpa racemosa
Caulerpa verticillata
Chaetomorpha media
Cladophora catenifera
Cladophora fuliginosa
Dictyosphaeria cavernosa

Phaeophyceae

Colpomenia sinuosa
Dictyopteris plagiogramma
Dictyota ciliata
Dictyota dentata
Dilophus guineensis
Pocockiella variegata
Sargassum bermudense
Spatoglossum schroederi
Turbinaria tricostata
Zonaria zonalis

Rhodophyceae

Asparagopsis taxiformis
Callithamnion herveyi
Corynomorpha clavata
Cottoniella arcuata
Dasya collinsiana
Falkenbergia hillebrandi
Galaxaura cylindrica
Galaxaura marginata
Galaxaura squalida
Heterosiphonia wurdemanni
Hypnea musciformis
Jania pumila
Jania rubens
Laurencia microcladia
Laurencia papillosa
Laurencia poitei
Liagora ceranoides
Liagora farinosa
Liagora valida
Lophocladia trichoclados
Polysiphonia ferulacea
Spyridia complanata

As would be expected, the stresses inflicted by surf and waves are reflected in the growth habits of the plants. Svedelius (1906b, p. 191) describes tufted Rhodophyceae with strong basal discs and deciduous upper parts as the most common inhabitants of battered reefs at Ceylon. Writing of the Hawaiian reefs, MacCaughey (1918, p. 48) reports an abundance of delicate species on the outer rim. Bell and MacFarlane (1933, p. 290) note that ribbon-like forms are prominent on exposed shores of Canada. Under similar active conditions in Bermuda, the floral elements agree to some extent with those mentioned above, but the most conspicuous feature is the turf or carpet of short plants which forms the belt washed by waves about low tide level. The plants are so firmly attached that the thallus usually breaks without the holdfast being pulled loose. These plants have the strong basal discs and deciduous upper parts described by Svedelius, and, indeed, one or two Rhodophycean species are abundant, but the dominant species is usually the Phaeophycean, Sargassum bermudense. Locally, however, Laurencia papillosa, Spyridia complanata, or some of the other Rhodophyceae may be very abundant. The delicate types, such as MacCaughey found, are represented by numerous species of Rhodophyceae, but these are smaller and less prominent than several of the coarser brown algae. Ribbon-shaped forms resembling those of Bell and MacFarlane are not usually found directly where the waves pound the Bermuda shore, but several of them become abundant in depths of a meter or more where the mechanical stress is probably less, or they may be in shallow water if local protection is afforded by irregularities of the shore. Dilophus guineensis is exceptional in that it is a ribbon-like species growing under the full force of the waves, but Dictyota dentata, Dictyopteris plagiogramma, and Zonaria zonalis, which are also flat and narrow, seem favored by the churning associated with active waters and not by the mechanical force of the

waves. Zonaria is brilliantly irridescent when submerged and is sometimes so abundant that it may be more conspicuous than even the Sargassum of the shore. Chlorophyceae are scantily represented in wave-swept habitats, and the marine phanerogams are completely absent.

Littoral algae.--Following several days of calm weather, the surf becomes sufficiently abated to disclose that some of the species listed as "infralittoral algae" extend above low tide level. These, however, are subject to constant wetting by surf. The more typical littoral species--those exposed by the falling tide and not kept wet by surf--are never found in the infralittoral region. The most abundant among these are three Rhodophyceae, namely, Bostrychia binderi, Bostrychia tenella, and Polysiphonia howei.

Examples of Wave-Swept Shores

A few of the shores which fit the description of a wave-swept habitat include Gates Point at the east end of St. Georges Island, the southeast shore of Paget Island, the northeast shore of Smiths Island, Gunner Bay and Red Hole at the east end of St. Davids Island, the south shore of Charles Island, and Gravelly Bay and the mouth of Hungry Bay on the south shore of Hamilton Island.

SEASONAL SUCCESSIONS

The fluctuations of individual species at Bermuda combine to produce a rhythm in the vegetation as a whole, for, in general, a decrease in abundance of one species is not offset by an increase of another. Briefly stated, the cycle of growth of the vegetation starts in autumn, rises to a maximum in spring, and declines during the summer. This simplified picture will now be examined in detail from three viewpoints: (1) the aspects in the various types of habitats through the year, (2) the history of a few selected species, and (3) an analysis of the vegetation into its seasonal components. In addition, some of the characteristics of the climate of each season will be described.

Aspection in the Algal Habitats

Fish Ponds and Landlocked Pools

Because of their small size, the fish ponds and small pools of the Walsingham area are very conveniently inspected, and the limited number of species they support simplifies matters even more. Accordingly, it is convenient to describe the seasonal changes occurring in these habitats first.

Autumn.--Autumn was a transitional period when the remnants of the summer vegetation were being washed away and the new flora was still in young state. Early in November, for example, *Amphiroa fragilissima* and *Caulerpa racemosa* were the only algae of any considerable quantity. Reddish films of bacteria and microscopic blue-green algae formed patches on some of the rocks--reminders of the summer flora. Hidden among the tangled masses of *Amphiroa* and *Caulerpa racemosa* was a small amount of *Caulerpa crassifolia* and *Caulerpa sertularioides*, and only by closest search could *Halymenia*

bermudensis be located. Fully grown, Halymenia is a conspicuous foliaceous alga, but at this time of the year the fronds were only a few centimeters high and were easily hidden in crevices of the rocks. An occasional other species was present, depending on the specific pool in view, but none was destined to achieve any importance later in the year in these habitats. Growth was slow during November and December, and at the end of autumn there was practially no change to be described. Except for a new tuft of Bryopsis plumosa or Bryopsis hypnoides here and there, and a few fronds of Ulva lactuca, the aspect was static and would have been interpreted as a sparse growth existing under apparently unfavorable conditions with no promise of future richness.

Winter.--Once established, the species of Bryopsis grew rapidly, and even with slow growth the earlier species produced a considerable effect after two or three months. Consequently, the pools displayed a volume of vegetation in February and March which, accentuated by the small size of the places and the showy appearance of some of the species, gave the pools and fish ponds a richer aspect than could be seen in any other type of habitat. Bryopsis plumosa and Halymenia bermudensis were the most conspicuous algae, the former a deep green and the latter a winey red in color. Toward the end of March, Ulva lactuca also achieved prominence, and its broad, green, membranous fronds complemented Halymenia, the two species covering much of the original Amphiroa on the bottom. Although the total bulk of Caulerpa seemed unchanged, the increase of the other algae reduced somewhat the original dominance of Caulerpa racemosa.

Spring.--There were increases in numbers and size during spring, and a luxuriant vegetation developed in the fish ponds. In April it would have been difficult to select any one of the species as preponderant, for the few species present were all noteworthy and the plants seemed

to be vigorous and healthy. Later in the spring the species of Bryopsis took the lead to the extent that some of the pools appeared choked by them. The Caulerpas and Amphiroa were still important members of their communities, but Ulva and Halymenia showed signs of aging. Decay and animal browsing had produced holes in the Ulva plants, while the fronds of Halymenia were discolored in spots, and a few small epiphytic red algae had become established on both species. By June, Halymenia had disappeared from several stations. Through the spring period no new species were recognized except for a few very minor elements.

Summer.--The deterioration of Ulva and Halymenia marked the beginning of a process of rapid decline in the flora of the small pools. During summer the masses of Bryopsis were greatly reduced and Ulva vanished from most of the pools. Some of the former richness was still visible in August, but with September the aspect became comparatively sparse. Amphiroa, Caulerpa crassifolia, and C. sertularioides were less affected than some of the other species, but Caulerpa racemosa persisted only in the most shaded niches, while Ulva and the two species of Bryopsis were lacking or represented by a few relics. In terms of bulk Amphiroa and the Caulerpas were foremost, but the general aspect of these pools in late summer was dominated by thin films and gelatinous tufts of Myxophyceae and sulphur-bacteria growing on the vegetable debris and creeping over the rocks and living plants.

With only slight changes--the decay and disappearance of the vegetable debris and a reduction of the scum of microscopic things--the scene in November and December was essentially the same as that in September, and the cycle was now ready for repetition.

Summary.--If we omit mention of the species, the seasonal cycle of vegetation in these protected places is seen to have followed a simple pattern. The cycle started in autumn with only two species abundant, but before

the end of autumn all the major species had appeared. Steady growth through the winter and spring produced a maximum vegetation in April and May, which was followed by decline of some species before spring was over. In the summer Myxophyceae increased, but there was a general decrease of other algae, and at the close of summer the aspect was similar to that of autumn.

The seasonal fluctuations of the individual species are shown diagrammatically in Plate XI.

Quiet Coves

The larger number of species involved renders the seasonal changes in the quiet, sand-bottomed coves more difficult to describe, and it shall be necessary to restrict the narrative to a few of the chief elements.

Autumn.--Several of the conspicuous algae of these coves were present throughout the year and their bulk and numbers in November mitigated the sparseness which would be expected at the beginning of the seasonal cycle. Among these, Sargassum was paramount, and its species formed the main part of the plant growth wherever rock was available for attachment. In sandy and muddy areas Sargassum gave way to several of the calcareous Chlorophyceae, especially the species of Penicillus (see Plate VIII) and the quiet-water Halimedae. Locally, shallow areas of some coves contained a profuse growth of Cymopolia barbata and Acetabularia crenulata (see Plate V), and in slightly deeper parts of almost all coves extensive mats of Amphiroa fragilissima lay among the sea grasses. Tufts of Myxophyceae and occasional colonies of Acanthophora spicifera, relics of the past season, were seen here and there but they soon vanished. The intertidal rock surfaces bore associations of small Rhodophyceae whose appearance remained unchanged through the year. The mangrove roots were also covered by small red algae but a conspicuous green alga, Monostroma, was soon to appear.

Winter.--Before the end of November three important new species had appeared in many of the coves, and they were soon followed by several others. The three earliest arrivals were Colpomenia sinuosa, Ectocarpus mitchellae, and Spyridia filamentosa, species which quickly came to the front and affected the aspect of the coves. The other species, which arrived in December and January, were Aegira zosterae, Hydroclathrus clathratus, and Scytosiphon lomentaria. In some of the mangrove thickets Monostroma oxycoccum spread over large areas, especially toward the landward sides of the thickets, where Avicennia rather than Rhizophora was dominant.

The rapidity with which some of these newcomers developed deserves emphasis. Entangled in the tops of the Sargassum plants and floating on the surface of the water, Ectocarpus and Spyridia came to obscure much of the bottom vegetation in a matter of two or three weeks. Colpomenia and Hydroclathrus, less generally distributed in quiet coves, grew prodigiously about low tide level if the proper substratum was available. A colony of Colpomenia plants about a month old is shown in Plate IX, and some specimens of Hydroclathrus of about the same age and proportions are shown in Plate X. The pocket knife in Plate X is about 16 centimeters long, indicating the approximate size of the thalli.

The appearance of the quiet coves was markedly drab through this period and continued to be so in February and March. The Phaeophyceae were more buff than brown in color, and the most abundant Rhodophyceae, Amphiroa and Spyridia, were strikingly pale in comparison to the deep red colors seen in the fish ponds at the same time.

Spring.--During the early spring most of these annual species reached a maximum of volume which they maintained throughout April and into May. The consequent fullness of the flora was further enhanced by an increased growth among many of the algae which had been present through the year.

The highest development of the flora of quiet coves was reached in May, but even as some species were ascendant others had started to dwindle. Scytosiphon and Aegira were among the most short-lived and vanished from some areas in April, leaving only a few stands until May. Ectocarpus, Colpomenia, and Hydroclathrus died away in May and June, as did the single annual of the mangrove thickets, Monostroma.

Summer.- Through the summer the outstanding feature was probably the disappearance of Spyridia from the surface, with the resultant disclosure of the steadily increasing numbers of two families of the green algae, Codiaceae and Dasycladaceae. Most of the species of these families are calcareous, and at this season they flourished. Among the Phaeophyceae a lime-encrusted species of Padina had been conspicuous since June and added to the general impression that the flora was largely of calcareous algae. In the most protected parts of the coves, where the only possible disturbance of the water was a slight ripple, a delicate bloom of filamentous Myxophyceae had become established and masked some of the rotting remnants of the earlier vegetation. As the summer drew to a close the scene resembled more and more the conditions which have been described for the beginning of the cycle, in November.

Summary.--In brief, we note that the cycle started in autumn with a preponderance of perennial species, which were soon joined by several annuals. Some of the early annuals quickly passed their maxima and were replaced by later annuals; others persisted to the end of spring, at which time the greatest bulk of vegetation developed. A rapid mortality set in at the end of spring and continued through summer, but there was little replacement by new species. Instead, the perennial species resumed their prominance, together with occasional growths of blue-green algae. The behavior of some of the key species is diagrammed in Plate XII.

Moderately Exposed Bays

Autumn.--To one not familiar with the conditions which obtain during other seasons of the year, the November flora of places such as Whalebone Bay would give little promise of reward, for the aspect at this time was surprisingly bare. The principal alga here, as almost everywhere in Bermuda, was a Sargassum, in this case Sargassum bermudense. In shaded niches Bryopsis pennata var. leprieurii was not to be overlooked, and occasional large colonies of Padina vickersiae were locally important. In deeper water Caulerpa racemosa was fairly common, but much of the submerged rock surface was bare or populated only by small plants of several of the Phaeophycean genera, of which the most common was Pocockiella.

Winter.--Closely spaced visits in November and December disclosed that several species were on the ascendancy and the bare portions of the bottom were being covered rapidly, albeit the individual plants were small. Dictyopteris justii, Pocockiella variegata, and Zonaria zonalis may be singled out for special attention because of their later prominence. Near the surface, either as epiphytes or lithophytes, Colpomenia sinuosa, Sphacelaria tribuloides, and Laurencia microcladia entered the scene. Colpomenia grew more slowly here than in the quiet coves and was not abundant until the middle of winter. Indeed, growth of all the species was slow and as late as January the most characteristic feature of these coves was the multitude of small things. Many species were present but the plants were poorly developed and few of the species grew in great quantity.

Spring.--Early in the spring the changes in aspect were accelerated when a few species of Rhodophyceae made their first appearance, and the existing elements grew more rapidly. Dudresnaya crassa, Liagora farinosa, and Trichogloea herveyi deserve mention because of their sudden rise, and, as will be noted later, their brief term of life.

From the standpoint of vigor and variety of the vegetation, the high point in moderately exposed bays was reached late in the spring. Caulerpa racemosa, originally common about a meter below the surface, attained full size and luxuriance near low tide level in May, and thereby became exceedingly conspicuous. Even more conspicuous were several of the Phaeophyceae. Sargassum, Dictyopteris, and Zonaria attracted attention by virtue of their relatively great size, while Pocockiella and Colpomenia stood out because of their abundance. The Rhodophyceae were represented comparatively weakly at this time. Dudresnaya and Trichogloea had vanished from most bays before the end of May, and the numbers of Liagora plants were greatly reduced. The most abundant red algae were Lophocladia trichoclados and Laurencia obtusa, neither of which approached the size of the large brown algae.

Summer.--In late summer the changes were again considerable. Caulerpa racemosa was still present in some quantity but was obviously past its peak. The number of species of Phaeophyceae had fallen off, but the remaining species were still the dominants. Nevertheless, even they appeared to be waning. For example, Dictyopteris justii was at its largest size in August and September, but the plants were battered and epiphytized, and great masses of this species were being washed ashore. Pocockiella, although plentiful, was not so generally distributed as before, which seemed to indicate that some of the colonies had died out. The great masses of Colpomenia were quite gone. The Rhodophyceae fared worst of all, for not a single species was seen in quantity sufficient to affect the over-all aspect. Instead, frequent gelatinous tufts of Myxophyceae floated from the remnants of larger algae and added to the impression of a moribund flora.

Summary.--We may summarize the seasonal changes in moderately exposed

bays as beginning with a period of relatively slow growth in autumn and early winter. Numerous small plants were present before the end of winter, and these were joined by new elements in the spring. The Rhodophyceae for the most part showed only a brief period of ascendance while the Phaeophyceae grew rapidly in the spring and persisted to rule the late spring and summer scene. Only a few Phaeophyceae carried through the summer. As in both of the calmer habitats, Myxophyceae were more prominent in late summer than at any other time. A diagram of the rise and fall of the chief elements is shown in Plate XIII.

Wave-Swept Shores

Autumn.--In contrast to the more sheltered habitats, the shores which are subjected to considerable surf appeared to have a luxuriant flora in November. The richness was superficial, however, for the appearance was due almost completely to the short turf of densely growing tough plants which made a broad band on the rocks about low tide level (see Plate VII). The foaming waters obscured the conditions of the bottom, and only during the occasional periods when calm seas occurred at the time of low tide was it possible to see that the submerged vegetation was not as dense as the luxuriant higher growth. The species responsible for the deceptive show of richness were Sargassum bermudense, Dilophus guineensis, Laurencia papillosa, and Spyridia complanata--ranked in approximate order of abundance. Falkenbergia hillebrandi was a common epiphyte at this time and its matted delicate filaments added bright red variety to the brown and rust colors of the larger species. Numerous other species were present, but only later did any of them become notable.

Winter.--Before the end of December Antithamnion cruciatum and Dasya collinsiana, which were inconspicuous in November, increased to the point of

abundance near the surface, while on rocks a meter or more below the surface Caulerpa racemosa and several species of Dictyota dominated the scene. It was characteristic that during the winter none of these species disappeared or declined, but all increased and were joined by several Rhodophyceae, a few Phaeophyceae, and one or two Chlorophyceae. Accordingly, in February and March there was a considerable variety of species in view, all of them small in size.

Spring.--There was no addition to the number of species in spring, but those already present became more abundant and increased in size. Most of the algae of active waters did not attain any great dimensions, but at least one of them deserves rank among the larger algae of Bermuda. This is Zonaria zonalis, a foliaceous member of the Phaeophyceae, which did not reach its full length of 20 centimeters until April. Beneath the water it was brilliantly irridescent in shades of purple and blue, and late in the spring its colonies made a spectacular display of color at levels below the brown zones of the shore. Other species also reached a peak of development in April or May, so that the end of spring brought with it a truly luxuriant vegetation. Colpomenia sinuosa, which had been pale brown in quieter areas, formed magnificent golden masses in the full glare of the sun on exposed shores, and Caulerpa racemosa spread from the deeper waters to cover many of the rocks with great sprawling clusters of miniature grapes. Each crevice of the submerged rocks was populated by one or more of the Rhodophyceae, and it was difficult to find a rock surface, either above or below low tide level, which was not completely covered by algae.

Summer.--Although the general impression of fullness was retained during June, several of the species thinned out, and the flora started to fall away from its peak. By August Caulerpa was the only green alga of consequence, and it was far below its earlier maximum, Colpemenia had been gone since

June and had not been replaced by any other species, and such Rhodophycean genera as Jania, Liagora, and Galaxaura were very scarce. With the disappearance of Zonaria in September, the wave-swept shores assumed essentially the same aspect which has been described as the November condition.

Summary.--Briefly reviewed, the seasonal cycle in wave-swept habitats began with a superficial appearance of richness in autumn because of the crowded growth of a few species in the surf zone, but the number of species at this level and below was much less than the maximum. An increase in numbers of species and of individuals took place in winter, although the plants remained small. During the spring there was no increase in species, but all species became more abundant and reached full size, so that the highest point of vegetation occurred at this season. As in other habitats, summer was a period of decline, and the end of summer or the beginning of autumn saw the lowest point in the vegetation.

The species mentioned in the narrative were selected merely to indicate the degree and direction of change from season to season. Plate XIV, illustrating the behavior of a larger number of species, may provide a more realistic picture of the complexity of the successions.

Specific Examples of Growth Cycles

To break down the complex flux of successions into its elements and to treat the species individually would be unnecessarily repetitious, but a few examples may help to make the several types of growth cycle more clear.

Acanthophora spicifera.--This red alga started its growing season in May, several months after most species had appeared. It grew very rapidly and contributed considerably to the spring maximum. Unlike other algae which flourished in spring, Acanthophora retained its abundance through the summer and many colonies were still present in November. Tetrasporic plants

were common in spring and summer, but sexual plants were found only in November. A unique feature was the continued presence of isolated relics long after the species was absent from familiar stations. For instance, in December the species was seen only once, in January three small clumps were found, and in an especially protected spot a few plants were found on the first day of February.

Caulerpa racemosa.--This species is an example of a perennial which exhibits periodicity. The low point in its cycle occurred in late fall or winter, at which time it was relatively scarce. Near low water mark only a scanty growth of the erect assimilatory branch system was present, or even this was lacking and the plant appeared to be perennating by means of its coarse stolons. In depths of a meter or more large colonies could be found, but these were by no means as large as the colonies which appeared later. At its height, in May, the species was enormously abundant in many bays and showed its best development about low tide level, with little growth extending down further than about 0.6 meter. Following this maximum, there was a period of retrogression in the summer, but the species never completely faded from the scene.

The shift in abundance from deeper water in winter to low tide level and above in spring by Caulerpa racemosa is a response to the changing seasons which was not observed in any other species at Bermuda. Similar so-called "migrations" have been said to occur in Sweden (Kylin 1917), the British Isles (Rees 1940; Blackler 1951), and the Mediterranean (Feldmann 1951). Kylin's investigations led him to conclude that the low temperatures of surface waters in winter prevented certain species from growing near low tide level, and that they were able to spread upward when the temperatures were higher. Feldmann thinks the reverse is true in the Mediterranean--that is, certain algae cannot grow at the surface during the hot days of

summer. At first glance, this would seem to be the case with the Bermuda example, for it began to decline during the warmest months. However, temperature records for 1949 (Macky 1950) show that the mean maximum air temperature and sea temperature for July, August, and September differed by only a fraction of a degree, and that during some days the sea temperature was higher than the air temperature. It seems safe to rule out temperature as the cause for the disappearance of Caulerpa racemosa from the surface in summer, then. A possible factor is the intense sunlight of summer. This is supported by the observation that in fish ponds, where the water is very shallow, Caulerpa racemosa persisted at the end of summer only in the most shaded niches. Apparently, in other habitats depths of a meter or more represent equivalent "shaded niches".

