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TABLE 2
Kinds of Plants in the Marine Environment

Phylum or Division*	Approx. No. Living Species	Proportion Marine	Predominant Size	Marine Occurrence
Algae				
CHLOROPHYTA				
Green algae	7000	13%	microscopic to massive	benthos
CHAROPHYTA				
Stoneworts	76	(13%)	macroscopic	(brackish benthic)
EUGLENOPHYTA				
Euglenoids	400	3%	microscopic unicellular	benthos: mud and shallows
CHRYSOPHYTA				
Golden-brown algae	650	± 20%	microscopic unicellular	plankton
Coccolithophorids	200	96%	microscopic unicellular	plankton
Diatoms	6000–10,000	30–50%	microscopic unicellular	plankton; benthos
XANTHOPHYTA				
Vaucheria	60	15%	filamentous macroscopic	benthos: mud
PYRROPHYTA				
Dinoflagellates	1100 +	93%	microscopic unicellular	plankton
PHAEOPHYTA				
Brown algae	1500	99.7%	microscopic to massive	benthos
RHODOPHYTA				
Red algae	4000	98%	microscopic to massive	benthos
CYANOPHYTA				
Blue-green algae	7500 described taxa; probably < 200 autonomous species	± 75%	microscopic to macroscopic	benthos (marine to brackish and fresh water)
SCHIZOMYCOPHYTA				
Bacteria	1500	12%	microscopic	ubiquitous
MYXOMYCOPHYTA				
Slime molds	450	0	[± microscopic]	– – – – – –
MYCOPHYTA				
Fungi	75,000	0.4%	microscopic	benthos
Lichens	16,000	0.1%	essentially microscopic	high intertidal
BRYOPHYTA				
Liverworts and mosses	25,000	0	[macroscopic]	– – – – – –
TRACHEOPHYTA				
Psilopsida, club-mosses, horsetails, ferns, cycads, conifers	10,000	0	[macroscopic to massive]	– – – – – –
Flowering plants	250,000	0.018	macroscopic to massive	benthos

lowlier assemblage, the algae, now enormously diversified in unconnected major groups. In this age the algae are altogether dominant in the marine environment. On the land the algae are scantily present as aerial organisms and are for the most part confined to specialized aquatic situations and to soil.

Two major groups of spore plants widely successful on land, the ferns and the bryophytes, are completely absent from the sea, even though in some tropical seashore areas the two environments are separated precisely by only a few centimeters.

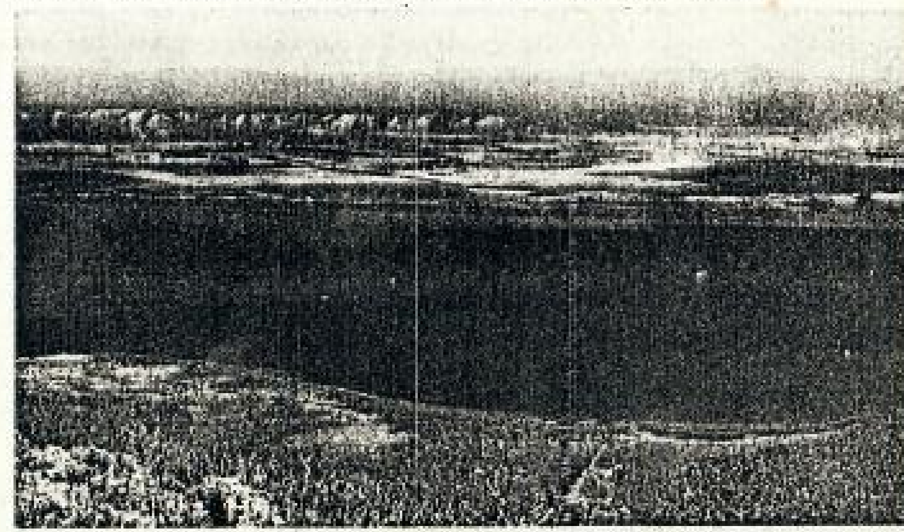
The study of marine bacteriology only a few decades ago began to reveal a diverse and important occurrence of bacterial organisms in virtually every habitat, while marine mycologists, developing their field even more recently, are now discovering marine fungi in far greater numbers than had been anticipated only a few years ago. The marine fungi, however ubiquitous, are all of small and obscure forms, and one does not find in the sea anything comparable to our terrestrial mushrooms.