Codium decorticatum.--Most Chlorophyceae are relatively small, but this one is almost the largest of Bermuda algae. An exceptionally bulky specimen was 0.42 meter long and weighed 2.5 kilograms, while less abundantly branched specimens, although lighter in weight, attain 0.6 meter in length. Whether a species is a perennial or an annual has no apparent relation to its size, however, for Codium decorticatum reaches maturity and dies away in less than a year. The earliest specimens were found in December and were both rare and small at that time, whereas in April and May plants from 0.4 to 0.6 meter long were abundant. The species as a whole died away during the summer, with only a few individuals surviving as late as September. Throughout its growing season, fruiting plants of this species were common.

Codium intertextum.--More than 80 observations were recorded concerning this species, and only when all of them were considered in sum was it possible to interpret its seasonal cycle. The difficulty is due to the fact that Codium intertextum was found in every month of the periods spent at Bermuda, and it was seen in abundance at least once during every season.

The colonies occur as dark rubbery expansions with the whole lower surface firmly appressed to vertical rock faces. The first collection in 1949 was made on February 25 from a small colony at Whalebone Bay and was quickly followed by three other collections, all in small quantity, at other places. A return visit to Whalebone Bay on March 16 disclosed an astonishing spread of the species throughout the bay. For the remainder of spring Codium intertextum was one of the most familiar algae at Bermuda. In June, a few days before the end of the first visit to Bermuda, I noted that it remained prevalent at Whalebone Bay, but that the colony from which the first collection was taken still showed marks of the scraping tool which had been used to remove the plants. Apparently, despite its rapid growth on other rocks, the species did not regenerate rapidly.

Notes made during the next trip to Bermuda, in August and September, show that the species had not appreciably changed in quantity at Whalebone Bay and was also plentiful in another locality, but that it was scanty or lacking at eleven other collecting sites. On the basis of all the records, summer must be considered the season of decline for Codium intertextum. The points may be made here that the behavior of a species is not precisely synchronous in all stations, and that inspection of only a few stations may provide very inconclusive results.

During November and December the species was found very often and in all degrees of plenty. At Whalebone Bay none could be found in November and only small isolated patches were found in December, while at several different places extensive confluent colonies were seen at the same period. Apparently, the species was recovering from its summer decline, and the spotty differences in quantity were the result of its potential for sudden growth. At Whalebone Bay, this ability to grow rapidly was seen the previous March, and another example was observed at Achilles Bay in January of

1951. On January 3 the species was scarce in the bay, whereas on January 24 it covered large areas of the shore rock and was as abundant here as at any other place in Bermuda.

From these records it seems clear that Codium intertextum started its cycle in autumn, and spread during autumn and winter, but showed wide disparity in development at different stations, presumably because of dissimilar local conditions. Ultimately, however, it became established as one of the most common algae of the spring flora at Bermuda. A period of decline set in during the summer, and recovery from this period in autumn brings the account back to its starting point. Reproductive material was found only once--in December.

Dictyopteris justii.--A much more orderly pattern than that of the foregoing is shown by Dictyopteris justii. During November the species was very hard to find, and the few plants seen were so small that they were barely recognizable. Through the winter and spring there was a steady increase in numbers and size, so that this species became one of the major elements of the algal vegetation of rocky shores where there is sufficient wave action. Late in the spring it was commonplace to find the plants covered by a delicate plush of one or more epiphytic Rhodophyceae, and the species became a frequent constituent of the "driftweed" which was cast ashore. However, there was no noticeable decrease in the standing crop until August. At this time the plants were the largest ever seen, but enormous numbers of individuals were being washed ashore and many stations were obviously depleted. Some stands of the species persisted into September, but in most places only a few battered fronds remained.

Most of the specimens thrown up by the sea were complete plants, even to the holdfast. It follows that the next season's growth must have arisen from spores, and not by regeneration from basal parts. In this

connection, it is of interest that the only fertile plants were found in November, and these were old and tattered relics of the summer flora. Collins and Hervey (1917) report fertile plants in August. Some species of algae are known to start a new season's growth from persisent portions of the old thallus (Svedelius 1906b, p. 191; Oltmanns 1923, p. 437) but for most species it has not been established whether regeneration or spores alone initiate the seasonal cycle. Consequently, it is difficult to distinguish annual from perennial algae. Dictyopteris justii, however, would appear to be truly an annual, whether we consider only its marked seasonal variation in size, or its lack of a perennial vegetative phase.

Jania pumila.--One of the most interesting of the seasonal phenomena was the synchronism existing between this species and its host. Jania pumila is a minute coralline red alga which I have found growing only on the brown alga, Zonaria zonalis. Because of its small size, Jania passed unnoticed until May, when it so abundantly covered some of the Zonaria plants that it attracted attention. Similar conspicuous infestations were seen in August and September on old specimens of the host. A re-examination of the collections of Zonaria which had been brought back to Ann Arbor disclosed that the epiphyte was present in twelve collections and absent from five. Although these specimens yield no record for Jania during December, January, and February, they do show that it was present in November, at the beginning of the host's growth cycle, and it was recorded every month after February. There seems little reason to doubt that the epiphyte was also present from December to February.

What is unique here is not that the epiphyte was found on only a single species, but that the host is an annual which disappears for part of the year. It would be very interesting to detect the means by which Zonaria and Jania pass over their unfavorable season and become associated

again at the beginning of the next cycle. An alternate host may be the explanation, but there is little evidence to favor this hypothesis. Børgesen (1913-20) found Jania pumila on both Zonaria and Turbinaria at the Danish West Indies, but Howe (1918), while noting that Jania has been reported on Turbinaria elsewhere only mentions Zonaria as the host in the Collins collections from Bermuda, and I was unable to find Jania on Turbinaria from Bermuda. Taylor (1928) reports the epiphyte on Dictyopteris justii at Florida, but again I was unable to confirm this alternate host at Bermuda. In any case, D. justii parallels Zonaria in its seasonality and both are absent at the same time, so Jania could not re-infect one from the other. Whatever the explanation, the adaptation of the epiphyte to its host is one of the more interesting problems associated with seasonal successions.

Sargassum bermudense.--No doubt the most commonly found alga in Bermuda and one which is usually the dominant alga of its habitat is this endemic species. Unlike Dictyopteris and Zonaria, the other large brown algae which compete with it and occasionally exceed it in prominence, Sargassum does not exhibit any seasonal fluctuation in quantity. On the contrary, at all seasons a plenitude of vigorous plants can be found, and conversely there are always some scraggly partially denuded individuals present. Apparently, there is a regular replacement through the year of aged plants by new growth. Fertile plants were seen almost every month and were undoubtedly responsible for some of the new growth, but there is also some regular replacement from persistent basal parts of the old plants. There is no wholesale sweeping away of one year's crop with establishement of the next year's crop dependent on the survival of a limited number of colonies or on perennating portions of the old plants, as is the case with Caulerpa racemosa.

Trichogloea herveyi.--This especially handsome fleshy red alga has a very brief growing season and one which is sharply delimited at both ends.

The first observation was made on March 16, at which time only 2 plants of Trichogloea were found on a stone, and no more could be found in spite of careful search. Twelve days later a larger stand was located in another bay, and this find was followed by other collections in rapid order, so that the species was considered as firmly established by the end of April. On April 27 a memorandum for future reference was made concerning a stand of 20 large plants growing a few meters away from the spot where the first 2 plants had been found.

Near the end of May, Trichogloea began to occur among the algae cast ashore, and its numbers rapidly dwindled from collecting sites. On June 10 a survey of the original station disclosed that only 2 plants remained of the earlier 20. The next visit to Bermuda was made in August, and at that time the species was completely absent from the flora.

Parenthetically, we may note that no periodicity was detected in the reproduction of Trichogloea herveyi. Only sexual plants are known, and they were found in most collections, including the first and last.

Seasonal Components of the Algal Flora of Bermuda

From the diagrams which show the annual variation of various species and from the examples of specific growth cycles, it is apparent that the species can be grouped according to their periodicity. To describe seasonal changes of abundance, it is convenient to distinguish between species which are obviously present at all seasons and those which are apparently absent for part of the year. The first group comprises the perennial forms; the second will be called annuals in accordance with the usual practice of phycologists. Some phycologists (Knight and Parke 1931,

p. 13; Fritsch 1945, p. 5) do not feel that the concepts of annuals and perennials as understood by terrestrial ecologists are completely applicable to the algae, but even these authors follow the common usage, commendably refraining from devising new terms in the present state of our knowledge. These groups, with subdivisions according to the seasons when particular annuals flourished, make it possible to present an analysis of the algal flora into its seasonal components.

Perennials

Chlorophyceae

Acetabularia crenulata
Avrainvillea nigricans
Caulerpa crassifolia
Caulerpa cupressoides
Caulerpa prolifera
Caulerpa racemosa
Caulerpa sertularioides
Caulerpa verticillata
Cladophoropsis membranacea
Codium pilgeri
Cymopolia barbata
Dichotomosiphon pusillus
Halimeda monile
Halimeda tridens
Halimeda tuna
Neomeris annulata
Penicillus capitatus
Penicillus pyriformis
Rhizoclonium hookeri
Udotea flabellum

Phaeophyceae

Dictyota dentata
Padina vickersiae
Sargassum bermudense

Rhodophyceae

Amphiroa fragilissima
Bostrychia binderi
Bostrychia montagnei
Bostrychia tenella
Catenella repens
Eucheuma isiforme
Galaxaura obtusata
Galaxaura squalida
Gelidium pusillum
Halymenia pseudofloresia
Polysiphonia howei
Wurdemannia miniata

Seasonal changes among perennials.--Although the perennials are present through the year, it should be emphasized that some of them exhibit periodic growth. Among these, Caulerpa racemosa, Amphiroa fragilissima, and Galaxaura squalida have a maximum in spring, and their volume is considerably less in the other seasons. Another group, comprising Caulerpa crassifolia, C. sertularioides, Cymopolia barbata, Halimeda monile, H. tridens, Penicillus capitatus, P. pyriformis, and Padina vickersiae, becomes more

prominent in both spring and summer than in autumn and winter. Among the species of Caulerpa which alternate periods of slow growth with periods of rapid growth, it is possible to see evidence of this periodicity even in individual specimens. In Caulerpa crassifolia and C. sertularioides the periodic growth may be revealed by the appearance of the assimilatory branches, whose upper parts often look fresh and new in comparison to the basal parts. In Caulerpa racemosa the whole assimilatory branch may be obviously younger than the prostrate runner from which it arises.

I have not been able to detect any seasonal variation in quantity of Udotea flabellum, but occasional plants of this species also show thin, greener zones, apparently new growth, in the upper parts of the blade. The few plants seen with this character were collected in April, but since most of the plants collected at the same time did not show any such distinction between upper and lower portions of the frond, it does not seem possible to designate spring as a season of new growth for Udotea. Furthermore, the growth rate of this species should be studied to determine whether the greener zones represent the growth of a few days or a few months, or, indeed, whether they represent new growth at all. The pressing need for more knowledge of growth rates of this and other species is illustrated by the recent findings of Knight and Parke (1950, p. 450) in species of Fucus. Inspection of some plants suggested that there might be periods during the first year of growth in which extension of the frond was slower. Serial records of growth through the periods in question did not bear out the hypothesis, however. Instead, the authors conclude that the impression of new growth was caused by a wearing away of reproductive organs, with consequent exposure of previously hidden vegetative parts. These were very conspicuous because they were lighter in color than the reproductive organs, but there was no evidence that they represented

accelerated growth. The case of Fucus, with its differentiation between reproductive organs and vegetative parts, is quite unlike that in Udotea, for reproduction is unknown in Udotea. In the absence of growth studies, we can only surmise that the greener parts of Udotea are areas of new growth.

Preponderance of perennials in the littoral belt.--I have mentioned earlier that the intertidal associations showed little change through the year, and the reason for this uniformity is apparent from the list of perennials. That is, most of the species which are never found below low tide level are perennials, for example, Dichotomosiphon, Cladophoropsis, Rhizoclonium hookeri, the species of Bostrychia, Catenella, Gelidium, and Polysiphonia howei. A notable exception is Monostroma oxycoccum, which has a well defined seasonality, but the other apparent exceptions, such as Colpomenia and Codium intertextum, grow at levels where they are exposed only briefly by low tides, or where part of the colony extends below low tide level.

The factors involved in this preponderance of perennials in the littoral are not definitely known. For the British flora, Rees (1940, p. 435) is of the opinion that species which are present through the year are at an advantage in the intertidal region because they can maintain their own dominance by copious propagation at the same time that their bulky overlapping thalli prevent the seeding of the shore by annuals. At Bermuda, however, the intertidal forms are small and do not completely cover the shore; consequently, it is not competition for space which excludes the annuals. Several authors have made assertions which point to the possibility that growth in the intertidal region is too slow for the development of annuals. Thus, Baker (1909, p. 202) and Stephenson (1943, p. 228), among others, have stated that the availability of nutrients decreases at

higher levels. Chapman (1943, p. 247) claims that assimilation and respiration take place during submergence and the algae with long periods of emersion would consequently grow slowly. On the other hand, Børgesen (1908, p. 827) found that most of the short-lived species of the Faeröes grow in the littoral belt, and he supposes that "only algae growing in full daylight are able to go through all stages of development in so short a time". Actual measurements of photosynthesis and respiration by Stocker and Holdheide (1937) and by Kaltwasser (1938) show that the effect of desiccation on these functions is not easily evaluated. Both photosynthesis and respiration are reduced during desiccation, but neither is completely suppressed. The net effect on the growth rate remains to be determined. Indeed, the very premise that annuals have a higher growth rate than perennials is questionable, for Northcraft (1948, p. 397) finds it necessary to distinguish between perennials of rapid growth and perennials of slow growth in his survey of algal recolonization on denuded intertidal surfaces. The scarcity of annuals in the littoral region is, in short, simply another problem awaiting investigation.

Annuals

Even though some of the perennials display noticeable variation in numbers with the seasons, it is the algae whose gross thalli are present only for part of the year that are mainly responsible for the striking changes of the flora at different seasons. The life term of some of these species may be more than 9 months, or it may be as short as 3 months. To group all relatively short-lived algae together as "annuals" would ignore their seasonality; to group them in accordance with the seasons at which they are present would give equal weight to juveniles, to relics, and to full-grown, typical plants. Rather, it would seem that a better perspective can be obtained by listing these algae according to the seasons when they flourish.

Algae of the winter and spring.--Many species of this, the largest, category make their first appearance in late autumn, but not until sometime in the winter are any of them characteristic members of the flora. Their quantity continues unabated into the spring and most of them reach their peak at this season. Only rarely are they found in the summer, and never in large quantity. Most of these "early annuals" have a growing period of 6 or 7 months, and a few are present for 9 months.

Chlorophyceae

Batophora oerstedi
Bryopsis hypnoides
Cladophora catenifera
Enteromorpha clathrata
Enteromorpha lingulata
Enteromorpha plumosa
Monostroma oxycoccum
Ulva lactuca
Vaucheria bermudensis*
Vaucheria piloboloides

Phaeophyceae

Aegira zosterae
Colpomenia sinuosa
Dictyota bartayresii
Dictyota cervicornis
Dictyota ciliata
Ectocarpus duchassaingianus
Ectocarpus mitchellae
Hydroclathrus clathratus
Padina pavonia

Rhodophyceae

Antithamnion cruciatum
Asparagopsis taxiformis
Botryocladia occidentalis
Botryocladia pyriformis
Callithamnion byssoideum
Ceramium byssoideum
Coelothrix irregularis
Cottoniella arcuata
Dasya collinsiana
Erythrotrichia carnea
Falkenbergia hillebrandi
Halymenia bermudensis
Herposiphonia secunda
Herposiphonia tenella
Heterosiphonia gibbesii
Heterosiphonia wurdemanni
Jania rubens
Laurencia microcladia
Laurencia poitei
Liagora ceranoides
Liagora farinosa
Liagora mucosa
Liagora valida
Polysiphonia opaca
Polysiphonia variegata
Polysiphonia ferulacea
Pterocladia capillacea
Spyridia complanata
Wrangelia penicillata

Spring algae.--The few species comprising this group are among the most short-lived of Bermuda algae, for they complete a generation in a period of only 2 to 4 months, between March and June. Unlike the algae of other

*Recent work suggests that the affinities of Vaucheria are with the Xanthophyceae (Smith 1950, p. 402).

seasonal categories, they do not undergo a period of slow growth in winter or a period of protracted decline in summer, but are neatly restricted to their single season, spring.

Phaeophyceae

Sporochnus bolleanus

Rhodophyceae

Acrosymphyton caribaeum
Dudresnaya crassa
Helminthocladia calvadosii
Nemastoma gelatinosum
Trichogloea herveyi

The foregoing brief list of spring algae demonstrates strikingly the need and advantages of studying a flora at all seasons. With the exception of Dudresnaya crassa, these species are the only members of their respective genera which have been reported from Bermuda. Since the congener of Dudresnaya crassa, D. bermudensis, was not found during the present survey, all the species comprising this list represent genera which would have been unrecorded if collections had not been made in the spring. Furthermore, the brown alga is the sole example of the order Sporochnales at Bermuda. Another remarkable feature of the spring algae is the fact that three of the six species have never been reported outside of Bermuda. The three endemics are Dudresnaya crassa, Nemastoma gelatinosum, and Trichogloea herveyi. Under the circumstances, it is not surprising that our knowledge of most of these species has heretofore been very incomplete. However, the collections made during the spring of 1949 have made it possible to clarify several aspects of the taxonomy and morphology of three members of the group--Acrosymphyton caribaeum, Dudresnaya crassa, and Trichogloea herveyi (Taylor 1950, 1951, 1952).

Algae of the spring and summer.--A goodly number of species are present at Bermuda through the greater part of the year but make their principal display in spring and summer. Although some of them begin their growth in autumn, the majority appear in winter. They grow slowly in winter, but

during spring they quickly come to the front. In the summer months new plants of these species are not found. Instead, the typical plants are large and often infested with epiphytes. As the end of summer draws near, the members of this group become more and more uncommon in their familiar habitats. Meanwhile, those among them which ordinarily grow under conditions of wave action contribute enormously to the drift vegetation which litters the beaches after each tide. In autumn only an occasional trace remains, giving no indication of the luxuriance of the earlier growth.

Chlorophyceae

Anadyomene stellata
Bryopsis plumosa
Cladophora fuliginosa
Codium decorticatum
Codium intertextum
Codium isthmocladum
Dasycladus clavaeformis
Ulva fasciata
Valonia macrophysa

Phaeophyceae

Dictyopteris delicatula
Dictyopteris justii
Dictyopteris plagiogramma
Dictyota dichotoma
Dictyota divaricata
Dictyota linearis
Pocockiella variegata
Spatoglossum schroederi
Zonaria zonalis

Rhodophyceae

Centroceras clavulatum
Crouania attenuata
Crouania pleonospora
Jania pumila
Laurencia corallopsis
Laurencia gemmifera
Laurencia obtusa
Lophocladia trichoclados
Polysiphonia havanensis
Seirospora purpurea
Spyridia filamentosa

Algae of the summer and autumn.--Only two species seem to find the summer and autumn especially favorable for growth, and a third species may be added to this category with some reservation. The first two, Dictyota indica and Padina sanctae-crucis, both Phaeophyceae, were most often found in summer, but carried over well into the winter. The third, Acanthophora spicifera, arose very rapidly in May and achieved considerable prominence even before spring was over. Unlike the other algae of that season, it showed very little sign of diminishing in the summer and was still plentiful

in November, with a few specimens persisting until February. Acanthophora should perhaps be considered an alga of the spring, summer, and fall, and is included here only because of its late arrival in the spring and its tolerance of the seasons which seem unfavorable to most other algae.

Winter algae.--By excluding the algae which are present in the winter and are also strongly developed throughout the spring, we are left with only three species which may be considered truly winter algae. Two of these three, Scytosiphon lomentaria and Sphacelaria tribuloides, are Phaeophyceae, and the third, Callithamnion corymbosum, is a red alga. The single season of these algae is not so cleanly delimited as was the case with the spring algae, but the overlap into adjacent periods is not sufficient to warrant placing the winter algae in one of the other groups.

Recapitulation.--A summary of the seasonal categories of annuals, using only the total number of species in each group, has been tabulated in Table 2. The general trend of seasonal fluctuations shown by these totals was

TABLE 2

NUMBER OF SPECIES OF ANNUAL ALGAE WHICH FLOURISH AT EACH SEASON

	Autumn	Winter	Spring	Summer
Chlorophyceae		10	19	9
Phaeophyceae	2	9	19	11
Rhodophyceae	1	32	45	12
Totals	3	51	83	32

essentially the same in each class of algae as for the whole flora. The low point occurred in the autumn, when, although many species were present, only three species seemed to be at or near their best condition. The great increase in winter was due not only to new arrivals but also to an increase in frequency and size of many algae which were scarce and poorly developed

earlier. A further increase led to the spring maximum, which included practically all the winter species in addition to a number which were also prominent in the summer. At the end of spring, this last component of the spring flora formed almost all the summer flora.

Monthly Records of Algae at Bermuda

A list of all the algae observed during this survey and the months when each was found is provided in the appendix (Table 6). This list represents the "raw data" of the survey and, as such, requires some interpretation. It does not, for instance, distinguish between the months when a species was rarely found and the months when it was widespread. Furthermore, at the beginning and end of each trip to Bermuda less than a full month of observations was possible. Consequently, the records for the incomplete months (February, June, August, and September) are not strictly comparable with the records for other months.

Algae of sporadic occurrence.--It will be noted that Table 6 contains many species which have not been listed among the perennials or the several groups of annuals. These species were found only sporadically and the data are insufficient to permit placing them in any of the seasonal categories. Knight and Parke (1931, p. 25) consider algae which are found sporadically on the Isle of Man to be invaders from other regions and call them "casual annuals", but it is doubtful whether the Bermuda sporadics are invaders and there is no certainty that they are all annuals, "casual" or otherwise. More probably, they are native but of limited distribution within Bermuda, and observations over several years would determine whether they exhibit seasonal fluctuations. Meanwhile, it seemed advisable to include the records of the months when the sporadics were found during this survey.

Comparison of monthly totals with seasonal totals.--The total number of species seen each month is shown in Table 3. These totals provide an interesting supplement to the totals of the annuals which flourish at each season (Table 2).

TABLE 3

NUMBER OF SPECIES OF ALGAE SEEN EACH MONTH AT BERMUDA

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
Chlorophyceae		44	43	54	50	54	55	53	37		36	32
Phaeophyceae		24	26	29	27	31	30	28	22		18	13
Rhodophyceae		62	61	72	66	79	79	83	44		42	37
Totals		130	130	155	143	164	164	163	103		96	82

The outstanding difference between the two tables is the disparity in totals. The lower figures of Table 2 are caused by the omission of the following three groups: (1) perennials; (2) "out of season" algae, that is, new growth and relics; and (3) algae of sporadic occurrence. Inclusion of these groups in Table 3 shows very clearly that a large variety of algae may be found at Bermuda in all seasons. Even during autumn, when the volume of vegetation was lowest, the number of species present was high. The fact that November and December were populated by a multitude of young plants is the reason that the fall season has been taken as the beginning of the seasonal cycle throughout the descriptions in the preceding pages.

Together, Tables 2 and 3 show that the height of the flora was reached in spring, both in the number of species that were especially favored by this season (Table 2) and in the total number of species found in these months (Table 3).

The deterioration of the flora in summer is reflected by the abrupt decrease in number of species seen during June, August, and September.

However, it is probable that some relics of the spring flora would have been found if time had permitted inspection of all stations in each month of the summer.

Proportions of Annuals and Perennials

Ratio of annuals to perennials at Bermuda.--The perennial Bermuda algae which were listed above comprise 35 species, and the several lists of annuals include 89 species. In addition, among the algae of sporadic occurrence there are several species which appear to be annuals. For example, the species of Enteromorpha, Ectocarpus, and Callithamnion were not found during the summer months, and it therefore seems reasonable to consider all the species of these genera annuals, even though the records for some of them were inadequate to reveal definitely which seasons were most favorable. In other cases (Rosenvingea intricata, Dasya pedicellata, etc.) the discovery of a conspicuous alga in an area where it had not been seen earlier suggested that the alga was an annual, but its rarity precluded precise determination of its season. These presumptive annuals have been added to the annuals of known seasonality, and the totals are compared with the total perennials in Table 4.

TABLE 4

NUMBERS OF ANNUALS AND PERENNIALS BY CLASS

Class	Annuals	Perennials
Chlorophyceae	27	20
Phaeophyceae	24	3
Rhodophyceae	65	12
Totals	116	35

The ratio of annuals to perennials is approximately 3.3:1. The extremely high proportion of annuals among the Phaeophyceae is especially

significant from the viewpoint of aspection. On the average, plants of this class are comparatively large, and their seasonal waxing and waning can affect the volume of vegetation enormously, whereas if they were mainly perennials the bulk of the vegetation would show little seasonal fluctuation.

Ratio of annuals to perennials outside Bermuda.--With the exception of Hoyt (1920), there seems to be no report of the proportions of annuals in floras outside Bermuda. However, a few authors have furnished lists containing remarks on the seasonality of most of the species, and from these lists some very tentative ratios may be estimated (Table 5). In

TABLE 5

RATIO OF ANNUALS TO PERENNIALS IN VARIOUS REGIONS OF THE WORLD

Region	Reference	Annuals: Perennials	Temperature Range, °C
Nova Scotia	MacFarlane and Bell 1933	1.4:1	-1 - 14
Firth of Forth	Traill 1885	1.6:1	5 - 14
Orkney Islands	Traill 1891	1.7:1	6 - 13
Berwick (England)	Batters 1890	1.9:1	5 - 13
Isle of Man	Knight and Parke 1931	2.6:1	7 - 15
Venetian Lagoons:	Schiffner and Vatova 1938		5 - 26
Porti-Canali		1.6:1	
Citta		2.3:1	
Media e Bassa		3.5:1	
Alta		3.7:1	
Isole Veneta		3.9:1	
Rovigno (Italy)	Vatova 1948	3.3:1	9 - 24
Beaufort, N.C.	Hoyt 1920	6.0:1	10 - 25
Bermuda	Present Study	3.3:1	15 - 30

order to place all the ratios on as nearly an equal basis as possible,

species of Myxophyceae and the coralline red algae have not been included, since these groups are treated with varying degrees of thoroughness in the several lists. The Bermuda ratio has also been calculated without these two groups. The temperature ranges for Nova Scotia and the British Isles have been taken from Deutsche Seewarte (1902) and Mohn (1870); the other ranges were furnished by the respective authors. It must be emphasized that the ratios are merely a first approximation, but there is sufficient agreement among the figures for the British Isles and for the Gulf of Venice to suggest that the orders of magnitude are fairly reliable. The inequalities among the Venetian lagoons are perplexing. The lists given by the authors (Schiffner and Vatova 1938) show that a given species may grow at different seasons or even be perennial in different portions of the lagoon system. Apparently, local conditions strongly modify the general climatic responses. Nevertheless, there is considerable similarity between ratios calculated for the Venetian lagoons and that for Rovigno, which is also in the Gulf of Venice.

From the few examples given in the table, it appears that temperate floras contain more annuals than perennials--an observation which, so far as I know, has not been made previously. Furthermore, although the data are by no means conclusive, there seems to be a higher proportion of annuals in warmer waters than in cold waters. Bermuda, with sea temperatures ranging from 15 to 30°C, is the warmest area under consideration and it also has a relatively high proportion of annuals. The especially high ratio reported for Beaufort requires interpretation because of the peculiar conditions in that area. Parr (1933, p. 88) has shown that temperature barriers shifting between Cape Cod and Cape Hatteras place Beaufort in open temperature continuity with New England waters in the winter but with southern waters in the summer. Consequently, it is not surprising that Beaufort supports two

floras--a winter flora of northern affinities and a summer flora of southern affinities (Hoyt 1920; Williams 1949)--and the seasonal alternation of these two floras is reflected in the high ratio of annuals to perennials.

It would be interesting to know whether the excess of annuals over perennials increases with warmer waters even into the tropics. Setchell (1915, p. 300), without indicating his sources, says that seasonal changes in the flora are most pronounced in the temperate zone and are least in the tropic zone. If this be true, it may be expected that the ratio of annuals to perennials would be relatively small in tropical regions. The relatively high proportion of annuals in Bermuda does not support this contention, for, although the Bermuda vegetation would be considered warm-temperate by Stephenson (1948, p. 215) on the basis of temperatures, floristically it is tropical. Our only other information from the tropics comes from Svedelius (1906b, p. 218), who states that the greater part of Ceylon vegetation is composed of perennials. This lends some support to Setchell's assertion, but more evidence is needed before generalizations can be made safely.

When appropriate data become available from the several geographical zones, the ratio of annuals to perennials, as a rough index of the extent of seasonal changes, may facilitate correlations with climatic phenomena. It is quite possible that the correlation with temperature seen in Table 5 applies only to the temperate zone, and that in other zones, where temperatures are less variable through the year, light or some other factor may be more important.

Seasonal Changes of the Climate

Data provided by W. A. Macky, Bermuda Meteorologist, on rainfall, sunlight, and sea temperature at Bermuda are summarized in the graphs of

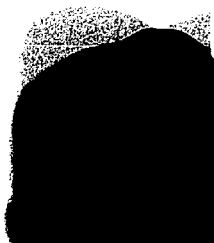


Plate XV. Each graph shows the conditions during the months included within this study, as well as the mean monthly values derived from the longest records available.

Rainfall

The rainfall during the period covered by this study deviated markedly from the averages expected on the basis of previous records (Plate XV, Figure a). In 1949, the amount of rain was less in January than in any previous January except that of 1907 and that of 1937, and the rainfall in May was higher than any since 1904 (Macky 1950, p. 94). In 1951, the January rainfall was again extraordinary, and was the greatest since January, 1910 (Macky 1952, p. 116).

The effect of rainfall in an aquatic environment has been variously interpreted. According to Transeau (1916, p. 131), heavy rains increase the salt concentration of fresh waters, and Newcombe and Brust (1940, p. 87) found that rainfall had a significant and immediate effect on the phosphorus content of river waters near an estuary. The latter authors and Riley (1937) present data showing tht rivers contribute measurably to the nutrients of inshore oceanic waters, but no direct correlation has been pointed out between rainfall and the phosphorus or nitrogen content of the inshore waters. In sum, the evidence suggests that the run-off, which is increased by rain, carries nutrients from the land toward the ocean.

At Bermuda, drainage from the land enters the ocean directly or by percolation through the limestone, without the intervention of streams or rivers. If this drainage enriches the inshore waters, the extreme rainfall of May, 1949, may possibly be interpreted as having been of immediate benefit to the maximal vegetation of that period. However, since there are no data to indicate whether drainage has any effect on the nutrient content

of the Bermuda waters, the correlation between extreme rainfall and rich vegetation must be considered of dubious significance.

Furthermore, no correlations are evident between the unusually low and high rainfalls of January, 1949, and January, 1951, and the conditions of the vegetation soon after. That is, although the precipitation was much greater in January, 1951, than in January, 1949, the flora was not noticeably richer in February, 1951, than in February, 1949.

An inimical effect has been attributed to rainfall by Lami and Priou (1949, p. 48) and Williams (1949, p. 6), who report mortality of certain species due to heavy rains. Presumably, this will affect only species growing near or above low tide level and is due to intolerance of fresh water. Generalizations concerning this harmful effect are not safe, for Brown (1917) has shown experimentally that there is a wide variation of tolerance to fresh water among different species of marine algae.

Two Bermuda species were especially vulnerable to effects of rain. Colpomenia sinuosa and Caulerpa racemosa were among the most abundant species growing about low tide level during the frequent rains of May. Both species diminished in June. There was, however, no suggestion of catastrophic mortality during their decline, and many colonies in places shielded from the rain dwindled away during the same period. Other species also showed no signs of harm from the rain. At best, any unfavorable influence of the rain must be considered local and temporary, rather than a seasonal effect.

Sea Temperatures

The temperatures which are shown graphically in Plate XV, Figure b, were measured at St. Georges Island and at Hamilton Island, and are not necessarily typical of the open ocean around Bermuda. The mean sea temperatures are based on records compiled during only six years (U.S. Department

of Commerce, 1951), but more extended observations are not available. The means obtained through the term of this study did not deviate from the six-year means by more than one degree, and therefore have been omitted from the graph. The monthly maximum and minimum readings for the present period have been plotted to indicate the range of temperatures.

It has been asserted frequently that temperatures are important in determining the seasonal ranges of algae (Setchell 1915, 1920; Hoyt 1920; Grubb 1924, 1936; Isaac 1938), but the claims seem to have been unsupported by evidence. Kylin (1917) has reported on the sensitivity of some species to low temperatures, and Biebl (1939) demonstrated that the upper limits of certain algae may be very sharp, but whether it is temperature or some other seasonal factor which is limiting under natural conditions has not been adequately determined.

Inspection of the graph of Bermuda sea temperatures discloses very little concerning the role of temperature in controlling seasonal fluctuations of the algae. The period of rapid growth of algae between March and May took place within a range of about 16.8 to 25°C, but, on the other hand, most of the same species were present but poorly developed and slowly growing between November and January, within a similar temperature range. This does not suggest a causative relation between temperature and the spring flourishing, unless we attribute some effect to the fact that the gradient of heat is upward in one season and downward in the other--and such a surmise would be premature at this time.

The lack of agreement between the low point on the graph and the state of the vegetation at that period is very interesting. The coldest months were January, February, and March, yet most of the algae began their new growth before this period and seemed unaffected by the low temperatures, in spite of the fact that a considerable number of the species

involved have Caribbean affinities (Siphonales, Dictyotales, diverse Rhodophyceae) and Bermuda represents their northernmost limit of range. In other words, although the Bermuda flora is largely a warm-water flora, it does not undergo a period of generalized decline during the coldest months.

It is also interesting that the highest temperatures are associated with a vegetation which was greatly reduced in vigor and bulk. The warmest months were July, August, and September, at which time many species were absent and most of those which remained were far below their earlier abundance, with the individual plants showing signs of senescence. As has just been pointed out, we are concerned with an essentially warm-water flora at its northern limit, and it was somewhat unexpected that the deterioration should occur in the warmest season.

Quite possibly, simple correlations such as the foregoing between temperature and the state of the vegetation are the main basis for claims that temperature has an important influence on the seasonal cycle of growth, but such "evidence" is very inconclusive. A special reason for reserving opinion is the difficulty of dissociating temperature from insolation, since these two climatic factors tend to vary in the same direction about the same time. Consequently, correlations between temperature and the vegetation are likely to be similar to those between insolation and the vegetation.

Insolation

The total hours of sunlight recorded by meteorological instruments during each month of this investigation are shown in Plate XV, Figure c, together with the mean monthly totals. The means were taken from unpublished data of the Bermuda Meteorological Office and cover a twenty-year period.

The noon altitudes of the sun about the twenty-first of each month were calculated from tables in the American Ephemeris and Nautical Almanac (U.S. Nautical Almanac Office, 1946), and are presented diagrammatically (Plate XV, Figure d).

Svedelius (1906b, p. 218), Setchell (1915, p. 300), and others have postulated that seasonal changes of the vegetation are largely dependent on light relationships in certain geographical zones, but the evidence bearing on the role of light is scarcely better than the evidence for the role of temperature. This is a not unnatural consequence of the concurrent rise and fall of these variables. However, in at least two investigations it was found possible to correlate a change in vegetation with a change in sunlight while no corresponding change in the temperature occurred. Thus, Atkins and Harris (1924, p. 20) were able to detect a seasonal increase of phytoplankton in a fresh-water pond at the time of the vernal increase of sunlight, while the temperature during this period remained low, and even fell at some times. Knight and Parke (1931, p. 29) report effectively similar observations for marine algae. These authors conclude that temperature is subordinate to insolation as a controlling factor, at least at some phases of the growth cycle.

We may now examine the situation as it existed at Bermuda. If we refer to the altitude of the sun and duration of sunlight, it can be seen that during the summer not only was the altitude of the sun greatest, but also the intense sunlight resulting from this high elevation was little mitigated by cloud cover, for the total hours of sunlight were greatest in the summer months. It has already been pointed out that the decline of the flora occurred at a time of maximum temperatures, and it is now to be emphasized that the same period was distinguished also by maximum insolation. Therefore, it does not seem feasible to postulate special

significance for either of these factors with respect to the end of the growth cycle.

On the other hand, it becomes possible to separate insolation from temperature if we consider the different conditions of autumn and spring. I have remarked that the temperatures of autumn and spring were approximately the same while identical species were poorly developed in the one season but grew rapidly to a maximum in the other. However, the light conditions were by no means equivalent at these seasons. The number of hours of sunlight were approximately equal for each season, but the intensity of sunlight, as shown by the altitude of the sun, was considerably higher in the spring. Accordingly, without insisting on any cause and effect relationship, it may be said that the difference between the vegetation of autumn and that of spring is associated with a difference in light and not with any difference in temperature.

REPRODUCTION

Previous Studies

In the introductory chapter it was pointed out that our knowledge of aspection in all parts of the world is very scanty, and it may now be mentioned that such information as we have is largely concerned with vegetative phases of the topic; data concerning reproduction are even more meager. A few workers have furnished tables or lists, or have suggested the general trend of reproduction in their areas, but most of the records of fruiting periods are in taxonomic works, and here the emphasis is on individual species with little or no attempt to uncover trends of the vegetation as a whole. Nevertheless, some valuable information can be gleaned from these works, especially when the authors have had access to material from all seasons.

Europe

The subject has attracted more interest in the British Isles than in any other region. Tables showing the times of reproduction have been provided by Turner (1800), Knight and Parke (1931), and E. Lewis (1936). In addition, the taxonomic lists of Traill (1885, 1891) and Batters (1890) indicate the seasons when many species were found in fruit.

Elsewhere in Europe no such concentration of work has been published. Data for some of the species of the Faeröes, Denmark, and Sweden are to be found in the taxonomic works of Børgesen (1903), Rosenvinge (1909-1931), and Kylin (1944, 1947), respectively. Several pages and a long table are devoted to a discussion of the problem in the Gulf of Naples by Funk (1927), although he limits the convenience of his table by listing many of the

plants only by genus. The marine vegetation in the vicinity of Albères, on the Mediterranean coast of France, has been very extensively treated by Feldmann (1937), and his ecological observations include the fruiting periods, which he summarizes in a table but which he discusses only briefly. A surprising volume of work has been published in Italian concerning the algae of the Gulf of Venice (Schiffner and Vatova 1938; Vatova 1940, 1948), and the extensive use of tables and lists to minimize the text does much to overcome the difficulty imposed by the language.

North America

Apart from the European reports, we have records only from North America, and these are very few indeed. The largest body of data is contained in Taylor's (1937) marine algal flora of the northeastern coast. For the Pacific Coast there is only Hurd's (1917) discussion of the fruiting condition of some species found at Puget Sound during the winter. Of the several catalogues dealing with the warm Atlantic floras, only two include information on our subject, and these are fragmentary. One of these, Børgesen (1913-20), often mentions when a species was found in fruit at the Danish West Indies (now the Virgin Islands), but the collections include only the months from December to April. Furthermore, Børgesen does not say whether he examined all his material for reproductive structures or if he merely noticed them on particular specimens which he happened to be studying for morphological purposes. The other work is that of Collins and Hervey (1917) on Bermuda algae. These authors made collections over a period of six or seven years and arranged their visits to include every month except June, but they too fail to declare whether their occasional comments on the months when certain species were fruiting are based on deliberate search or on incidental observations. They give no records at all of the fruiting times of the majority of the species.

Reproduction in the Bermuda Algal Flora

Monthly Data

During the present study, the collections of 151 species of algae were examined for reproductive structures. Notes were made of the type of reproductive organ found each month, and where no evidence of reproductive activity was found, this fact was also recorded. The results are shown in Table 7, in the appendix.

There are limitations associated with a brief tabulation which should be kept in mind when analyses or inferences are being made from the table, and especially when comparisons are being made with other tables, which are probably subject to the same or other limitations. One limitation is the absence of any indication of relative frequency of fertile as against sterile plants in any month. The list merely shows whether fruiting material of a species was found in a particular month and does not suggest whether all, most, or few of the collections of that species during the month were fertile. This drawback will be corrected somewhat by a discussion of fruiting trends in the next pages, but for the most part the danger of postulating too much from observations of only one cycle of seasons argues against making an already complicated table more complicated by the addition of dubious quantitative estimates. Another point to be remembered in the use of this and other tables is that certain species are only identifiable from fruiting material and so are listed as if they were always fruiting. Actually, it is probable that some of the species of Ectocarpus, Derbesia, and Vaucheria were present in the vegetative condition only at times, but they could not be shown on the table because specific identification was impossible or questionable. Further limitation occurs in the difficulty of detecting reproduction stages in many algae. The

Chlorophyceae in particular include many genera which produce either gametes or zoospores in cells which are little or not at all different visibly from vegetative cells. Under these conditions there is little profit for much labor expended in searching for signs of fertility, and the resultant poverty of data is probably more an indication that the reproductive stages were not detected than a trustworthy sign that fruiting was uncommon. Consequently, attempts to determine the fruiting condition of many Chlorophyceae were given up and the species not listed in the table. It follows that any percentages or other calculations which may be attempted from the tables must take cognizance of only the species which are shown to have been checked for reproduction, and not of all species collected during this survey.

A recapitulation, showing (a) number of species examined each month, (b) number of species found in reproductive condition each month, and (c) the proportion (b/a) of examined species which were fruiting, is provided at the end of the table. In a general way, the recapitulation agrees with expectations based on the vegetative cycle, and it suggests some tentative patterns of reproduction for the whole flora. For example, since the number of species examined varies with the number of species seen each month (cfr. Table 3), the rise and fall of the vegetation are reflected in the first set of totals of the recapitulation. The number of species found in fruit each month also follows the general pattern of the vegetative cycle. This is not surprising, for it seems reasonable to expect more species in fruit during the maximum period of the vegetation, since at that period more species were available for examination. However, it was felt necessary to verify the presumption, especially in view of the rather common belief that fruiting occurs at the close of the life cycle. Such a premise suggests that early in the growing season and during the period of

maximum vegetation, there may be fewer species in fruit than at the end of the growing season, but the figures show that this is not markedly so. Rather, we find that there is a correlation between the number of species examined and the number of species found to be undergoing reproduction. How close this correlation is can be seen in the percentage of species found in fruit each month. In almost every month reproductive structures were found among collections of approximately 50 per cent of the species examined. A notable exception is September, when only 39 per cent of the species were found in fruit. Since September was a month when the vegetation was at a low point and the individual plants showed signs of senescence, it is very tempting to offer theories concerning the relation of the vigor of the population to its reproductive potential, but more rigorous statistical treatment is necessary before we can assess the significance of the low percentage of September.

The main value of these preliminary calculations lies in that they suggest definite problems to be attacked by statistical methods in the future, either at Bermuda or elsewhere: (1) Is it true that, whether or not the fruiting population is composed of different species from month to month, it forms approximately the same proportion of the total population from month to month? (2) What is this proportion? (3) As the total population declines at the end of the season, is its reproductive potential less than the average? To answer these questions the reproductive capacity of each species will have to be calculated from examination of many plants each month, and the figures so derived must replace the bare "presence or absence" designations used in the present survey.

An attempt was made to abstract from Table 7 lists of the species according to the seasons when they fruit, but it was found that the number of lists necessary was so high that such an analysis did little to simplify

the data. Furthermore, it was felt that reproduction should be considered in connection with the life history of the species, and not as an independent phenomenon. From this point of view, it is possible to classify algae according to the place of reproduction in the growth cycle, and to examine several concepts which have been proposed by other investigators.