As shown in Table 2, the conspicuous and macroscopic components of the marine vegetation are all members of but five divisions (or phyla) of the "Plant Kingdom"; other divisions are represented only by microscopic organisms of principal occurrence in the plankton.

Marine Flowering Plants

Few as are the kinds of angiosperms in the marine environment, they are, nevertheless, often dominantly conspicuous. The eel grass, *Zostera marina,* is a common inhabitant of bays and estuaries on both coasts of the United States (Figure 1-4), while the receding tide on rocky shores of the north Pacific re-

FIGURE 1-4. A narrow ship's channel into the harbor of San Quintin, Baja California, is outlined by dark beds of *Zostera marina* occupying the silty shallows.



14

Spermatophytes; Mangrove Associations; Salt Marshes

SPERMATOPHYTES

The marine flowering plants, commonly known as the "sea grasses," all belong to two closely related families of aquatic plants, the Hydrocharitaceae and the Potamogetonaceae. In the first of these are three marine genera: *Halophila, Thalassia,* and *Enhalus.* In the second, there are eight genera: *Phyllospadix, Zostera, Posidonia, Halodule (Diplanthera), Cymodocea, Syringodium, Amphibolis,* and *Ruppia.* Some 45 species have been described in all, but many of these remain poorly understood, and a few are known only from a single collection (Figure 14-1).

The marine angiosperms for the most part live in areas seldom visited by terrestrial botanists, and, since they usually do not lend themselves to inclusion in marine algal floras, they have generally been overlooked except by a very few specialists. Furthermore, most species live well submerged, and seldom if ever are uncovered by low tides. Some occur in waters too deep and murky for shore collecting, yet too shallow for a ship's dredge. Such habitats will probably yield additional species when they have been more thoroughly explored, just as happened in Pacific Central America in 1959, when the writer found two undescribed species in a series of shallow dives in muddy bays.

FIGURE 14-1. *A–D, Halophila: A,* part of a leafy plant; *B,* a male flower; *C,* a female flower; *D,* young fruit. *E, Syringodium filiforme,* showing terete leaves and part of a rhizome. *F–J, Halodule (Diplanthera): F,* part of a leafy plant with a rhizome; *G,* a leaf tip; *H,* a female flower; *I,* a male flower (anther); *J,* a young fruit.

The majority of the genera and species of sea grasses are of strictly tropical distribution. All of the genera of Hydrocharitaceae are characteristically tropical, and, in the Potamogetonaceae, only *Zostera* and *Phyllospadix* are typically of temperate range. *Posidonia* is of warm-temperate to subtropical distribution. *Ruppia* is essentially cosmopolitan and exceptional in occurring both in purely marine habitats and in brackish or inland alkaline waters.

Several points of geographical distribution of the tropical sea grasses are especially notable.

1) There is almost complete oceanic segregation of the species of the Old World from those of the New World.

2) About three-quarters of the species occur only in the Old World. The center of distribution appears to be in the Indo-Malaysian region. A second area of important occurrence is in the Caribbean Sea. This distribution, according to Ostenfeld, den Hartog, and others, indicates that the sea grasses are old plant types that originated not later than early Tertiary while the Panamanian isthmus was still open. Distribution between Indo-Malaysia and the Caribbean evidently occurred before the Panama land barrier arose, and subsequent speciation in the two areas has provided for several vicarious pairs of closely related species such as: *Thalassia hemprichii* and *T. testudinum; Syringodium isoetifolium* and *S. filiforme; Halodule uninervis* and *H. beaudettei.* The effectiveness of land barriers to sea-grass dispersal is evidenced by the fact that *Halophila stipulacea* did not occur in the Mediterranean until after the opening of the Suez Canal, through which it then quickly moved to establishment along the coasts of Greece.