The Place of Reproduction in the Growth Cycle

In the lists which follow, the symbols used to designate the kind of reproductive structure will be the same as those used in Table 7, namely, G for gametangia and cystocarps, ⊕ for tetrasporangia, P for purilocular sporangia, and U for unilocular sporangia.

Perennials exhibiting fructification through the year.--Of the 35 or more algae which grow at all seasons in Bermuda, 8 of the more common species were found with reproductive bodies in almost every month and without noticeable concentration of reproductive activity to any part of the year. With one exception (Cymopolia) these species are generally distributed throughout the islands, and each is a prominent or even dominant member of its community.

Chlorophyceae

Acetabularia crenulata (G)
Cymopolia barbata (G)
Neomeris annulata (G)

Phaeophyceae

Padina vickersiae ⊕
Sargassum bermudense (G)

Rhodophyceae

Bostrychia binderi ⊕
Bostrychia tenella ⊕
Galaxaura squalida ⊕

Perennials not exhibiting fructification at any time.--The members of this category were not found in fruiting condition at Bermuda, although there was an abundance of material. Most of the species involved are less common than those of the preceding list, yet they are by no means rare algae.

Although it seems reasonable to infer that the abundance and wide distribution of the species in the first group is related to the frequency of reproduction, it must be admitted that there are other factors to be considered, since the species which were never found in fruit are also fairly common.

Chlorophyceae

Caulerpa crassifolia
Caulerpa prolifera
Caulerpa sertularioides
Halimeda monile
Halimeda tridens
Halimeda tuna

Rhodophyceae

Catenella repens
Digenea simplex
Eucheuma isiforme
Galaxaura obtusata
Gelidium pusillum

It is not certain whether Digenea is a perennial or an annual, but the bulk of evidence suggests it belongs in this list.

I have not included here any genera whose reproductive processes are completely unknown and which therefore may be escaping detection because of our lack of knowledge. It is true, however, that only one or two species of Caulerpa have ever been found in fruit and these only rarely. Consequently, it is not surprising that the Bermuda material of this genus was all sterile. Similarly, fertile material of Halimeda is so rare that Howe (1907) considered it advisable to place on record the discovery of some fruiting plants of Halimeda tuna in Bermuda during the month of June. Annuals fruiting throughout their growing season.--A considerable number of species which were macroscopically present only during a part of the year were found to fertile in every month of their season. This does not mean necessarily that every individual was fertile, although a few species approached such a condition, but it means that each species as a whole had some individuals in fruit every month. Apparently, the time lag between germination and reproductive maturity is very short in these species, since

even the specimens found in the first months of their respective seasons were fertile.

Chlorophyceae

Codium decorticatum (G)
Codium isthmocladum (G)
Batophora oerstedi (G)

Phaeophyceae

Aegira zosterae (U,P)
Colpomenia sinuosa (P)
Ectocarpus duchassaingianus (P)
Padina pavonia ⊖
Pocockiella variegata ⊖
Scytosiphon lomentaria (P)
Spatoglossum schroederi ⊖

Rhodophyceae

Callithamnion herveyi ⊖
Champia parvula ⊖
Crouania attenuata ⊖
Dasya collinsiana ⊖
Dudresnaya crassa (G)
Helminthocladia calvadosii (G)
Liagora ceranoides (G)
Liagora farinosa (G)
Liagora mucosa (G)
Lophocladia trichoclados ⊖
Seirospora purpurea ⊖
Trichogloea herveyi (G)

Several of the species are indicated as being continuously in tetrasporic condition. Sexual plants of these species were found rarely or not at all. Other species have been omitted from this list, even though they were fertile at all months of their seasons, because they showed a seasonal separation of sexual and asexual generations.

Although these species fall into one group on the basis of their reproductive behavior, there is a considerable diversity about other phases of their natural history at Bermuda. For example, the species of Codium, Pocockiella, Lophocladia, and Seirospora were present through almost the whole year, whereas Helminthocladia and Trichogloea had a very short growing season. Aegira, Colpomenia, Scytosiphon, and most of the others were intermediate in this respect.

There is also considerable difference in abundance and extent of distribution shown by the members of this group. Colpomenia, Pocockiella, and Lophocladia were found in all parts of the islands in great abundance at the proper seasons, but Batophora, Callithamnion herveyi, and Champia

were found in only a few localities, and only Batophora was abundant where it grew. Indeed, Champia was found so sporadically that its season of maximum growth was not determinable, and it is included among these annuals only because every collection contained an abundance of fruiting material.

Annuals never found in reproductive condition.--Among the species which were not found in fruit at any time, a few were collected sufficiently often to suggest that the lack of records was due to a real rarity of reproductive stages and not to inadequate sampling.

Phaeophyceae

Dictyota linearis

Rhodophyceae

Callithamnion byssoideum
Cottoniella arcuata
Laurencia corallopsis

Cottoniella is especially perplexing in this connection. The means of reproduction of the other members of the above list are well established in the literature, but there seems to be no record of the reproduction of any species of Cottoniella (Schotter 1951). On morphological grounds, it is placed in the family Delesseriaceae--a family in which cystocarps and tetrasporangia are of a size easy to detect. The presumption is that reproduction in Cottoniella is excessively rare, and not that it has been overlooked. Inasmuch as the Bermuda species is only present for a short part of the year and is, in addition, an epiphyte on other algae, the problem of how its numbers rise and fall, and how the individuals carry over to the next season, is very interesting.

Annuals with a fruiting maximum early in the growing season.--A number of species were collected in fertile state more often at the beginning of their growing season than at the end. As has been mentioned in discussing the limitations of a tabular arrangement, some species appear from the table to be fertile at all months, whereas they actually have a periodicity. This list,

and some of the list which follow, will serve to compensate somewhat for the limitation of the table.

Phaeophyceae

Dictyota cervicornis ⊖
Dictyota indica ⊖
Ectocarpus mitchellae (P)

Rhodophyceae

Antithamnion cruciatum ⊖
Asparagopsis taxiformis (G)
Heterosiphonia wurdemanni ⊖
Polysiphonia havanensis (G) ⊖
Spyridia filamentosa (G) ⊖

The fact that only one type of reproductive structure was found among some of the above species suggests that more or less reclassification may be necessary when the complete picture is known. For example, the sexual phases of Dictyota indica and Antithamnion cruciatum were not found, but it is almost certain that they occur, perhaps in small quantity. If the sexual phases of these species are also present early in the growing season, there can be no reason to doubt the appropriateness of this category. On the other hand, if the sexual phase were found to develop late in the growing season, the species would be more appropriately considered under a later topic (seasonal alternation of generations). Asparagopsis taxiformis is also listed with only one type of fructification, but the life cycle of this species is not similar to those of Dictyota or Antithamnion. That is, the plants which are called Asparagopsis taxiformis are never tetrasporic, either at Bermuda or elsewhere, but there is strong evidence (Feldmann 1939; Harder 1948) that the tetrasporic phase of the species is a plant called Falkenbergia hillebrandi, which is common at Bermuda. Fruiting material of Falkenbergia was too scarce to indicate whether this sporophytic plant reproduces early in the growing season as does the gametophytic Asparagopsis, but the single collection of fruiting Falkenbergia was made in November, so it is at least not inconsistent with the records for Asparagopsis.

Annuals with a fruiting maximum late in the growing season.--Just as with

the preceding group of algae, this list may help to interpret the data shown in the table of monthly records by giving an idea of an increase of frequency of fruiting plants as the growing season of certain species came to a close.

Chlorophyceae

Dasycladus clavaeformis (G)

Phaeophyceae

Dictyopteris justii ⊖
Dictyopteris plagiogramma ⊖
Dictyota dichotoma ⊖
Sporochnus bolleanus (U)

Rhodophyceae

Wrangelia penicillata ⊖

Only one type of reproductive structure is known for Dasycladus clavaeformis, but in the other species of this list both sporophytes and gametophytes are known. It is regrettable that the data from Bermuda are restricted to only one of the generations.

Species found fruiting sporadically.--Inspection of the table discloses several species which were found in reproductive condition at various times during the year, but there is apparently no increased incidence of reproductive structures at either the beginning or the end of the growth cycle. However desirable it may be to arrange a classification in which categories can be erected for all species according to their reproductive behavior, it seems unwise to predicate at this time relatively complicated categories into which the "sporadically fruiting" algae will fit. Only if observations during several years were to confirm the irregular fruiting periods of these species would such a course be justified. Meanwhile, the members of this group may be considered analogous to the species which were found in the vegetative condition sporadically, in that data are not lacking but are inconclusive.

Phaeophyceae

Dictyota bartayresii ⊖
Dictyota divaricata ⊖

Rhodophyceae

Botryocladia occidentalis ⊖
Botryocladia pyriformis ⊖ (G)
Ceramium byssoideum ⊖
Crouania pleonospora ⊖
Dasya rigidula ⊖
Halymenia agardhii ⊖ (G)
Hypnea musciformis ⊖

Seasonal Alternation of Generations

A very interesting concept has been proposed concerning the sequence of asexual and sexual periods in certain algae. The phenomenon, called "seasonal alternation of generations" by Svedelius (1927), seems to have been first described for marine algae by I. F. Lewis (1912; 1914). Since his investigations provided the most clean-cut results yet reported, they would appear to merit repetition in some detail here.

Lewis sowed tetraspores and carpospores of three species of red algae on oyster shells in July at Woods Hole. After 24 hours, when germlings were established, the shells were fastened to pilings which were known to be uninhabited previously by these algae. By August the germlings from tetraspores had produced sexual plants, but the plants arising from carpospores sown at the same time were not yet fertile. The shells were left on the pilings until June of the next year, at which time no identifiable red algae could be found on the shells but red dots were present. These red dots proved to be holdfasts. In July the three species were sparingly present on the shells but were abundant on the pilings. The plants were prevailingly tetrasporic, the ratio of asexual to sexual plants being about 10:1. However, by August the majority of individuals were sexual. Lewis says this shift of relative frequencies is true of many other species. He explains the life cycle disclosed by his experiments as encompassing a production of tetraspores in abundance but of relatively few carpospores at the beginning of the season. This inequality accounts for the preponderance of sexual (carposporic) plants later in the season. The carpospores from the sexual plants are released and germinate before the end of the

season. With the approach of cold weather, all plants but the youngest sporelings die, and the greater number of sporelings at this time are those which developed from the carpospores. The next year, these sporelings mature as tetrasporophytes and the cycle starts over again. There is, of course, a certain amount of overlap, so that some sexual and some asexual plants can be found at all times. From field observations on other red algae, Lewis concludes that this is "the complete and typical life cycle for the New England coast", although exceptions exist.

It is difficult to find other reports of such a seasonal separation of generations which are as well substantiated as Lewis', but references to the phenomenon are not lacking. Coulter (1914, p. 29) states that a cycle consisting of early asexual reproduction followed by sexual activity at the close of the season is usual among spore-producing plants, although he does not identify it with an alternation of generations, nor does he try to show how one phase would follow the other. Bonnet (1914) calls attention to several early reports of sexual and asexual reproduction occurring at different times and considers them to be convincing proof of the reality of an alternation of generations in the algae. An attempt by Hurd (1917) to find evidence for a seasonal alternation of generations at Puget Sound was not successful, although she admits that the sexual and asexual generations of one species "may be at least partly conditioned by seasons".

A rather complicated alternation is reported by Sturch (1924). He found Harveyella pachyderma with two asexual periods and two sexual periods occurring in alternate order as if each sexual generation were the consequence of the previous asexual one and vice versa. One set of the alternating generations was composed of the plants collected in shallow water and the other pair grew in deeper water, so that the cycle is

not fundamentally different from that described by Lewis.

It was not until 1927 (Svedelius) that the name "seasonal alternation of generations" was applied to this sequential fruiting. Svedelius at that time reported on field studies in the Baltic which had convinced him that the life cycle of Ceramium corticulatum consists of an early sporophytic stage which repeats itself over and over by means of paraspores, and of sexual plants which arise at the end of the season. The data are not so convincing as those of Lewis, resulting in disagreement from Sjöstedt (1928), an acrimonious rebuttal (Svedelius 1929), and criticism of both sides of the argument by DuRietz (1930). In short, there were as many interpretations as there were investigators.

In the Mediterranean, Feldmann (1937, p. 162) says he was not able to discover seasonal alternation of generations. Feldmann-Mazoyer (1940, p. 230), also discussing the Mediterranean, reports that she was able to find suggestion of a seasonal alternation of generations in only two species of Ceramiaceae, and that neither species gave conclusive evidence.

Finally, we may mention the assertion by Rees (1940, p. 411) that in several Rhodophyceae and Chlorophyceae the sexual and asexual reproductive bodies mature and are liberated at different seasons of the year. He gives species of Enteromorpha and Porphyra as examples but without evidence comparable to that shown by Lewis.

From the foregoing review, it is apparent that although a seasonal alternation of generations may be the typical life cycle for the Rhodophyceae of New England, the evidence permits no such generalization for other regions, and at best only a few species seem to exhibit the phenomenon. This is essentially the case at Bermuda, also, for the data from Bermuda do not show an indubitable seasonal alternation of generations in any species, but at least three species deserve further observation. Acanthophora

spicifera was found to be tetrasporic from the beginning of its season in May until August, but almost the last plants seen were a few sexual plants in November. Another species, Laurencia microcladia, has a growing season starting in November and lasting until the end of the next summer, with a maximum in May-June. The only sexual individuals seen were among the collections of November, December, and January, whereas tetrasporic plants were common throughout the season. If further observation can substantiate this pattern as an actual seasonal alternation and not a mere accident of collection, we have here the reverse of the cycle described by Lewis, Bonnet, Svedelius, and Feldmann-Mazoyer. That is, our species displays sexuality at the beginning of the season, not at the end. The same results were obtained with Laurencia obtusa, which starts in spring and lasts into the next winter, in that the sexual plants were only found early in the growing season while tetrasporic plants were present at all times.

The inconclusiveness of the data observed at Bermuda is due to a difficulty which is probably operating at other places also, namely, the scarcity of sexual plants of Rhodophyceae in comparison to the numbers of asexual plants. What is needed is an experimental study such as that by Lewis. Lewis does not mention whether his first attempts to culture the plants were successful; consequently, attempts to duplicate his methods may be expected to require at least two seasons of observations if all cultures "take". The Bermudian species listed above show most promise for such an investigation, but their long growing seasons will probably require at least two years of residence before a complete alternation would develop from cultures. A highly desirable refinement of Lewis' data would be a statistical analysis based on valid random samples.

Parenthetically, it may be mentioned that the alleged heteromorphic alternation of generations between Asparagopsis and Falkenbergia (Feldmann

1939; Harder 1948) and between Derbesia and Halicystis (Kornmann 1938, Feldmann 1950) was borne in mind during the present studies with the hope that a seasonal alternation of generations might be detected. However, the species were not found often enough to provide evidence either for or against such an alternation.

Reproduction as the End of the Seasonal Cycle

Here and there in the literature are statements from which one might infer that reproduction in the algae marks the end of the seasonal cycle and that the plants die when this function is fulfilled. There is a reiteration of this idea in Coulter's book on the evolution of sex in plants (1914, pp. 23, 24, and especially 29 and 32). It is a common feature of the life cycle of Spirogyra and other fresh water algae, according to Transeau (1916, p. 121). The same idea is implied when the scarcity of male plants of Rhodophyceae is explained by Svedelius (1929, p. 385) as due to the fact that they have "fulfilled their function when they have dispersed the spermatia, while the female individuals must nourish the whole mass of carpospores and bring it to full maturity". Knight and Parke (1931, p. 37) emphasize that the last act of a vegetation threatened by unfavorable conditions is the production of propagative cells.

I have found very little evidence at Bermuda to support this idea for the majority of species. Coulter's emphasis on sexual activity at the end of the season is reflected in two species, Dasycladus clavaeformis and Acanthophora spicifera, but, conversely, sexual plants of Laurencia microcladia and Laurencia obtusa were found at the beginnings of their seasons. Transeau's remarks are only mentioned to show the general acceptance of the idea of reproduction at the end of the season; investigations on the very scant fresh water algal flora of Bermuda have been purely taxonomic

(Collins and Hervey 1917, Rich 1938) and provide no information on this question. The explanation offered by Svedelius for the scarcity of male plants seems to be merely a matter of conjecture and not verifiable. An alternative explanation is that, since male plants are difficult or impossible to recognize once they have dispersed the spermatia, they may be passing under the guise of sterile specimens.

There is some evidence that annuals do not necessarily disappear after fruiting. Grubb (1936, pp. 405, 410) reports that Porphyra and Ulva in Great Britain reproduce during the winter but do not wane until May or June. Nereocystis, the famous bull-kelp of the Pacific Coast, has an analogous history (Rigg 1917). In this case the sporangia are most abundant in summer but the plants survive for several months after. At Bermuda, also, there is a small number of species which are listed above as apparently having a reproductive maximum at the beginning of the season and persisting until months later. If we may judge from the literature, Hydroclathrus clathratus should also be on this list, and quite possibly it is the extreme example of an alga which does not die soon after fruiting. According to Thuret and Bornet (1878, p. 12), the young, unperforated thalli of this species bear sporangia as a continuous covering, but the characteristic reticulate mature thalli are sterile or have only small groups of sporangia here and there. Børgesen (1913-20) considers this the explanation for his inability to find sporangia on his specimens from the Danish West Indies, for he collected only plants with the characteristic perforations. The same difficulty obtains with the Bermuda material--only full-grown plants were collected and they seem to be sterile. In the absence of positive evidence that this plant in Bermuda reproduces largely during its young stages, the species has not been listed under any category on the basis of fruiting habits, but the literature indicates that at least in so

places Hydroclathrus does not "fruit and die".

Of course, it may be held that the individual plant and not the whole population must be considered, and that the individuals found in fruit at the beginning of a species' season die before the species completely disappears. In the case of Hydroclathrus and the species which were listed as having a reproductive maximum at the beginning of the season, this premise seems to require the corollary that those sterile plants found late in the season would have died without issue. Such a conclusion cannot be proved or disproved, but its acceptance would restrict the idea that algae fruit and die to a relatively few individuals so far as these species are concerned.

Cultural studies would be of great help in elucidating this question, especially since it is very difficult from field studies to uncover direct evidence that any individual plant vanishes soon after fruiting. On the basis of field studies, however, very few of the Bermuda algae can unequivocally be said to "fruit and die".

Variation of Reproductive Periods with Depth

Whereas the concepts of definite fruiting periods, seasonal alternation of generations, and reproduction as the end of a life cycle are familiar to the literature, another phenomenon associated with reproduction does not seem to have been reported often enough to attract much attention. I am referring to a difference in time of reproduction according to the depth at which the species grow. First, we may reconsider Sturch's report (1924) of a seasonal alternation of generations in Harveyella pachyderma. For our present purposes this report is interesting because the sexual plants occurred in deep waters during May and June and in shallow waters from November to January, with asexual plants occurring between these generations. Whereas Sturch investigated only the one species, Funk (1927,

p. 289) makes a much more inclusive report on the algae of Naples. He claims that the deep water vegetation has a maximum of reproduction during summer and fall, in contrast to the species near the surface which have winter and spring maxima. Vatova (1948, p. 48) states that his findings concerning the perennial algae of Rovigno, in the Adriatic Sea, correspond to those of Funk. In support of his conclusion Vatova declares that the perennial species of Phaeophyceae are generally restricted to the coast and the majority of them reproduce in winter and spring, but most of the perennial Rhodophycean species are deep water forms and they reproduce mainly in summer and autumn. Without attempting such broad generalizations, Feldmann (1937, p. 165) reports that a few Mediterranean species which can be found in both deep and shallow waters exhibit different periodicity of reproduction in each of these habitats. He does not discuss the matter.

According to E. Lewis (1936), the phenomenon is manifested even intertidally in Wales. That is, she writes that algae of the upper levels tend to fruit in summer, whereas those growing near sea level fruit in the winter for the most part.

Although it was not possible to dredge for deep water species and there is consequently no information about the fruiting periods of that segment of the vegetation, the experience at Bermuda furnishes a basis for some comments on the foregoing reports. First, it may be pointed out that the question is enormously more complex than Funk's simple generalization would suggest. If a seasonal alternation of generations obtained for any considerable number of species, then it may be expected that not one but two fruiting maxima must be considered--a period of sexual reproduction and a period of asexual reproduction. This is exactly what Sturch describes, but Funk's generalization does not provide for such alternations.

Another complexity arises from the high proportion of annuals at Bermuda. As was pointed out in a preceding section, the number of species found in reproductive condition is a function of the number of species available for examination. Since in almost every month about 50 per cent of the species examined at Bermuda were fertile, it follows that the greatest number of species were found in fruit during the period of maximum vegetation. The Bermuda data pertain only to the shallow water vegetation, but Funk admits that the period of maximum reproduction in deep water at Naples also agrees with the period of maximum vegetation in the deep water. Accordingly, his generalization does not seem to say much that is not already apparent from a study of the growing seasons. Vatova's inferences, if correct, seem to be more meaningful, since he considers only the perennial species. That is, his deductions indicate that it is not merely a difference in number of species present at various times which causes a reproductive maximum to appear in deep water at one period and in shallow water at another. However, it would be difficult or impossible to apply to the Bermuda vegetation Vatova's view that the Rhodophyceae represent the deep water vegetation. Except for 5 species which were found only cast ashore and may therefore be suspected of growing beyond the depths which were usually explored, all the Rhodophycean species of Bermuda can be found within the first meter of depth and several are actually intertidal. Consequently, reproduction in the Rhodophyceae and, for similar reasons, reproduction in any other class of algae, does not permit generalization concerning any difference of fruiting periods with depth at Bermuda. Parenthetically, it may be noted that Vatova's statement that Rhodophyceae are mainly deep water species is inapplicable not only at Bermuda but also in Puget Sound (Muenscher 1915, p. 83) and in portions of the Mediterranean (Feldmann 1937, p. 51).

With reference to the report by Miss Lewis that intertidal algae fruit at different periods according to the level at which they grow, it can only be said that the records for Bermuda intertidal species do not disclose any correlation between reproduction and tide levels. However, even by including the species which grow near low tide level and are as much infralittoral as intertidal, records of reproduction for only 12 species from Bermuda are available, whereas Miss Lewis bases her conclusion on 42 species. Consequently, it is not feasible to compare the results from Bermuda with those from Wales very closely.

Other Phenomena of Reproduction

Scarcity of sexual plants.--Perhaps the most serious difficulty in getting the complete picture of the reproductive habits of a species is the scarcity of sexual plants in the Phaeophyceae and Rhodophyceae. For the Phaeophyceae with a heteromorphic alternation of generations which includes a microscopic gametophyte, cultural studies are probably the only solution. For other Phaeophyceae, especially the Dictyotales, and for almost all the Rhodophyceae, there does not seem to be any solution except study of a great many individuals. The scarcity is not due to any difficulty in detecting the sexual phases, for the gametic plants of Dictyotales are as large and the reproductive organs are as prominent as the asexual plants and the tetraspores, and the cystocarps of the red algae are even more conspicuous than the alternate (tetrasporic) structures, although it must be admitted that the male plants are not so easy to detect. The scarcity is not peculiar to Bermuda. Haupt (1932) expresses difficulty in finding sexual phases of Zonaria, Dictyota, and Dictyopteris in California, and cites several authors who had noted the excess of asexual over sexual plants of Dictyotales in other regions. In her studies of the coralline red algae, Madame Weber-van Bosse (1904, p. 83) deplores the scarcity of sexual frui

and indeed the preponderance of tetrasporic plants seems to be a commonly accepted fact for the Rhodophyceae in general (Svedelius 1929). It is very interesting to speculate about explanations for this disparity, but the reason for bringing up the matter here was only to call attention to the phenomenon and the difficulties it produces. For example, sexual plants of Dictyota have been found to discharge gametes at fortnightly or monthly intervals in definite relation to the spring tides wherever they have been studied (J. Williams 1905, I. F. Lewis 1910, Hoyt 1927), but since almost no sexual plants of this genus were found at Bermuda no investigation of the topic was possible.

Scarcity of reproductive structures.--Even more puzzling than the infrequency of sexual plants is the scarcity or apparent absence of any reproductive bodies whatever in many species. Among the Bermuda members of the Chlorophyceae, none of the species of Caulerpa or Halimeda were found in reproductive condition, although fruiting structures have been described from other areas. With more than 30 generous collections to search through, I was able to find reproductive structures in Codium intertextum only once, and they apparently have not been recorded previously. As a matter of fact, the family Codiaceae, to which Halimeda and Codium belong, is very poorly known with respect to its fructification. Fruiting structures have never been described for most of the genera, including the Bermudian genera Penicillus and Udotea, and the evidence for reproductive structures in Avrainvillea rests on one incomplete report (Howe 1907). Since the Codiaceae and Caulerpaceae are very important features of the algal vegetation of Bermuda, our ignorance of their life cycles is a serious barrier to the full understanding of seasonal changes in the Bermuda flora. The difficulty is of the same nature in the Phaeophyceae, although not so large a portion of the vegetation is involved, and the Rhodophyceae which were rarely or never

found in fruit comprise a considerable number of common species. A list of these sparsely reproducing species will show better than a discussion how many members which give the tropical flora its characteristic stamp are involved.

Chlorophyceae

Avrainvillea (3 species)
Caulerpa (8 species)
Halimeda (4 species)
Penicillus (2 species)
Udotea (3 species)

Phaeophyceae

Dictyopteris (3 species)
Dictyota linearis

Rhodophyceae

Caloglossa leprieurii
Catenella repens
Centroceras clavulatum
Ceramium subtile
Cottoniella arcuata
Digenea simplex
Eucheuma isiforme
Falkenbergia hillebrandi
Galaxaura obtusata
Gelidium pusillum
Laurencia corallopsis
Spyridia filamentosa

Feldmann-Mazoyer (1940, p. 339) was unable to find fruiting Centroceras clavulatum in the western Mediterranean, and Taylor (1928, p. 190) records the species as "generally sterile" in Florida, but near São Paulo, Brazil, almost all individuals found were in tetrasporic condition according to Dr. A. B. Joly (personal communication). No doubt other species which rarely fruit in one region reproduce abundantly in other places, but the factors involved are unrecognized.

Differences in reproductive behavior among allied species.--I have not been able to recognize any reproductive trends which might be considered as typical of a genus or family, but some interesting irregularities or dissimilarities within taxa have appeared. The family Dasycladaceae is represented by 7 species in Bermuda, of which 5 were collected often enough to permit consideration of their periodicity. Of these 5, all the collections of Acetabularia crenulata, Cymopolia barbata, and Neomeris annulata contained fertile specimens and most of the plants in a collection were fertile. A

fourth species, Batophora oerstedi, approached this productiveness, although the proportion of fertile plants in its collections was less. However, a completely different picture was shown by Dasycladus clavaeformis, which was sterile in all collections but one.

Wide variance in reproductive habits was also shown within the genus Codium. Codium decorticatum had an abundance of gametangia on almost all plants. Codium isthmocladum was also fertile throughout its growing season, but the plants bore fewer gametangia and many plants were sterile. On the other hand, Codium pilgeri seemed to have two reproductive maxima, with a period of about 5 consecutive months when all plants examined proved to be sterile. Finally, there is Codium intertextum, which was found in fruit only once, although it was collected more often than any of the other members of the genus.

The differences between Laurencia microcladia and Laurencia obtusa are especially interesting because of their possible significance in the study of speciation in this difficult genus. The Bermuda plants in question have been referred to a single species, Laurencia obtusa (Hudson) Lamouroux, and a variety (var. gelatinosa (Desfontaines) J. Agardh) by Collins and Hervey (1917). More recently, the variety has been identified as a separate species, Laurencia microcladia Kuetzing, by Howe (1918) and Taylor (1928), and we shall follow this usage. Cystocarpic plants of Laurencia microcladia were found only in November, December, and January, whereas Laurencia obtusa was collected in sexual condition only in March and April. Furthermore, Laurencia microcladia grows only where it is subjected to at least moderate wave action, but Laurencia obtusa is a plant of quiet waters. More collections of sexual plants and observations over several years are required before conclusions can be safely drawn, but it is possible that a combination of seasonal isolation and ecological isolation

forms a barrier between the two species. It is probably just such combinations of different isolating mechanisms rather than single mechanisms which are the normal condition in nature, according to Stebbins (1950, p. 228), but so far as I am aware the algae have not been investigated from this point of view previously.

SUMMARY

1. Fluctuations in abundance and reproductive condition of marine algae through a cycle of seasons were studied in a variety of habitats at Bermuda. Four types of habitats are described, some ecological features of each are discussed, and the most common species in each are listed.

2. Fish ponds and landlocked pools are distinguished by extreme protection from waves and by deep shade. Phaeophyceae are rarely present.

3. Quiet coves, characteristically with mangroves at the heads and sea grasses on the bottoms, contain mud, sand, and rock substrata. Ecological features include strong insolation and periodic emersion of large areas of the bottom. There is indirect evidence that bacteria may be especially significant in the nutrient cycles of quiet coves.

4. Bays which are exposed to moderate wave action lack mangroves, but sea grasses are present. One of them, Thalassia testudinum, in some bays may be reclaiming portions of the bottom from the sea. Erosion of the shore rock, decreased light penetration, mechanical stresses, and temperature regulation are ecological effects of wave action. Substrata include sand and rock.

5. Habitats exposed to considerable wave action lack mangroves and sea grasses. Some sand may be present, but the substratum is mainly rock. A step-like configuration of the shore rock is especially pronounced in these localities, although it is also found on less battered shores. The causative agency is unknown.

6. The cycle of growth in each type of habitat started in autumn, rose to a maximum in spring, and declined during the summer. Myxophyceae became notable in summer in fish ponds, quiet coves, and moderately exposed

bays, but not on wave-swept shores.

7. The histories of a few species are recounted to illustrate different seasonal cycles. Codium decorticatum, Codium intertextum, and Dictyopteris justii exemplify the cycle which was typical of the vegetation as a whole. A cycle starting late in spring and continuing into the winter was manifested by Acanthophora spicifera. Trichogloea herveyi, which was found only from March to June, represents the truly spring annuals. Among perennials, Sargassum bermudense did not undergo seasonal fluctuations, whereas Caulerpa racemosa showed marked fluctuations. Jania pumila is particularly interesting as an example of a host-specific epiphyte which was absent during the period when its host was absent and become re-associated with its host by some undetected means at the beginning of the next cycle.

8. Of the Bermuda algae 35 species are considered to be perennials. Most of the intertidal algae are perennials.

9. Annuals are grouped according to the seasons when they flourished, even though some were present in reduced volume at other seasons. In this classification 48 species flourished in winter and spring, 6 species constitute the spring annuals, 29 species are listed as algae of the spring and summer, 3 other species were best developed during summer and autumn, and 3 species were restricted almost completely to winter.

10. Excluding Myxophyceae and coralline Rhodophyceae, there are about three times as many annuals as perennials in the Bermuda algal flora. Analysis of lists from several temperate and warm-temperate regions discloses a slight excess of annuals over perennials (1.4:1) in the coldest area (Nova Scotia) and an increase with warmer conditions until ratios equivalent to that of Bermuda are reached in the Gulf of Venice.

11. Although a warm water flora is involved, the cycle of growth for most species at Bermuda started before the coldest temperatures were

reached and continued, apparently unaffected, through the coldest months. The period of generalized decline occurred during the warmest months, which was also a period of maximum insolation.

12. The difference between the vegetation of autumn and that of spring was associated with changes in light conditions and not with a difference in temperature.

13. Some 151 species were examined for reproductive structures and the results, by month, are tabulated. Each month, reproductive structures were found among collections of about 50 per cent of the species examined.

14. Laurencia microcladia reproduced sexually at a different time from Laurencia obtusa, and the 2 species grew under different ecological conditions. It is suggested that a combination of reproductive and ecological isolation tends to keep these 2 related species distinct.

15. Among perennials, 8 species were found in reproductive condition through the year, and 11 species were not found in fruit at any time.

16. Among annuals, 22 species were found in fruit throughout their seasons; 4 species were never found in fruit although collections were ample; 8 species exhibited a fruiting maximum early in their seasons; and 6 species exhibited a late fruiting maximum.

17. In 3 species of annuals, sexual reproduction and asexual reproduction seemed to be somewhat separated in time.

18. The idea that reproduction occurs at the end of the growth cycle is examined and it is concluded that the evidence does not permit such a generalization for Bermuda algae.

19. The scarcity of sexual plants of Rhodophyceae and Phaeophyceae reported from other regions also obtains at Bermuda, and a considerable segment of the algal flora of Bermuda, including some of the most common species, was found in fruit sparingly or not at all, either sexually or asexually.

APPENDIX

PLATE I

MANGROVE COMMUNITY IN SANDY AREA

Rhizophora mangle and Avicennia nitida growing in areas of sand at Hungry Bay, Hamilton Island. Pads of Cladophoropsis membranacea are on the sand, and some are pierced by pneumatophores of Avicennia.



Plate I

PLATE II

MANGROVE COMMUNITY IN AREA OF SAND AND STONES

Avicennia nitida growing in an area of sand and stones at Hungry Bay, Hamilton Island. The pneumatophores of Avicennia are covered by short, curly growths of Bostrychia montagnei and other Rhodophyceae.



Plate II

PLATE III

EMERSION DURING LOW WATER OF SPRING TIDES

The head of a small unnamed cove on the south side of St. Georges Island during low water of spring tides. The phanerogam, Thalassia testudinum, is laid bare from shore to shore except for the narrow boat channel, but during neap tides the Thalassia is not uncovered. Rhizophora mangle is present on the far shore.



Plate III

PLATE IV

MULLET BAY, ST. GEORGES ISLAND,
DURING LOW WATER OF NEAP TIDES

The dense bottom vegetation is completely immersed during these average conditions.

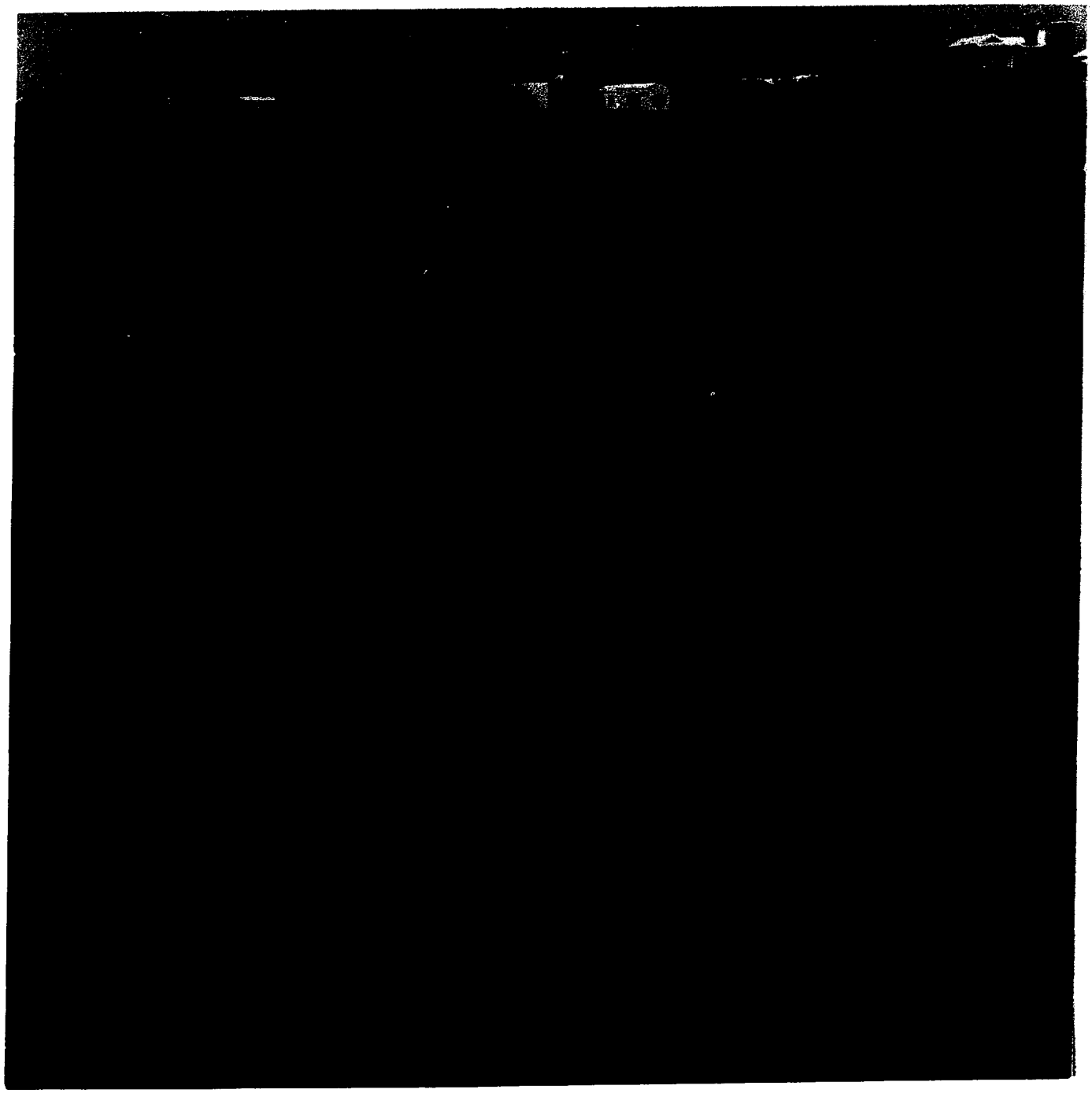


Plate IV

PLATE V

MULLET BAY, ST. GEORGES ISLAND,
DURING LOW WATER OF SPRING TIDES

This is the same area as that shown in Plate IV. The light-colored growth is largely Acetabularia crenulata and Cymopolia barbata, with considerable Halimeda monile and Penicillus capitatus included. The gray portion is a meadow of Thalassia testudinum.



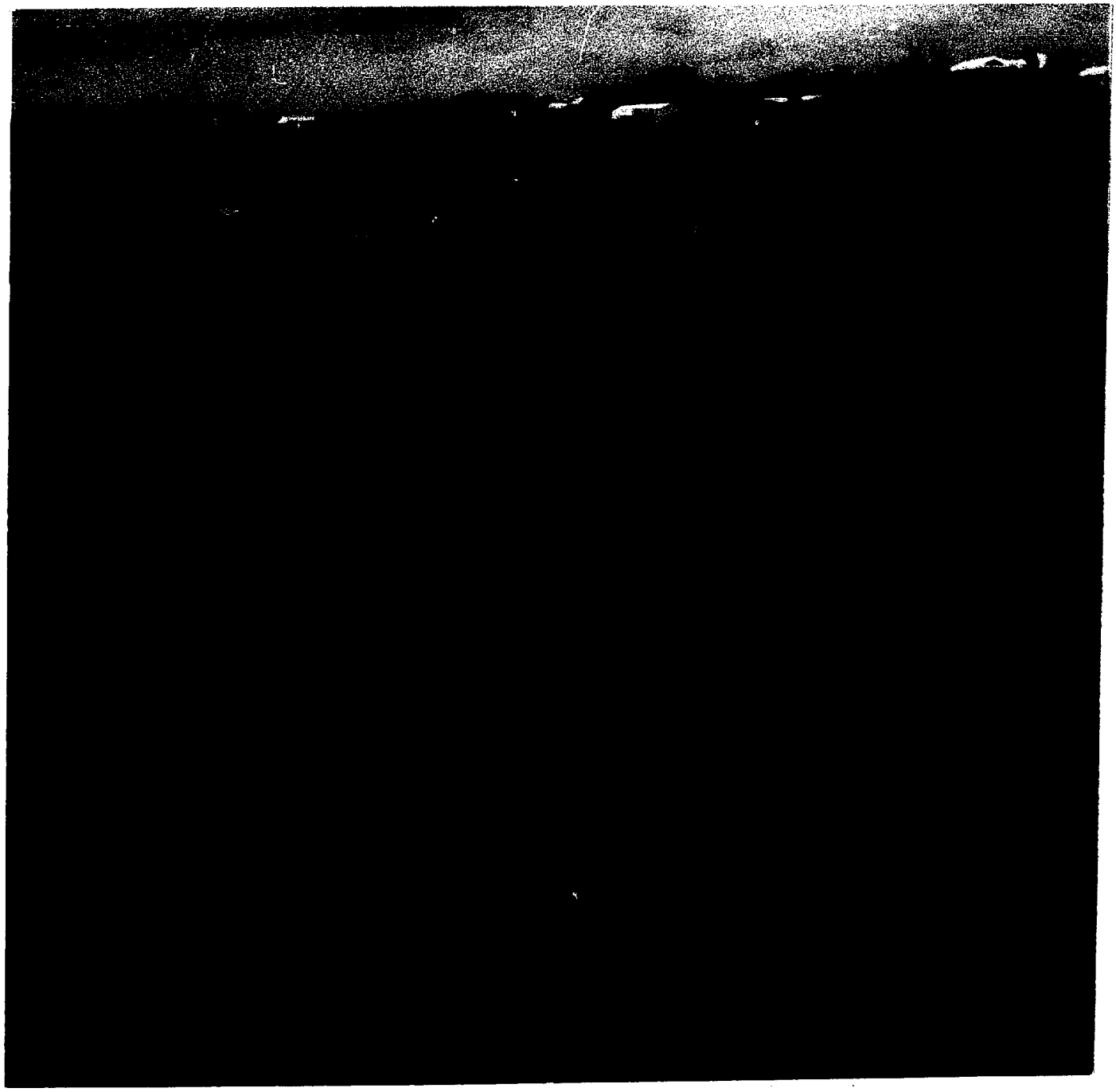


Plate V

PLATE VI

PORTION OF WAVE-SWEPT SHORE
AT
RED HOLE, ST. DAVIDS ISLAND

The "upper platform" is much dissected, but the "lower platform" is neatly delimited at the water level. The surf obscures the abrupt declivity between the "lower platform" and the bottom of the bay.

The algal growth is mainly Sargassum bermudense. Its short turf-like appearance is characteristic on exposed shores.