3) The west coasts of Africa and the west coasts of tropical America are markedly deficient in sea grasses. Although several species are now known to occur in both these areas, they are sparsely represented. There is evidently a marked connection between the presence of tropical sea grasses and the occurrence of abundant coral-reef formations. This, in turn, is related to the occurrence of large tidal amplitudes that inhibit coral and coralline-algal reef development.

The coasts of North America have a good representation of both the temperate and the tropical sea grasses (seven genera), while South America, except for the Caribbean coast is almost without these plants. The more important and abundant of the North American marine phanerogams are *Zostera, Phyllospadix,* and *Thalassia,* which will be taken up in turn.

Zostera

The most widely distributed sea grass in America is *Zostera marina,* the eel grass, which occurs on the Pacific Coast from Port Clarence, Alaska, to Baja California and Sinaloa, Mexico. On the Atlantic it ranges from southwest Greenland to South Carolina. It is generally a plant of shallow lagoons and bays, but may occur at depths as great as 50 meters. In areas of its abundance it supports a great variety of marine animal life and serves as the staple winter food for sea brant. Canada geese and black ducks also depend upon it to a considerable extent. Because of these interrelations, great attention attended its sudden disappearance by "wasting disease" on the Atlantic Coast in 1931–

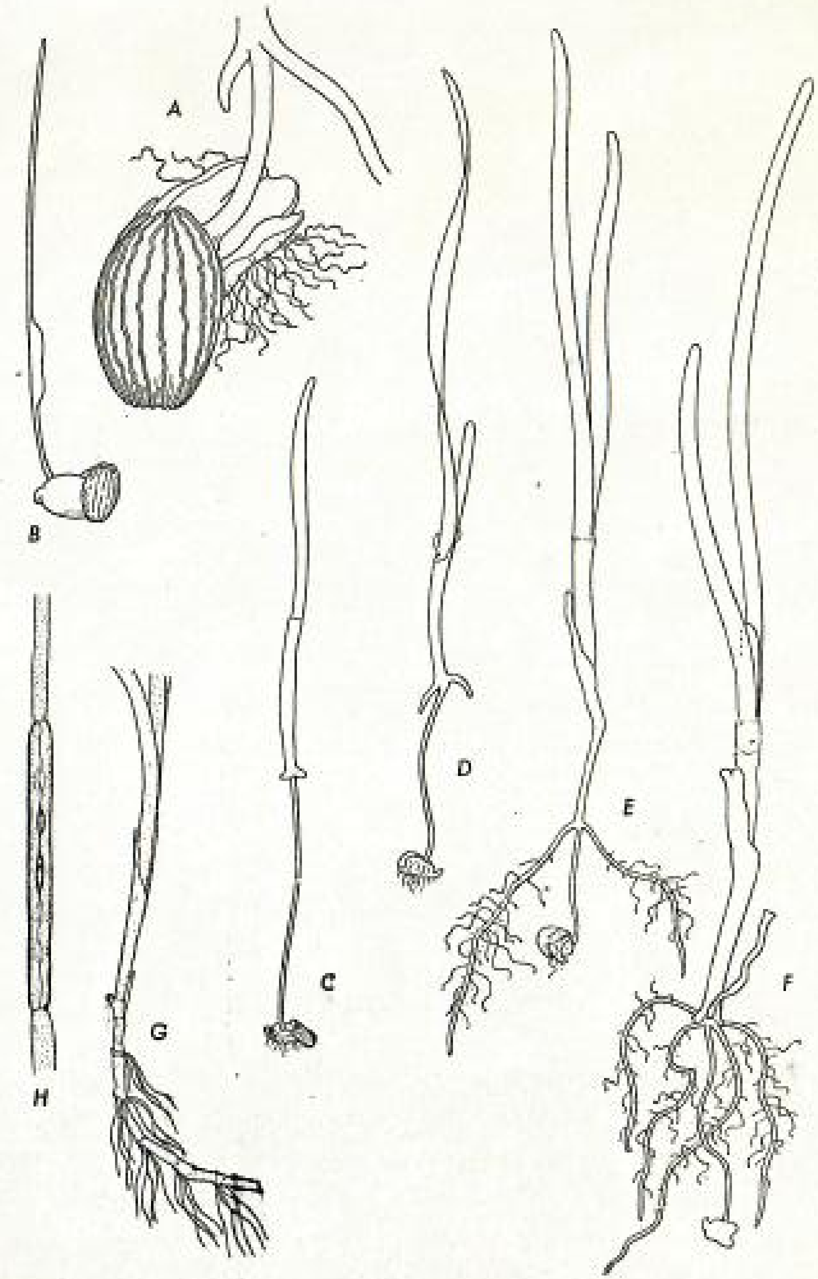


FIGURE 14-2. *Zostera marina: A,* seed and lower part of a young seedling showing costate testa, protruding flattened portion of radicle with root hairs, caulicle, and first pair of secondary roots; *B–F,* stages in development of seedlings; *G,* lower part of an older plant showing rhizome and roots from nodes; *H,* a spathe with ripening fruits partly evident (*A–F* after Setchell).

1932. Such decline resulted in reduction of wintering populations of Atlantic brant in some areas to as little as 2 percent of earlier years. (See Chapter 3 for comments on a possible causative organism, *Labyrinthula.*)

Setchell has provided several accounts of the morphology and phenology of *Zostera* in America, especially with regard to seasonal periodicity of growth and anthesis in response to temperature.