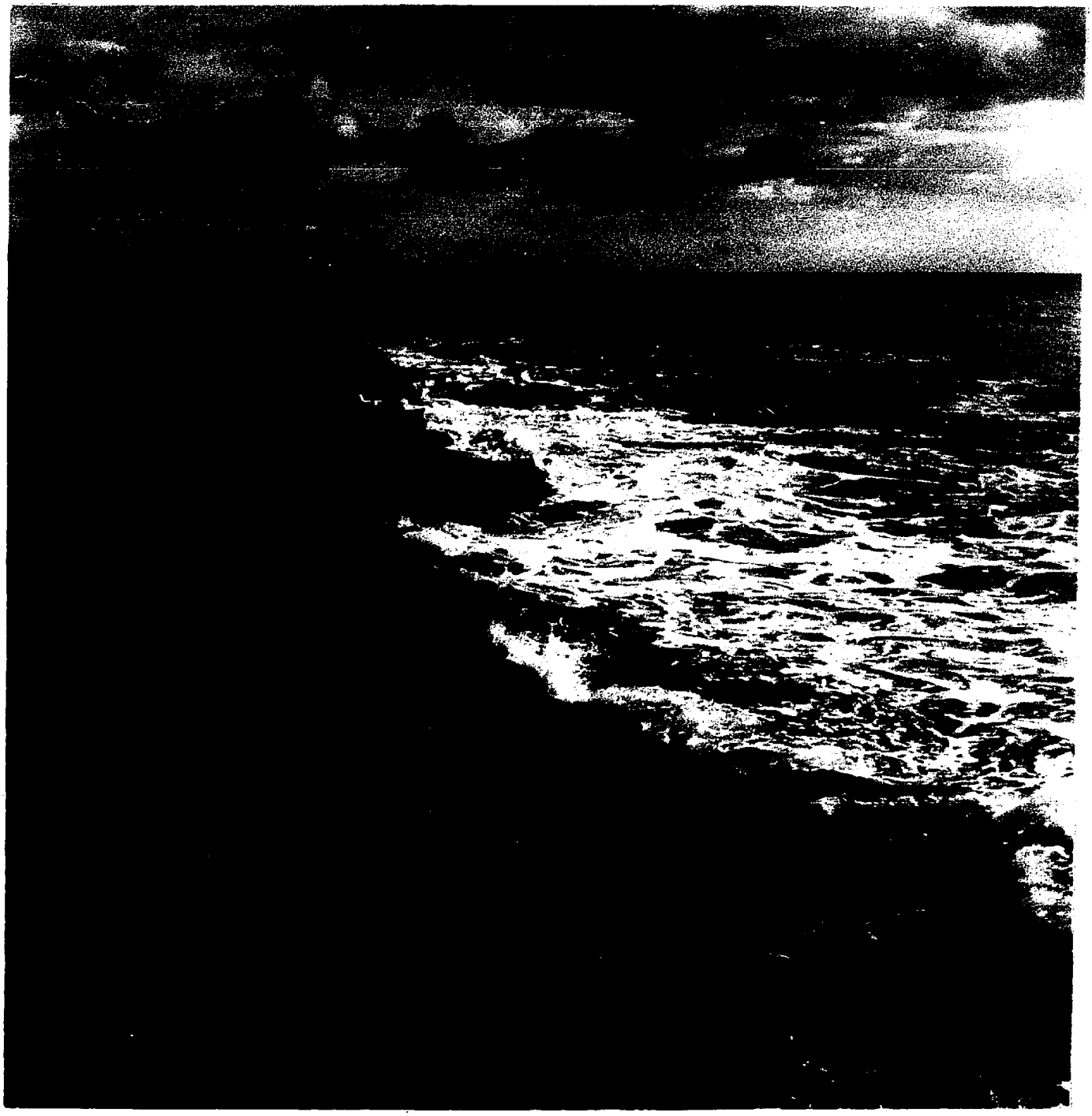


Plate VI

PLATE VII

WAVE-SWEPT SHORE AT GRAVELLY BAY, HAMILTON ISLAND

Several terraces occur below the extremely eroded "upper platform", but these are lacking at the more protected parts of the bay.

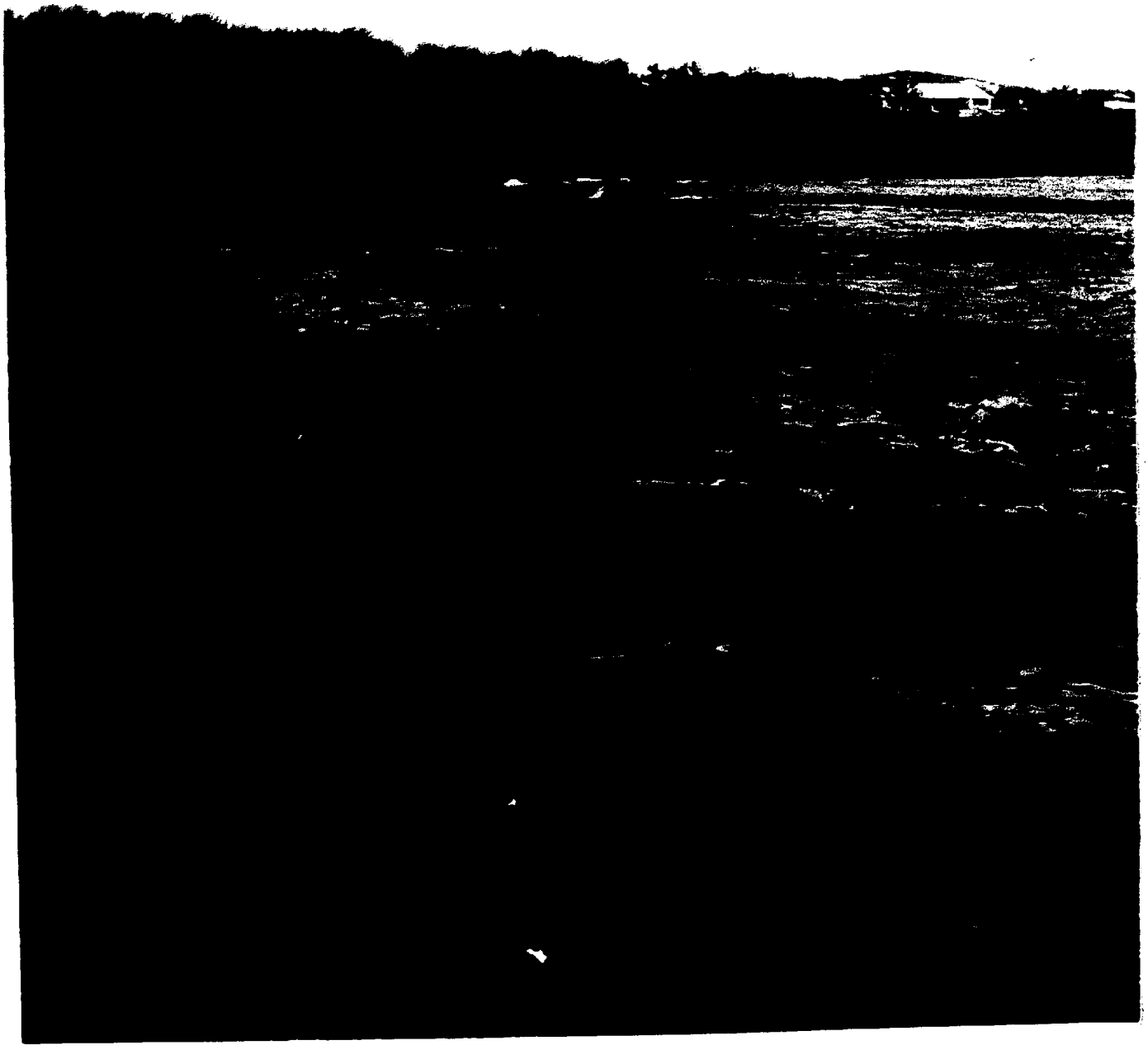


Plate VII

PLATE VIII

COLONY OF PENICILLUS CAPITATUS
AT
HUNGRY BAY, HAMILTON ISLAND

Perennial species such as the one shown here dominated the autumnal aspect of quiet coves.

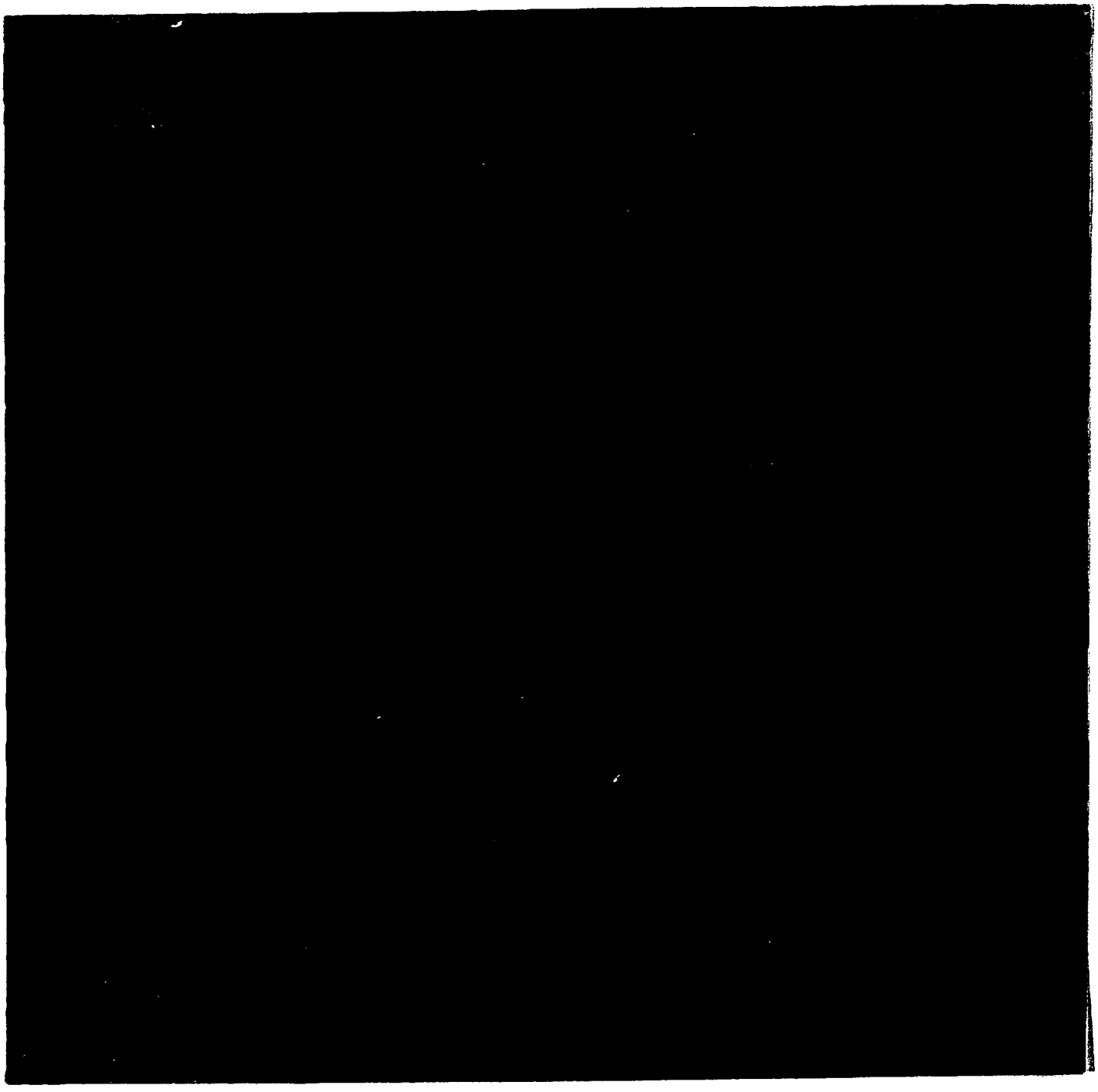


Plate VIII

PLATE IX

COLONY OF *COLPOMENIA SINUOSA*
AT
HUNGRY BAY, HAMILTON ISLAND

This colony had not yet appeared at the end of December, but the development shown here was attained before the end of January.

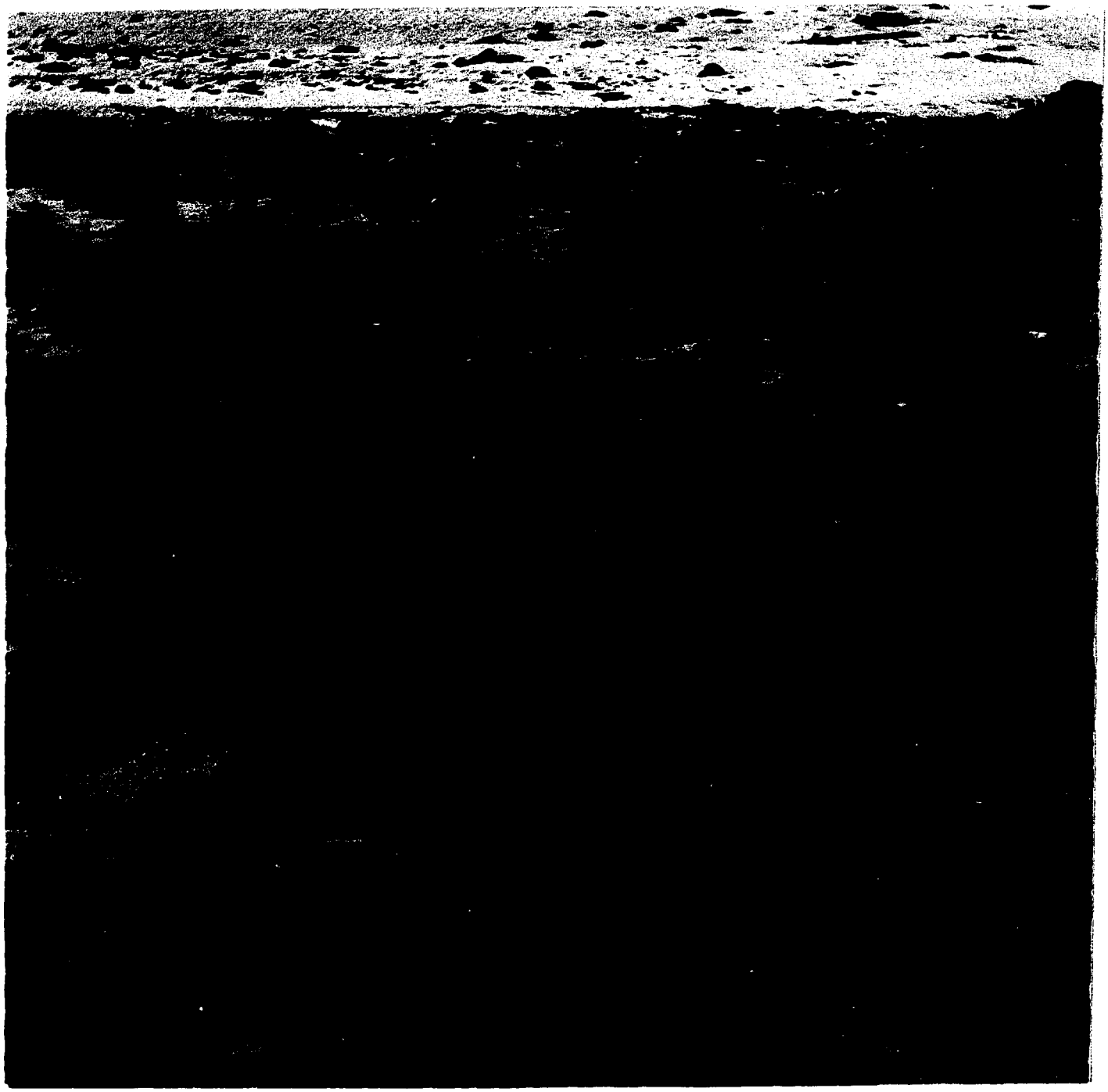


Plate IX

PLATE X

HYDROCLATHRUS CLATHRATUS
AT
THE CAUSEWAY, HAMILTON ISLAND

Although no individuals of this species were present in the locality at the end of November, these fully-grown plants were seen at the end of December.

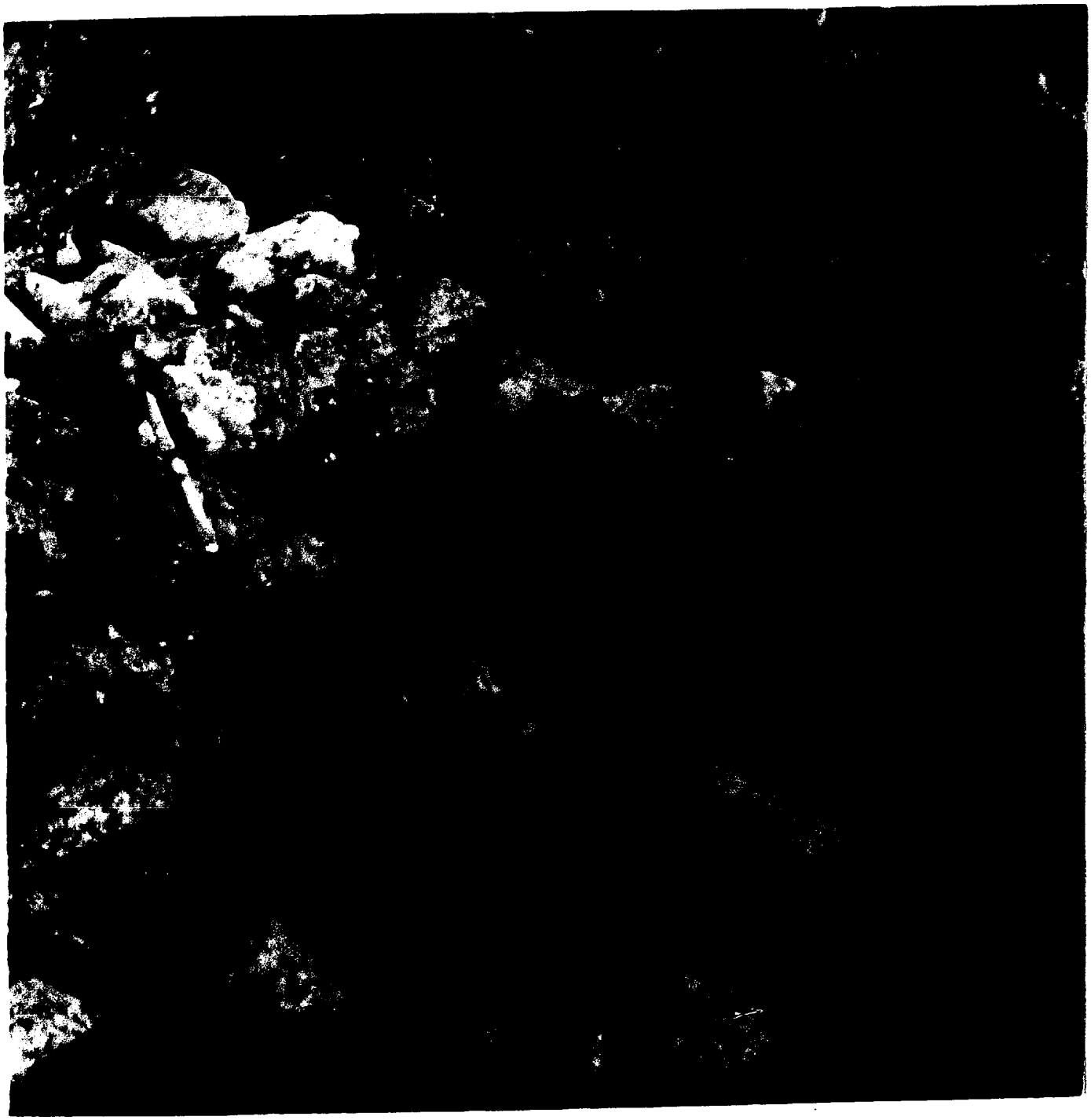


Plate X

PLATE XI

SEASONAL VARIATION IN VOLUME OF SOME SPECIES OF ALGAE GROWING IN FISH PONDS AND LANDLOCKED SALT WATER POOLS AT BERMUDA

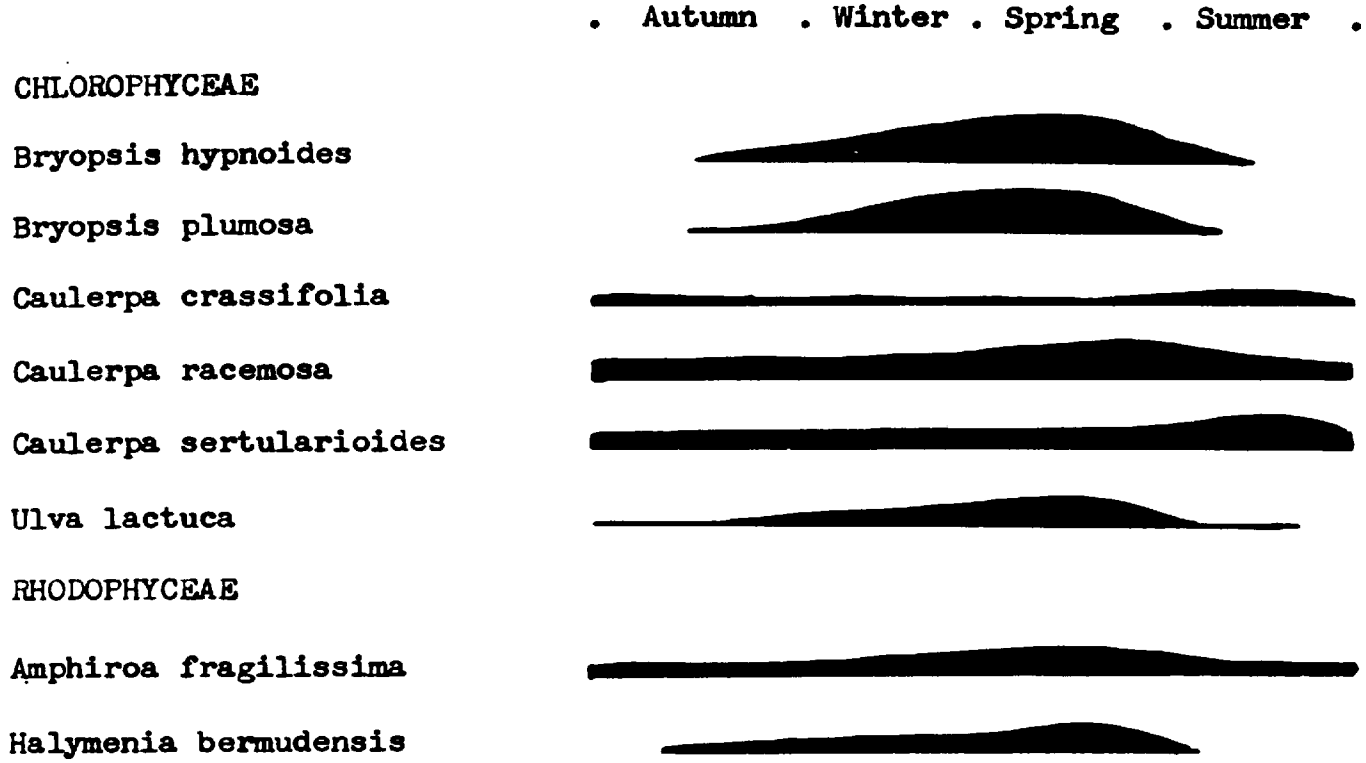

. Autumn . Winter . Spring . Summer .
CHLOROPHYCEAE
Bryopsis hypnoides
Bryopsis plumosa
Caulerpa crassifolia
Caulerpa racemosa
Caulerpa sertularioides
Ulva lactuca
RHODOPHYCEAE
Amphiroa fragilissima
Halymenia bermudensis