The seed of *Zostera* is more or less cylindrical, about 1 millimeter wide and 2 to 3 millimeters long. Its seed coat is marked with 16 to 25 ribs. Upon germination the testa splits longitudinally and allows the enlarging embryo to protrude. The radicle produces abundant root hairs, while the caulicle elongates through several centimeters of muddy substrate and carries up the plumule enwrapped by the cotyledon (Figure 14-2). The cotyledonary sheath ruptures along one side as the leaves expand and project beyond it. Meanwhile, adventitious roots appear from opposite sides of the first node and develop root hairs as they elongate. Further growth involves development of a rhizome by elongation of the internode and loss of the first leaves. Adventitious roots develop from each node, and from time to time lateral buds are initiated at the nodes. Depending upon environmental conditions, 1 to 2 years may be required to develop a plant to the stage shown in Figure 14-2,*F*).

The next stage of growth, which follows a period of quiescence, involves extensive development of the rhizome and its leafy branches, some of which become erect and produce the elongate fertile branches with 20 or more spadices enclosed within spathes. The fertile shoots are ephemeral and perish at the end of the season, while the prostrate shoots persist but become fragmented.

The flowers are imperfect, each consisting of either a pistil or a stamen. They are borne alternately in two rows in a series of about 12 on a spadix, and exhibit proterogyny. The style branches protrude first from the boat-like spathe, and only after these have fallen do the anthers project themselves. The ripening of seed is successive in the spadices upward in the fertile axis. From 500 to 1000 seeds may be produced on a luxuriant plant in a season, but most of these, falling into the mud, are grubbed up and swallowed by fish and water fowl. A few become favorably buried in the substrate by being carried into the cavities and tunnels of mud-burrowing organisms of the *Zostera* association.

Phyllospadix

The two Pacific coast species of this genus are unusual among sea grasses in being adapted to intertidal conditions often of considerable violence. They are the "surf grasses" which form emerald-green masses at or just below low water and are exposed generally to strong wave action and foaming surge. They are the cumaphytes or "surge plants," and are firmly fastened to rocky substrates by short, condensed rhizomes that often form a tough mat under a thin layer of shifting sand.

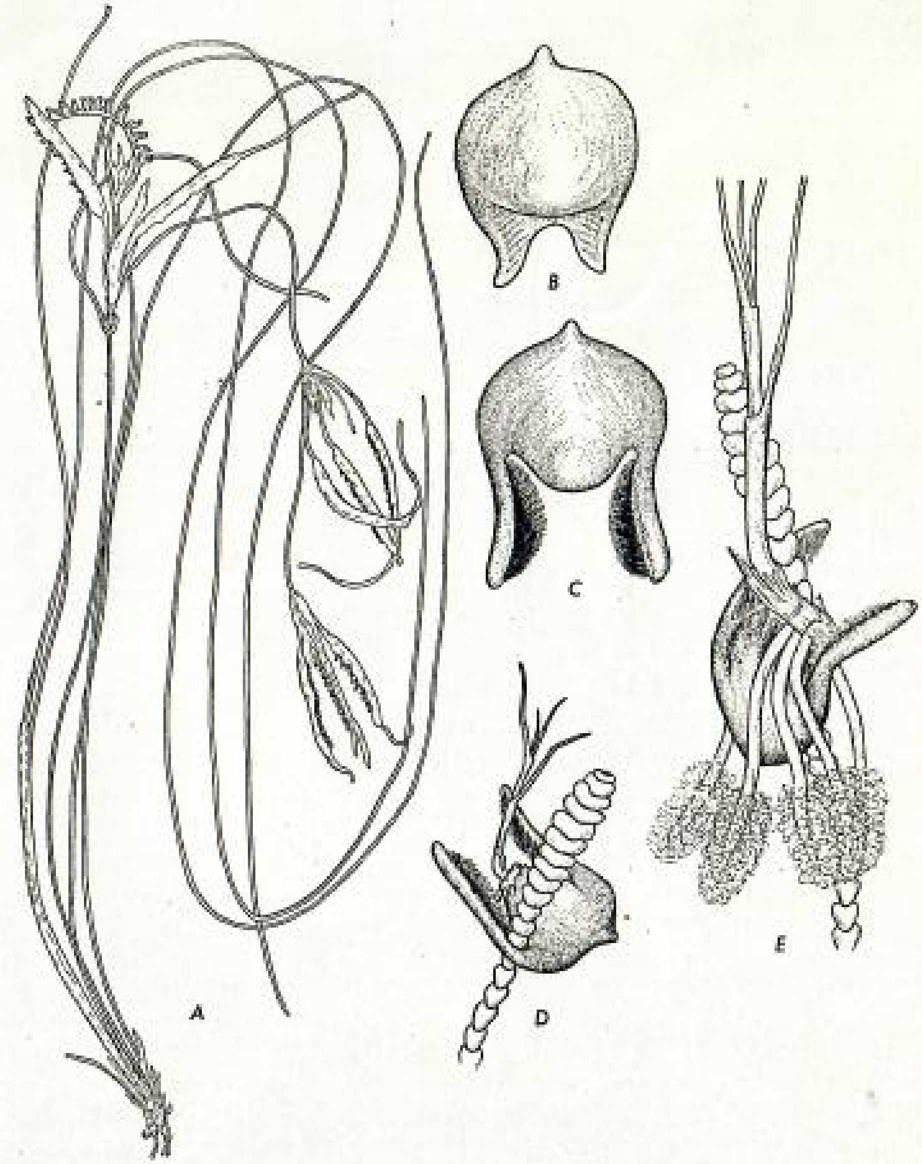


FIGURE 14-3. *Phyllospadix torreyi*: *A*, mature fruiting spadices; *B*, a young fruit; *C*, a mature fruit with exocarp worn away; *D*, germination of seed after attachment to a coralline; *E*, young plant with developing roots.

Sterile, leafy plants of *Phyllospadix* are usually encountered and are identified by leaf characters. *P. torreyi* has narrow, thick leaves 0.5 to 2 millimeters wide with inconspicuous nerves, while *P. scouleri* has broader, flat leaves 2 to 4 millimeters wide, with three distinct nerves.

Flowers are borne on dioecious plants in two rows on the side of a flattened spadix, and the whole inflorescence is enclosed by a spathe. In *P. torreyi* the flowering stems are 20 to 30 centimeters long and with two or three pairs of spadices (Figure 14-3). In *P. scouleri* the flowering stem consists of a peduncle only 1 to 6 centimeters long, supporting a solitary spadix.

Staminate plants are usually less numerous than pistillate ones, in the proportion of 1:12 or less. Pollination commonly occurs at time of flood following a low tide. The pollen is extraordinary in being filamentous, about 5 μ in diameter and 1000 μ long. It is often released by the first flood waves after a period of exposure, to be cast about among the more abundant pistillate plants. The pollen may at times move with the water to contact submerged stigmas, or may come to the surface, be deposited by receding waves, and refloated.