Plate XI

PLATE XII

SEASONAL VARIATION IN VOLUME OF SOME SPECIES OF ALGAE GROWING IN QUIET COVES AT BERMUDA

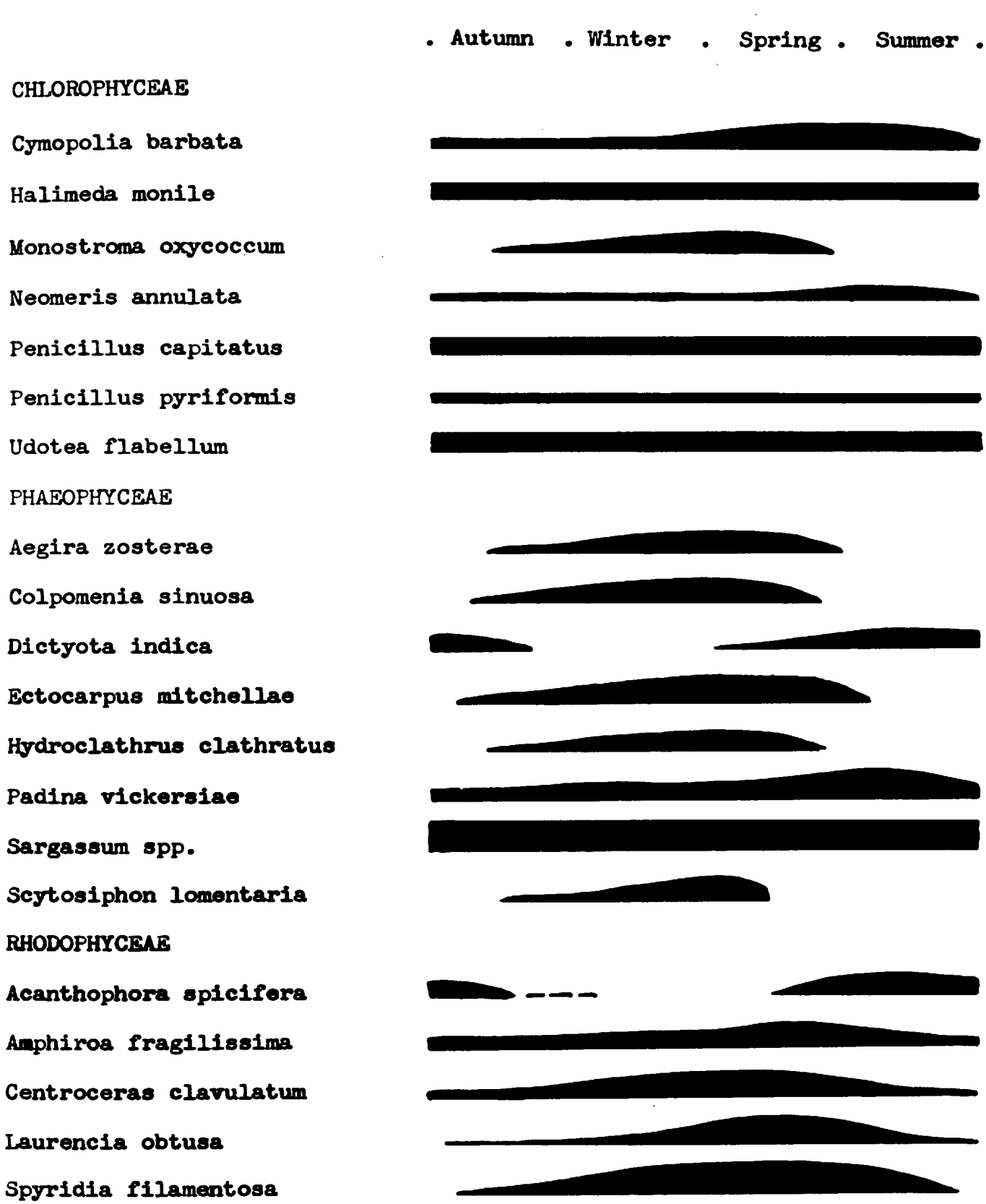

. Autumn . Winter . Spring . Summer .
CHLOROPHYCEAE
Cymopolia barbata
Halimeda monile
Monostroma oxycoccum
Neomeris annulata
Penicillus capitatus
Penicillus pyriformis
Udotea flabellum
PHAEOPHYCEAE
Aegira zosterae
Colpomenia sinuosa
Dictyota indica
Ectocarpus mitchellae
Hydroclathrus clathratus
Padina vickersiae
Sargassum spp.
Scytosiphon lomentaria
RHODOPHYCEAE
Acanthophora spicifera
Amphiroa fragilissima
Centroceras clavulatum
Laurencia obtusa
Spyridia filamentosa

Plate XII

PLATE XIII

SEASONAL VARIATION IN VOLUME OF SOME SPECIES OF ALGAE GROWING IN MODERATELY EXPOSED BAYS AT BERMUDA

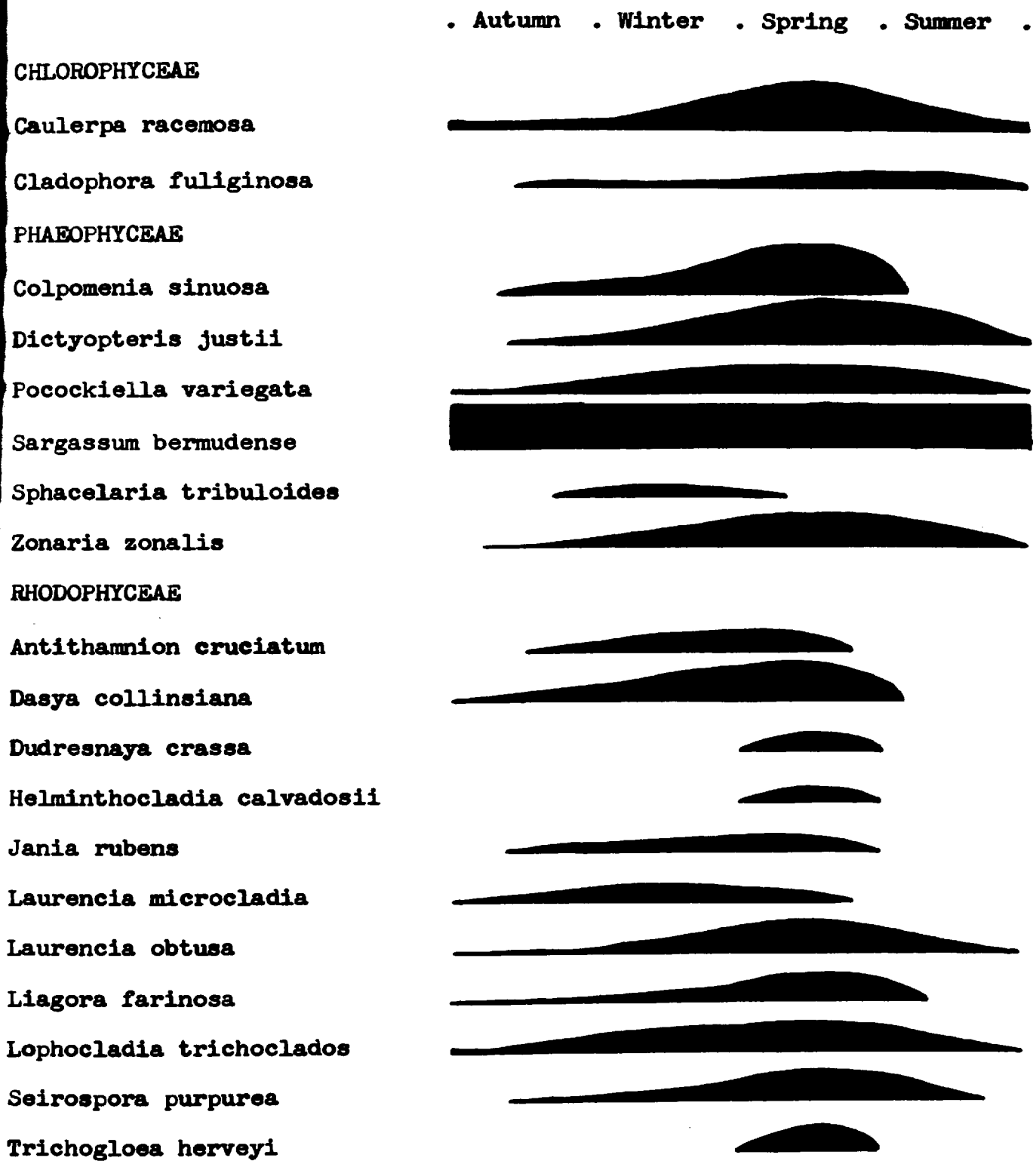

. Autumn . Winter . Spring . Summer .
CHLOROPHYCEAE
Caulerpa racemosa
Cladophora fuliginosa
PHAEOPHYCEAE
Colpomenia sinuosa
Dictyopteris justii
Pocockiella variegata
Sargassum bermudense
Sphacelaria tribuloides
Zonaria zonalis
RHODOPHYCEAE
Antithamnion cruciatum
Dasya collinsiana
Dudresnaya crassa
Helminthocladia calvadosii
Jania rubens
Laurencia microcladia
Laurencia obtusa
Liagora farinosa
Lophocladia trichoclados
Seirospora purpurea
Trichogloea herveyi

Plate XIII

PLATE XIV

SEASONAL VARIATION IN VOLUME OF SOME SPECIES OF ALGAE GROWING IN WAVE-SWEPT HABITATS AT BERMUDA

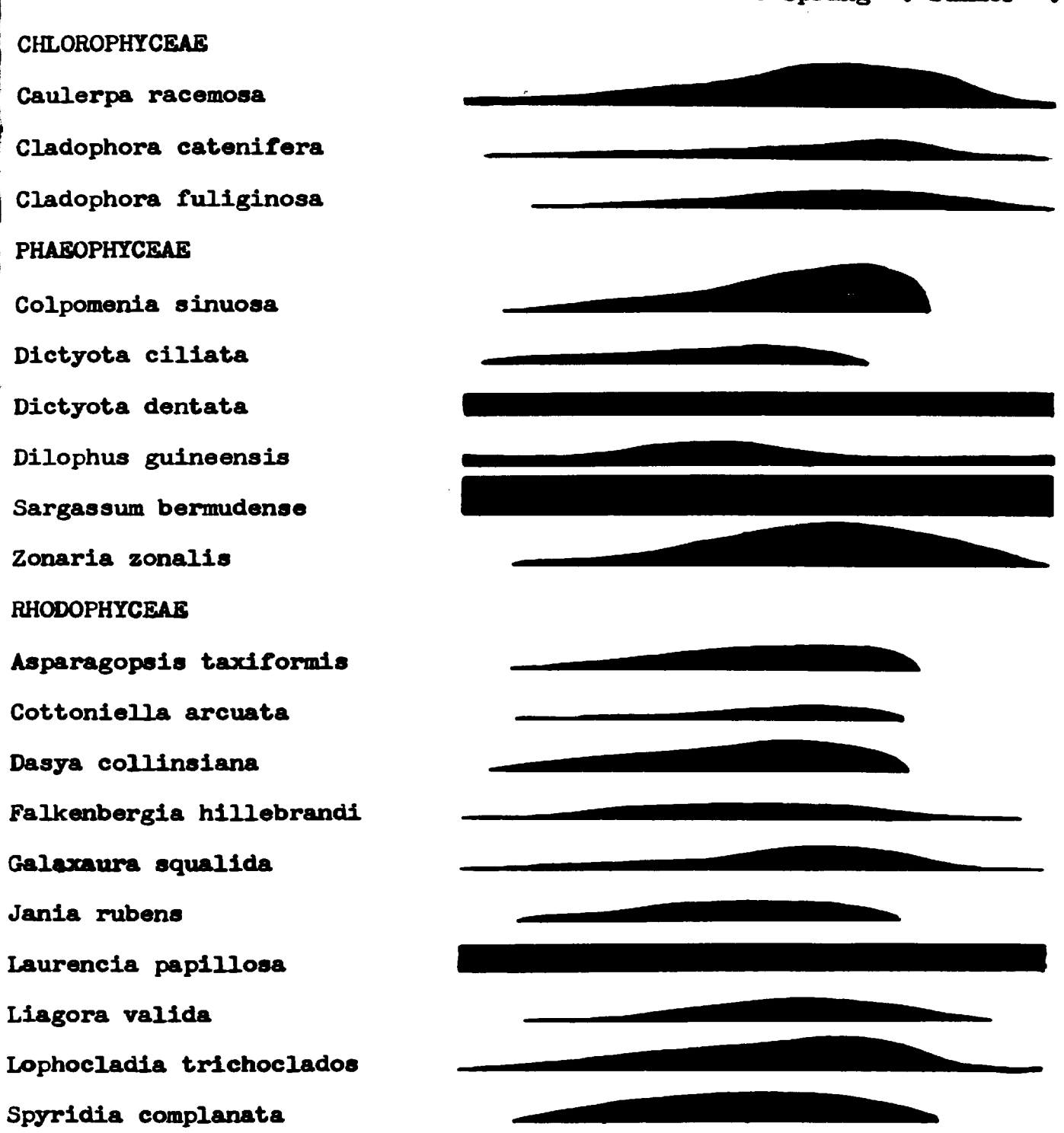

. Autumn . Winter . Spring . Summer .
CHLOROPHYCEAE
Caulerpa racemosa
Cladophora catenifera
Cladophora fuliginosa
PHAEOPHYCEAE
Colpomenia sinuosa
Dictyota ciliata
Dictyota dentata
Dilophus guineensis
Sargassum bermudense
Zonaria zonalis
RHODOPHYCEAE
Asparagopsis taxiformis
Cottoniella arcuata
Dasya collinsiana
Falkenbergia hillebrandi
Galaxaura squalida
Jania rubens
Laurencia papillosa
Liagora valida
Lophocladia trichoclados
Spyridia complanata

Plate XIV

PLATE XV

CLIMATOLOGICAL DATA FOR BERMUDA

a. Volume of Rainfall

o———————o Mean monthly rainfall during 52 years

x———————x Total monthly rainfall, January to September, 1949, and October, 1950, to January, 1951

b. Sea Temperatures

o———————o Mean monthly temperatures during 6 years

x———————x Maximum and minimum monthly temperatures, February to September, 1949, and October, 1950, to January, 1951

c. Duration of Sunshine

o———————o Mean hours of sunshine each month during 20 years

x———————x Total hours of sunshine each month, January to September, 1949, and October, 1950, to January, 1951

d. Noon Altitude of the Sun

The angle between each arrow and the horizontal is equivalent to the angle of elevation of the sun about the twenty-first day of the month.

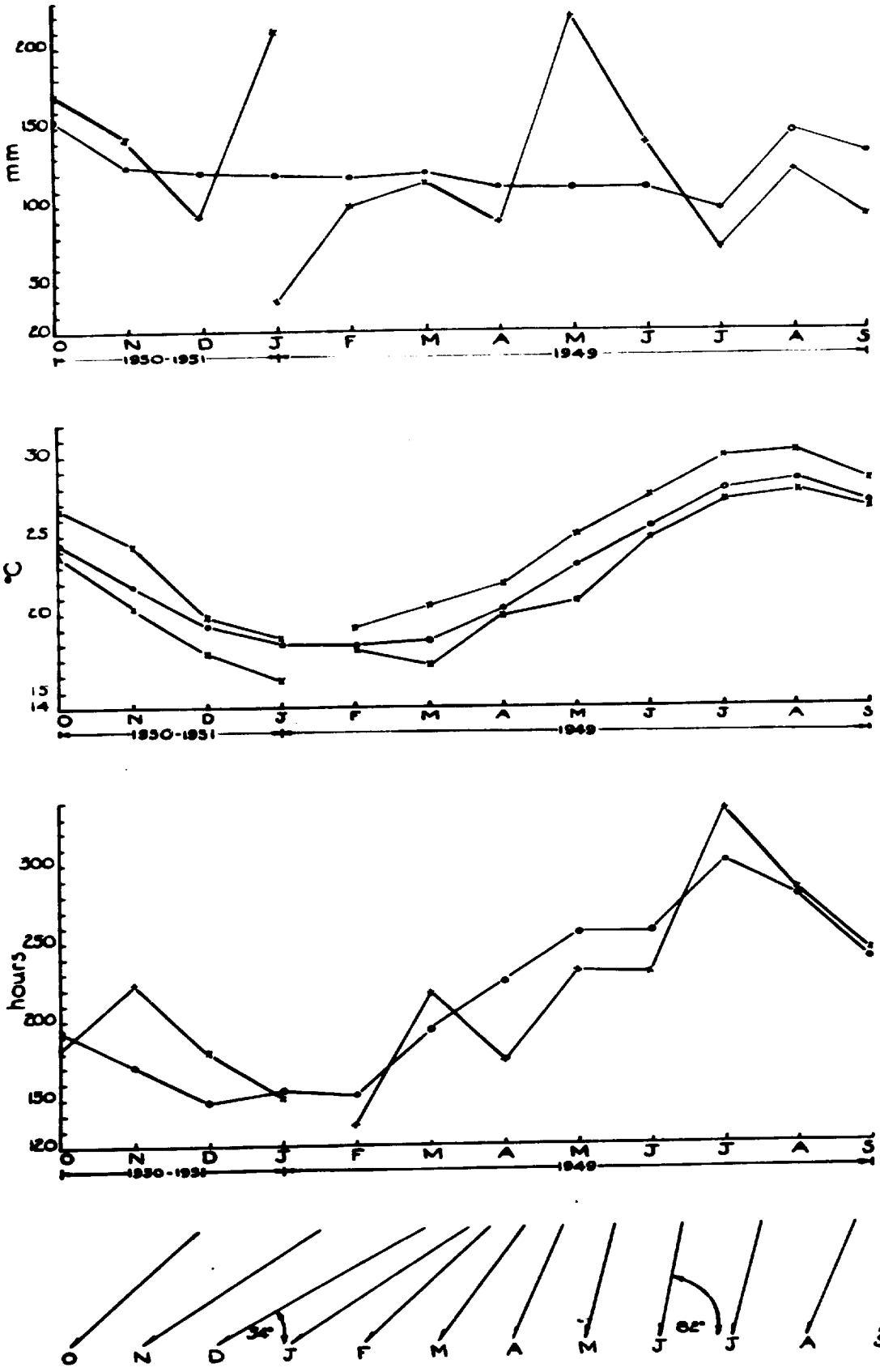

mm
200
150
100
50
20
O N D J F M A M J J A S
1950-1951
1949
a
°C
30
25
20
15
14
O N D J F M A M J J A S
1950-1951
1949
b
hours
300
250
200
150
120
O N D J F M A M J J A S
1950-1951
1949
c
O N D J F M A M J J A S
d

Plate XV

TABLE 6

MONTHLY RECORDS OF MARINE ALGAE FOUND AT BERMUDA DURING THE PERIODS 10 FEBRUARY 1949 TO 13 JUNE 1949, 17 AUGUST 1949 TO 13 SEPTEMBER 1949, AND 6 NOVEMBER 1950 TO 6 FEBRUARY 1951

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept
CHLOROPHYCEAE												
Acetabularia crenulata		x	x	x	x	x	x	x	x		x	x
Acetabularia polyphysoides				x							x	x
Acicularia schenckii		x		x								x
Anadyomene stellata		x	x	x	x	x	x	x	x		x	x
Avrainvillea longicaulis		x					x	x	x		x	x
Avrainvillea nigricans		x	x	x	x	x	x	x	x		x	
Avrainvillea rawsonii								x				
Batophora oerstedi			x	x	x	x	x	x	x			
Blastophysa rhizopus						x						
Bryopsis duchassaingii					x	x						
Bryopsis hypnoides		x			x	x	x	x				
Bryopsis pennata				x			x	x			x	
B. pennata var. leprieurii		x	x	x	x			x			x	
Bryopsis plumosa		x	x	x	x	x	x	x	x		x	x
Caulerpa crassifolia		x	x	x	x	x	x	x	x		x	x
Caulerpa cupressoides		x	x	x	x	x	x	x	x		x	
Caulerpa fastigiata		x	x	x	x		x					
Caulerpa peltata							x	x			x	
Caulerpa prolifera		x	x	x	x	x	x	x	x		x	x
Caulerpa racemosa		x	x	x	x	x	x	x	x		x	x
Caulerpa sertularioides		x	x	x	x	x	x	x	x		x	x
Caulerpa verticillata		x	x	x	x	x	x	x	x		x	x
Chaetomorpha brachygona		x			x	x	x					
Chaetomorpha crassa		x										x
Chaetomorpha gracilis								x				
Chaetomorpha linum				x	x	x	x					
Chaetomorpha media		x	x		x	x	x	x				
Cladophora catenifera		x	x	x	x	x	x	x	x		x	

TABLE 6--Continued

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept
CHLOROPHYCEAE--Continued												
Cladophora fuliginosa		x	x	x	x	x	x	x	x		x	x
Cladophoropsis membranacea		x	x	x	x	x	x	x	x		x	x
Codium decorticatum			x	x	x	x	x	x	x		x	x
Codium difforme									x			
Codium intertextum		x	x	x	x	x	x	x	x		x	x
Codium isthmocladum		x	x	x	x	x	x	x	x		x	x
Codium pilgeri		x	x	x	x	x	x	x	x		x	x
Cymopolia barbata		x	x	x	x	x	x	x	x		x	x
Dasycladus clavaeformis		x	x	x	x	x	x	x	x		x	x
Derbesia marina						x						
Derbesia vaucheriformis		x		x								
Dichotomosiphon pusillus		x	x	x	x	x	x	x	x		x	x
Dictyosphaeria cavernosa			x	x	x	x	x	x	x			
Enteromorpha clathrata			x			x	x					
Enteromorpha flexuosa						x	x	x				
Enteromorpha intestinalis		x		x	x	x						
Enteromorpha lingulata		x	x	x	x	x	x	x	x			
Enteromorpha linza				x				x				
Enteromorpha marginata				x								
Enteromorpha plumosa			x	x	x	x	x					
Ernodesmis verticillata				x				x				
Halicystis osterhoutii							x	x				
Halimeda monile		x	x	x	x	x	x	x	x		x	x
Halimeda simulans		x										
Halimeda tridens		x	x	x	x	x	x	x	x		x	x
Halimeda tuna		x	x	x	x	x	x	x	x		x	x
Monostroma oxycoccum			x	x	x	x	x	x	x			
Neomeris annulata		x	x	x	x	x	x	x	x		x	x
Penicillus capitatus		x	x	x	x	x	x	x	x		x	x
Penicillus pyriformis		x	x	x	x	x	x	x	x		x	x
Petrosiphon adhaerens			x									

TABLE 6--Continued

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept
CHLOROPHYCEAE--Continued												
Rhizoclonium crassipellitum						x	x	x				
Rhizoclonium hieroglyphicum						x						
Rhizoclonium hookeri		x	x	x	x	x	x	x	x		x	x
Rhizoclonium riparium						x	x					
Rhizoclonium tortuosum				x								
Siphonocladus tropicus							x					
Udotea conglutinata		x	x	x	x	x	x	x				
Udotea flabellum		x	x	x	x	x	x	x	x		x	x
Udotea wilsonii								x				
Ulva fasciata		x		x	x	x	x	x	x		x	
Ulva lactuca		x	x	x	x	x	x	x	x			x
Ulva lactuca var. rigida			x	x	x	x	x	x			x	
Valonia macrophysa		x	x	x	x	x	x	x	x		x	x
Valonia ocellata								x				
Valonia utricularis							x					
Vaucheria bermudensis				x	x	x	x					
Vaucheria dichotoma		x	x	x	x	x	x				x	
Vaucheria nasuta				x	x			x				
Vaucheria piloboloides			x	x	x							
PHAEOPHYCEAE												
Aegira zosterae			x	x	x	x	x	x	x			
Colpomenia sinuosa		x	x	x	x	x	x	x	x			
Dictyopteris delicatula		x	x	x			x	x	x		x	
Dictyopteris justii		x	x	x	x	x	x	x	x		x	x
Dictyopteris plagiogramma		x	x	x	x	x	x	x			x	x
Dictyota bartayresii		x		x	x	x	x	x	x			
Dictyota cervicornis		x	x	x	x	x	x					
Dictyota ciliata		x	x	x	x	x	x					
Dictyota dentata		x	x	x	x	x	x	x	x		x	x

TABLE 6--Continued

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept
PHAEOPHYCEAE--Continued												
Dictyota dichotoma				x	x	x	x	x	x		x	
Dictyota divaricata		x	x			x	x	x			x	
Dictyota indica		x		x			x	x	x		x	x
Dictyota linearis			x	x		x	x	x	x		x	x
Dilophus guineensis		x	x	x	x		x	x	x		x	x
Ectocarpus duchassaingianus		x	x	x	x	x	x	x				
Ectocarpus elachistaeformis							x					
Ectocarpus mitchellae		x	x	x	x	x	x	x				
Hydroclathrus clathratus			x	x	x	x	x	x				
Myriactula minor						x	x	x	x			
Padina gymnospora			x									
Padina pavonia				x		x	x	x	x			
Padina sanctae-crucis		x	x		x	x					x	x
Padina vickersiae		x	x	x	x	x	x	x	x		x	x
Pocockiella variegata		x	x	x	x	x	x	x	x		x	x
Rosenvingea intricata				x	x	x						
Sargassum bermudense		x	x	x	x	x	x	x	x		x	x
Sargassum fluitans		x	x		x	x	x	x	x			x
Sargassum natans		x	x		x	x	x	x	x		x	x
Sargassum polyceratium		x		x		x			x		x	
Sargassum vulgare				x	x	x		x				
Scytosiphon lomentaria			x	x	x	x	x	x				
Spatoglossum schroederi		x	x	x	x	x	x	x	x		x	
Sphacelaria tribuloides		x	x	x	x	x						
Sporochnus bolleanus						x	x	x	x			
Turbinaria tricostata		x		x	x		x	x	x		x	x
Zonaria zonalis		x	x	x	x	x	x	x	x		x	x
RHODOPHYCEAE												
Acanthophora spicifera		x	x	x	x			x	x		x	x

TABLE 6--Continued

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept
RHODOPHYCEAE--Continued												
Acrosymphyton caribaeum						x		x				
Amphiroa beauvoisii				x	x	x	x	x			x	
Amphiroa fragilissima		x	x	x	x	x	x	x	x		x	x
Amphiroa rigida antillana		x		x				x				
Antithamnion cruciatum		x	x	x	x	x	x					
Asparagopsis taxiformis		x	x	x	x	x	x	x	x			
Bangia fuscopurpurea			x			x	x					
Bostrychia binderi		x	x	x	x	x	x	x	x		x	x
Bostrychia binderi terrestre			x			x		x				
Bostrychia montagnei		x	x	x	x	x	x	x	x		x	x
Bostrychia radicans					x							
Bostrychia tenella		x	x	x	x	x	x	x	x		x	x
Botryocladia occidentalis		x		x		x	x	x			x	x
Botryocladia pyriformis					x	x	x	x				
Callithamnion byssoideum		x	x	x	x	x	x					
Callithamnion cordatum				x								
Callithamnion corymbosum		x	x	x				x				
Callithamnion halliae			x	x								
Callithamnion herveyi		x	x	x				x				
Callithamnion roseum		x							x			
Caloglossa leprieurii			x	x	x	x	x	x				x
Catenella repens		x	x	x	x	x	x	x	x		x	x
Centroceras clavulatum		x	x	x	x	x	x	x	x		x	x
Ceramium byssoideum		x	x		x	x	x	x				
Ceramium nitens		x		x			x				x	x
Ceramium subtile		x			x	x	x	x				x
Ceramium tenuissimum				x								
Champia parvula		x				x	x	x	x		x	
Champia salicornioides						x						
Chondria curvilineata		x			x			x				
Chondria dasyphylla						x	x					

TABLE 6--Continued

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept
RHODOPHYCEAE--Continued												
Chondria littoralis					x							
Chondria polyrhiza		x		x								
Chrysymenia halymenioides								x				
Chrysymenia ventricosa									x			
Coelarthrum albertisii				x		x	x					
Coelothrix irregularis		x		x	x	x	x	x				
Corynomorpha clavata			x	x	x		x					
Cottoniella arcuata		x			x	x	x	x	x			
Crouania attenuata		x	x	x	x	x	x	x				x
Crouania pleonospora				x	x	x	x	x				
Cryptonemia crenulata								x				
Dasya collinsiana		x	x	x	x	x	x	x	x			
Dasya pedicellata				x			x	x				
Dasya rigidula		x		x	x				x			x
Digenea simplex		x	x	x	x	x	x	x	x		x	x
Dudresnaya crassa			x				x	x	x			
Erythrocladia subintegra		x					x				x	
Erythrotrichea carnea				x	x	x	x					
Eucheuma isiforme		x	x	x	x	x	x	x	x		x	x
Falkenbergia hillebrandi		x	x	x	x	x	x	x	x		x	x
Galaxaura cylindrica		x	x		x	x		x				x
Galaxaura flagelliformis		x	x		x	x						
Galaxaura marginata		x	x			x	x	x				
Galaxaura obtusata		x	x	x	x	x	x	x	x		x	x
Galaxaura rugosa		x	x								x	
Galaxaura squalida		x	x	x	x	x	x	x	x		x	x
Galaxaura subverticillata											x	
Gelidiella acerosa		x	x			x	x	x			x	
Gelidium crinale		x		x				x				
Gelidium pusillum		x	x	x	x	x	x	x	x		x	x
Gigartina acicularis						x	x					

TABLE 6--Continued

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept
RHODOPHYCEAE--Continued												
Gracilaria confervoides		x										
Gracilaria cornea						x		x				
Gracilaria mammillaris				x								
Griffithsia globulifera					x			x				
Griffithsia schousboei			x		x	x						
Griffithsia tenuis				x			x					
Gymnothamnion elegans						x	x	x				
Halodictyon mirabile		x						x				
Halymenia agardhii			x	x	x	x	x	x	x		x	x
Halymenia bermudensis		x	x	x	x	x	x	x	x			
Halymenia floresia				x								
Halymenia gelinaria							x					
Halymenia pseudofloresia		x	x	x	x	x	x	x	x		x	x
Helminthocladia calvadosii						x	x	x				
Herposiphonia secunda		x				x	x	x	x			
Herposiphonia tenella				x	x			x				
Heterosiphonia gibbesii		x	x	x	x	x	x					
Heterosiphonia wurdemanni		x	x	x	x	x	x	x				
Hypoglossum tenuifolium				x		x		x				
Hypnea musciformis		x		x			x	x	x		x	
Jania adhaerens		x										
Jania capillacea					x							
Jania pumila		x				x	x	x	x		x	x
Jania rubens		x	x	x	x	x	x	x				
Laurencia corallopsis		x	x	x	x	x	x	x	x		x	x
Laurencia gemmifera						x	x	x			x	x
Laurencia intricata			x	x				x			x	x
Laurencia microcladia		x	x	x	x	x	x	x	x		x	x
Laurencia obtusa		x	x	x	x	x	x	x	x		x	x
Laurencia papillosa		x	x		x	x	x	x	x		x	x
Laurencia poitei			x	x	x	x	x	x	x			
Liagora ceranoides		x	x	x	x	x	x	x	x			

TABLE 6--Continued

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept
RHODOPHYCEAE--Continued												
Liagora farinosa		x	x	x	x	x	x	x	x			
Liagora mucosa			x			x	x					
Liagora valida			x	x	x	x	x	x	x		x	
Lomentaria baileyana			x	x								
Lophocladia trichoclados		x	x	x	x	x	x	x	x		x	x
Lophosiphonia bermudensis		x	x	x			x					
Lophosiphonia saccorhiza		x										
Lophosiphonia subadunca		x										
Murrayella periclados											x	
Nemastoma gelatinosum								x	x			
Nitophyllum wilkinsoniae							x	x	x			
Platoma cyclocolpa								x			x	
Polysiphonia binneyi							x					
Polysiphonia exilis						x						
Polysiphonia ferulacea		x	x	x			x	x				x
Polysiphonia gorgoniae						x						
Polysiphonia havanensis		x	x	x	x	x		x			x	x
Polysiphonia howei		x	x	x	x	x	x	x	x		x	x
Polysiphonia opaca				x	x	x	x					
Polysiphonia subtilissima			x	x								
Polysiphonia variegata		x	x		x	x	x	x				
Pterocladia americana		x				x	x	x			x	x
Pterocladia capillacea				x	x	x	x	x				
Seirospora purpurea		x	x	x	x	x	x	x	x		x	x
Spyridia aculeata		x		x				x				
Spyridia complanata			x		x	x	x	x				
Spyridia filamentosa		x	x	x	x	x	x	x	x		x	x
Thuretia bornetii		x		x	x			x				
Trichogloea herveyi						x	x	x	x			
Wrangelia bicuspidata		x	x			x			x			
Wrangelia penicillata				x	x	x	x					
Wrightiella blodgettii							x	x				
Wurdemannia miniata		x	x	x	x	x	x	x	x		x	x

TABLE 7

REPRODUCTIVE CONDITION OF MARINE ALGAE AT BERMUDA DURING THE PERIODS 10 FEBRUARY 1949 TO 13 JUNE 1949, 17 AUGUST 1949 TO 13 SEPTEMBER 1949, AND 6 NOVEMBER 1950 TO 6 FEBRUARY 1951

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept
CHLOROPHYCEAE												
Acetabularia crenulata		G*	G	G	G	G	G	G	G		G	G
Acetabularia polyphysoides				G							St	St
Acicularia schenckii		St		G								St
Batophora oerstedi			St	G	G	G	G	G	X			
Caulerpa crassifolia		St	St	St	St	St	St	St	X		St	X
Caulerpa prolifera		St	St	St	X	X	St	St	St		St	X
Caulerpa sertularioides		St	St	X	St	St	St	St	X		St	St
Codium decorticatum			G	G	G	G	G	G	G		G	G
Codium intertextum		St	G	St	St	St	St	St	St		St	St
Codium isthmocladum		St	G	G	X	St	G	G	St		G	X
Codium pilgeri		G	St	St	St	St	St	G	G		G	G
Cymopolia barbata		G	G	G	G	G	G	G	G		G	G
Dasycladus clavaeformis		St	St	St	St	St	St	St	St		G	St
Derbesia marina						Z						
Derbesia vaucheriformis		Z		St								
Halimeda monile		St	St	St	St	St	St	St	St		St	St
Halimeda simulans		St										
Halimeda tridens		St	St	St	St	St	St	St	St		St	St
Halimeda tuna		St	St	St	St	St	St	St	St		St	St
Neomeris annulata		G	G	G	G	G	G	G	G		G	G
Vaucheria bermudensis				G	G	G	G					
Vaucheria dichotoma		X	G	St	St	St	G				G	
Vaucheria nasuta				G	G			G				
Vaucheria piloboloides			G	G	G							

* See legend at end of table.

TABLE 7--Continued

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept
PHAEOPHYCEAE												
Aegira zosterae			U,P	U,P	U,P	U,P	U,P	U,P	U,P			
Colpomenia sinuosa		P	P	P	P	P	P	P	P			
Dictyopteris delicatula		St	St	St			St	X	0		St	
Dictyopteris justii		0	St	St	St	St	St	St	St		St	St
Dictyopteris plagiogramma		St	St	St	X	St	X	St			0	0
Dictyota bartayresii		0		St	0	0	0	St	X			
Dictyota cervicornis		0	0,G	St	X	0	St					
Dictyota ciliata		0,G	0	0	0	0,G	0					
Dictyota dentata		0	St	St	St	St	St	St	St		St	0
Dictyota dichotoma				St	X	St	St	0	St		0	
Dictyota divaricata		St	St			0	St	0			St	
Dictyota indica		St		St			0	0	0		St	St
Dictyota linearis			St	St		St	St	St	St		X	X
Dilophus guineensis		0	St	X	X	St	St	St	0		0	0
Ectocarpus duchassaingianus		P	P	P	P	P	P	P				
Ectocarpus elachistaeformis							P					
Ectocarpus mitchellae		X	P	P	P	P	P	P				
Myriactula minor						P	X	U,P	P			
Padina gymnospora			0									
Padina pavonia				0		0	0	0	0			
Padina sanctae-crucis		0	0		0	0					0	0
Padina vickersiae		0	0	0	0	0,G	0	0	0		0	X
Pocockiella variegata		0	0	0	0	0	0	0	0		0	0
Sargassum bermudense		G	G	G	G	G	G	G	X		St	X
Sargassum polyceratium		G		St		St			St		G	
Sargassum vulgare				St	G	St		X				
Scytosiphon lomentaria			P	P	P	P	P	P				
Spatoglossum schroederi		St	0	0	0	0	0	0	0		0	

* See legend at end of table.

TABLE 7--Continued

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept
PHAEOPHYCEAE--Continued												
Sporochnus bolleanus						St*	U	U	U			
Turbinaria tricostata		St		St	St		G	St	G		X	St
Zonaria zonalis		0,G	St	St	St	G	St	0	St		0	X
RHODOPHYCEAE												
Acanthophora spicifera		G	St	St	St			0	0		0	0
Acrosymphyton caribaeum						St		G				
Antithamnion cruciatum		St	0	St	St	St	St					
Asparagopsis taxiformis		G	G	G	G	G	St	G	St			
Bostrychia binderi		0	0	0	0	0	0	St	St		0	X
Bostrychia binderi terrestre			St			St		St				
Bostrychia montagnei		0	St	St	St	St	St	St	St		X	0
Bostrychia radicans					0							
Bostrychia tenella		0	St	0	St	0	0	St	St		X	X
Botryocladia occidentalis		St		0		St	St	St			St	St
Botryocladia pyriformis					St	St	St	0,G				
Callithamnion byssoideum		St	St	St	St	St	St					
Callithamnion cordatum				St								
Callithamnion corymbosum		St	St	G				St				
Callithamnion halliae			0	0								
Callithamnion herveyi		0	0	0,G				0				
Callithamnion roseum		St							0			
Caloglossa leprieurii			St	St	St	X	0	St				St
Catenella repens		St	St	St	St	St	St	St	X		St	X
Centroceras clavulatum		St	0	St	St	St	St	St	St		St	St
Ceramium byssoideum		St	0		0	St	St	St				

* See legend at end of table.

TABLE 7--Continued

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept
RHODOPHYCEAE--Continued												
Ceramium nitens		St*		St			St				St	St
Ceramium subtile		St			G	St	St	St				St
Ceramium tenuissimum				St								
Champia parvula		Θ				Θ	Θ	Θ,G	Θ		Θ	
Chondria curvilineata		St			St			St				
Chondria dasyphylla						St	St					
Chondria littoralis					St							
Chondria polyrhiza		St		St								
Chrysymenia ventricosa									G			
Coelarthrum albertisii				St		St	St					
Coelothrix irregularis		St		St	St	St	St	G				
Cottoniella arcuata		St			St	St	St	St	St			
Crouania attenuata		Θ	Θ	Θ,G	Θ	Θ	Θ	Θ				St
Crouania pleonospora				Θ	X	X	Θ	St				
Dasya collinsiana		Θ	Θ	Θ	Θ	Θ	Θ	Θ	Θ			
Dasya pedicellata				Θ			St	St				
Dasya rigidula		Θ		Θ	St				St			Θ
Digenea simplex		St	St	St	X	St	St	St	St		X	St
Dudresnaya crassa				G			G	G	G			
Eucheuma isiforme		St	St	St	X	St	St	St	St		X	St
Falkenbergia hillebrandi		Θ	St	St	St	St	St	St	St		St	St
Galaxaura cylindrica		G	G		G	G		G				St
Galaxaura marginata		St	St			St	St	St				
Galaxaura obtusata		St	St	St	St	St	St	St	St		St	St
Galaxaura rugosa		G	St								G	

* See legend at end of table.

TABLE 7--Continued

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept
RHODOPHYCEAE--Continued												
Galaxaura squalida		X*	G	G	G	G	G	G	G		G	G
Gelidiella acerosa		St	St			St	St	St			0	
Gelidium crinale		X		X				G				
Gelidium pusillum		St	St	St	St	St	St	St	X		St	St
Gracilaria mammillaris				G								
Gymnothamnion elegans						0	0	St				
Halymenia agardhii			0	0	0	G	0	St	0		St	0
Halymenia bermudensis		St	St	St	0	G	St	St	St			
Halymenia pseudofloresia		0	0	G	St	St	0	0	0		0	0
Helminthocladia calvadosii						G	G	G				
Herposiphonia secunda		0				0	0,G	0	St			
Herposiphonia tenella				0,G	St			St				
Heterosiphonia gibbesii		0	0	X	X	St	St					
Heterosiphonia wurdemanni		0	St	St	St	St	0	St				
Hypnea musciformis		St		0			0	St	0		0	
Laurencia corallopsis		St	St	St	St	St	St	St	St		X	St
Laurencia gemmifera						0	St	G			St	St
Laurencia intricata			St	St				St			St	St
Laurencia microcladia		0,G	0,G	0,G	St	0	0	0	St		0	St
Laurencia obtusa		0	0	St	St	G	0,G	0	St		0	0
Laurencia poitei			St	St	X	0,G	St	G	0			
Liagora ceranoides		G	G	X	St	G	G	G	X			
Liagora farinosa		St	G	G	G	G	G	St	X			
Liagora mucosa			G			G	G					
Liagora valida			G	St	St	G	G	G	G		X	

* See legend at end of table.

TABLE 7--Continued

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept
RHODOPHYCEAE--Continued												
Lomentaria baileyana			St*	ϴ								
Lophocladia trichoclados		ϴ	ϴ,G	St	ϴ	ϴ	ϴ	ϴ	ϴ		ϴ	ϴ
Lophosiphonia bermudensis		G	St	St			St					
Lophosiphonia saccorhiza		G										
Lophosiphonia subadunca		ϴ										
Murrayella periclados											ϴ	
Nemastoma gelatinosum								St	St			
Nitophyllum wilkinsoniae							St	ϴ	ϴ			
Platoma cyclocolpa								St			St	
Polysiphonia binneyi							ϴ,G					
Polysiphonia ferulacea		ϴ,G	St	G			ϴ	ϴ,G				
Polysiphonia havanensis		ϴ,G	ϴ,G	St	ϴ,G	St		St			St	St
Polysiphonia howei		ϴ	St	St	St	St	St	G	ϴ		ϴ	X
Polysiphonia opaca				G	X	St	St					
Polysiphonia subtilissima			St	St								
Pterocladia americana		St				St	ϴ,G	ϴ			ϴ,G	St
Pterocladia capillacea				ϴ,G	ϴ	ϴ	ϴ	ϴ,G				
Seirospora purpurea		X	ϴ	ϴ,G	St	ϴ	ϴ	ϴ	ϴ		ϴ	ϴ
Spyridia aculeata		St		ϴ,G				ϴ				
Spyridia complanata			St	X	X	ϴ,G	St	ϴ				
Spyridia filamentosa		ϴ	St	G	St	St	St	St	St		St	St
Trichogloea herveyi						G	G	G	G			
Wrangelia bicuspidata		St	St			St			St			
Wrangelia penicellata				St	St	St	ϴ					
Wrightiella blodgettii							St	ϴ				

* See legend at end of table.

TABLE 7--Continued

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept
RECAPITULATION												
A. Examined for reproduction		91	90	104	78	103	107	107	66		59	49
B. In reproductive condition		45	44	50	36	50	54	57	32		32	19
C. Percentage (B/A)		49	49	48	46	49	50	53	49		54	39

Legend:

- Θ Tetrasporangia
- G Gametangia, including cystocarps
- P Plurilocular sporangia or gametangia
- St Sterile
- U Unilocular sporangia
- X Species present but plants not examined for reproductive organs
- Z Zoosporangia

Blank spaces indicate months when species were not found.

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