The manner in which young *Phyllospadix* plants gain a foothold as seedlings in the surfy environment is an interesting adaptation of the mature fruit. The fruits remain in serial position in the spadix until they are fully ripe. When freed they have a pulpy exocarp which becomes gradually worn away as the ripe, drupe-like fruit is dashed about in the surf. This leaves a dark, horny mesocarp. The mesocarp has two projecting, incurved arm-like structures that bear inwardly-pointing, stout, fringing bristles. By means of these bristly arms the fruit is able upon occasion to become fastened to the branch of an articulated coralline growing on otherwise bare or smooth rock (Figure 14-3,*D*). It clings so tightly by these retuse bristles that it may germinate in position and send out a quantity of stout roots from each segment of the developing seedling rhizome (Figure 14-3,*E*). Root hairs are produced in abundance, attach themselves to whatever they contact, and tend to collect sand that forms a sandy patch about the developing plant. A tussock gradually takes shape and may reach a half-meter in diameter.

Thalassia

The Caribbean turtle grass, *Thalassia testudinum*, is the most abundant marine phanerogam in the tropical western Atlantic region. It occurs in the United States, with only minor discontinuity, from Sebastian Inlet, east Florida, around the whole arc of the Gulf of Mexico to southern Texas. It occurs in a variety of loose substrates from mud to sand and broken shell wherever these materials are maintained in position by relatively calm water. In quiet lagoons a dense intertidal growth may occur, while in open water beds may be found at depths of up to 30 meters. The plants evidently tolerate salinity variations from 10°/.. to 48°/.., with optimum range of 25°/.. to 38.8°/...

Thalassia develops its erect, leafy shoots from a creeping rhizome buried 5 to 10 centimeters in the substrate. New shoots arise successively from near the apex of the rhizome. The erect shoots consist of a short stem bearing a small group of four to five exposed, ligulate leaves with sheathing base. The leaves have a median main nerve and four to six smaller, lateral vascular

bundles on either side. Between the vascular bundles a number of rather conspicuous air spaces are arranged longitudinally in the leaf.

Thalassia is dioecious. Staminate flowers are long-pedicelled with a three-petaloid perianth and six stamens. Pistillate flowers are nearly sessile in the spathe and have a beaked, six- to nine-celled ovary. In Florida, flowering may occur from May through July. Phillips points out that when flowering is observed, only one kind of flower is noted. He cites several instances in which 5 to 15 percent of the plants observed were either staminate or pistillate, according to their flowers, but were not mixed. He also suggests that in view of the generally sparse production of flowers that vegetative reproduction is probably of greater importance in the maintenance and spread of *Thalassia* plants than is seeding. Careful observations on dissemination and growth of seeds and of vegetative fragments have, however, not yet been made. The peculiar stalked, oval, pointed fruits may float for long distances and roll about in the surf before opening to discharge seeds.

MANGROVE ASSOCIATIONS

Aside from the marine phanerogams that grow wholly submerged, there is a group of seed plants closely associated with the intertidal marine environment, but only partly submerged. The tidal woodland, or mangrove, occurs in muddy tidal waters throughout most of the tropical world, and into temperate latitudes in some areas, depending upon oceanic currents and the presence of favorable temperatures. Mangroves of some 30 species occur as shrubs or trees belonging to several different plant families. Like the sea grasses, most of the species are Old World ones. Only four species, in the broad sense, occur in America, while southeast Asia has 23. Three of the American mangroves are widespread on both East and West Coasts: *Rhizophora mangle* (Rhizophoraceae), *Laguncularia racemosa* (Combretaceae), and *Avicennia nitida* (Verbenaceae).

Mangrove plants characteristically grow in quiet lagoons and estuaries, and are provided with an intricate growth of prop roots that support the vegetative portions of the plants 1 to 2 meters above the mud bottom. Ordinarily the leafy parts hang down to the level of high tide, so that in areas of considerable tidal amplitude the most conspicuous feature at low water is the thicket of arching masses of prop roots standing in the mud.

The mangroves support a unique algal vegetation consisting mainly of the red algal genera *Bostrychia*, *Caloglossa*, *Catenella*, and *Murrayella*. The overhanging leafy branches provide protection from excess light and desiccation at low tide, so that the prop roots commonly support a rich vegetation of these small algal species (Figure 14-4). The shade also sometimes allows the development of thick carpets or felts of algae on the mud. These usually consist of species of *Caulerpa*, *Cladophoropsis*, or *Vaucheria*.

Some of the best-developed mangrove algal floras are encountered in the West Indies, while some of the poorest occur in tropical Pacific Mexico.

FIGURE 14-4. Muddy bottom of a sheltered cove bordered with mangroves in Bermuda. The *Rhizophora* stilt roots are covered between tide marks with shaggy *Bostrychia* coated with mud, while on the mud below are multitudinous small black snails (reprinted from *Marine Algae of the Eastern Tropical and Subtropical Coasts of the Americas* by W. R. Taylor, by permission of the University of Michigan Press, copyright 1960).

Børgesen has described the association in some detail as it occurs in the Virgin Islands. In a typical mangrove lagoon in that region the uppermost and most prevalent of the algae is *Bostrychia tenella*. This is a bi-tri-pinnately branched, bushy, creeping form fastened by means of discoid haptera and forming a soft bolster 2 to 3 centimeters thick around the mangrove roots. Intermingled with it is *Catenella opuntia*, a decumbent, jointed form of cartilaginous consistency, and frequently, also, the delicate, membranous *Caloglossa leprieurii*. All of these plants are commonly exposed by falling tide, but are adapted by their chemistry and by the water-holding character of the spongy mass of intergrown branches, to survive considerable desiccation. Furthermore, they are seldom found except on well-shaded roots and those protected from drying currents of air. On the other hand, very heavy shading of the interior of the mangrove thicket, together with the relative stagnation of the water, is unfavorable, and poor or negligible growths occur. At lower levels, where there is little or only brief exposure, the plants are nearly all very finely dissected, richly branched, filamentous forms such as *Murrayella*, *Polysiphonia*, *Ceramium*, and sometimes *Bryopsis*, and the delicate *Caulerpa verticillata*.

The world distributions of the algae associated with mangroves, often referred to ecologically as the Bostrychietum, has been long studied and extensively documented by Erika Post of Kiel. Some of the species of *Bostrychia*, *Caloglossa*, and *Catenella* are widely distributed in nearly all tropical mangrove habitats, while others are evidently localized or of exceedingly discontinuous distribution. Some have achieved peculiar ecological adjustments, such as *Bostrychia flagellifera*, known from several mangrove habitats in Australia, but found on lava rocks under reduced salinity in Japan and New Zealand. *Murrayella* is a characteristic mangrove inhabitant in the Atlantic American tropics, but does not occur in the Pacific. Its nearest relative, *Murrayellopsis*, is a remarkable plant known only from depths of 6 to 11 meters in California and northwest Mexico as the nesting plant of the ocean goldfish, *Hypsipops*.

SALT MARSHES

In the temperate regions of the world the quiet, muddy shores of marine lagoons and estuaries are not clothed with heavy brush and tree vegetation, but with a low marsh flora consisting of such plants as *Spartina*, *Limonium*, *Puccinellia*, *Spergularia*, and *Salicornia*. These halophytes often are subject to partial inundation, but are seldom completely submerged for more than a brief time. They, like the mangroves, are terrestrial plants rooted within tidal reach. The channels of the salt marshes, however, are the habitats of numerous algae. Some of the commonest ones are cosmopolitan or widespread, boreal green algae of the genera *Ulva*, *Enteromorpha*, *Rhizoclonium*, *Percursaria*, and *Ulothrix*. *Vaucheria* is often abundant, and there may be a variety of blue-green algae on the mud. A *Bostrychia-Catenella* association may occur, and there may be various fleshy red algae attached to shells or debris in the shallow waterways. Some of the especially interesting marsh algae are the marsh fucoids that live in several areas of the north Atlantic and Baltic. They are modified forms of species of *Pelvetia*, *Fucus*, and *Ascophyllum* living either free on the marsh, rising and falling with the tide, or embedded in the mud. They evidently arise as loose-lying plants by vegetative budding from fragments of normal plants. A free-living form of the southern fucoid, *Hormosira*, occurs in New Zealand on mangrove marshlands.

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