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Seagrass Ecosystems

A SCIENTIFIC PERSPECTIVE

about the book . . .

Seagrass Ecosystems: A Scientific Perspective consists of a review and summation of research to date in the field, as initially presented at the International Seagrass Workshop held in Leiden, the Netherlands, and revised and expanded in accord with criticism and information provided by workshop participants. Five general research aspects of seagrass ecosystems are covered: productivity/physiology, systematics, decomposition, consumers, and system oceanography. Additional papers, covering such topics as the wasting disease and geographic reviews of areas whose seagrass ecosystems have been little reported until now, including Mexico, Israel, and Australia, have also been incorporated into the book at the suggestion of those involved.

The only book available that addresses the ecosystems of seagrasses rather than their biology alone, *Seagrass Ecosystems: A Scientific Perspective* is a valuable source of information on the nearshore sea for students, scientists, and coastal managers.

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CONSUMER ECOLOGY OF SEAGRASS BEDS

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I. INTRODUCTION

The seagrass bed is one of the most conspicuous and widespread biotope types in the shallow marine environment throughout the world. A dense vegetation of seagrass produces a great quantity of organic material by itself, and also offers a good substrate for epiphytic smaller algae, diatoms, and sessile fauna. The vegetation plays the role of sediment trap, and minute suspended particles, both organic and inorganic, are deposited in this biotope. It also creates unique microhabitats for small animals.

It has been recognized that various kinds of animals live in the seagrass beds, and many papers dealing with the animal communities in this biotope have been published in recent years. Extensive data were accumulated on Mediterranean *Posidonia oceanica* beds, *Zostera marina* beds on both the Mediterranean and Atlantic coasts of France, mixed seagrass beds in Madagascar and some oceanic islands in the Indian Ocean, and in the Red Sea. Studies on the animal components in the *Zostera marina* beds were carried out in the Danish Belt Sea, Baltic Sea, Black Sea, Far East (Siberian coast of the USSR and Japan), Alaska, and the east coast of the United States. Animal components in the *Thalassia testudinum* and *Halodule beaudettei* beds have been investigated on the Gulf Coast of the United States and in the

Caribbean Sea. Some of the authors have exchanged their results with each other, but others have been working in isolation because of geographical and language barriers and other limitations. It would be useful to review and compile the present state of studies on animal components of seagrass beds of the world.

In the first part of this chapter, a general description of the animal communities of seagrass beds in various geographical regions will be given; after that, some problematic topics on consumer ecology in the seagrass beds will be discussed.

Before going further, we will discuss the problem of terms. When one has to describe the group of animals found in a habitat, many authors use the term "community," while some others may use the term "biota" or "fauna" to discuss the same object. In ecology, the term "community" or "biocoenosis" has been used with different implication by different authors and schools. Some authors demand definite taxonomic composition in a uniform habitat, others imply the existence of close interrelationships, either trophic or social, among members of the assemblage, and some others use the term more loosely, merely to indicate the assemblage of organisms in a biotope. If the seagrass grows sparsely or consists of small patches of vegetation, the boundary of a seagrass bed itself raises a rather complicated problem. In the case of an animal assemblage in the seagrass bed, epifaunal animal components attached to the seagrass may have close correlation with the seagrass bed, but some infaunal components may be a part of the benthic community on surrounding unvegetated bottom, and no positive correlations with the seagrass can be proved. If one considers the nekton, some fishes reside in the seagrass bed permanently, some others reside there only seasonally, and for some others the seagrass bed is only a part of their foraging area in the coastal shallow waters. Nevertheless, these various components are linked together by trophic relationships.

Dr. Pérès, the second author, favors prudent use of the term and has used "organismic assemblage" to describe the whole fauna of a seagrass bed instead of "community." His term is not commonly used, however, and we will use the term community rather flexibly and

pragmatically, according to the operational definition of Mills (1969). He stated: "Community means a group of organisms occurring in a particular environment, presumably interacting with each other and with the environment, and separable by means of ecological survey from other groups." For nektonic fauna in a semiclosed habitat like a seagrass bed, the measurement of the degree of independence in species composition or trophic relations is one of the objects of an ecological survey.

II. SEAGRASS ANIMAL COMMUNITIES IN VARIOUS REGIONS

A. Tropical Seagrass Beds in Madagascar

The shores of the Tuléar area, on the west coast of Madagascar, are fringed by coral reefs. Furthermore, a barrier reef ("Grand Récif") stretches off Tuléar Bay. Both reef types were studied in detail.

The most internal part of the on-reef works out as a retention area of the suspended material, mostly for the lightest and smallest particles; so there seagrass beds occur owing to both the increase of humic substances in the sediment and the more sheltered conditions. For instance, going leeward, and with slowly increasing depth on the Tuléar Great Reef, one finds the following series: a scattered seagrass bed with mixed *Thalassia*, *Cymodocea*, and *Halodule*, associating with some Scleractiniaria and a great deal of large actinians, *Cryptodendron adhesivum* and *Actinodendron plumosum*; a seagrass bed of more dense population of the same species, but with a much richer fauna; a seagrass bed of *Syringodium* and *Thalassodendron ciliatum* with impoverished fauna.

In spite of small discrepancies which exist among the fauna of these three different seagrass beds, one can admit they are inhabited by a common fauna (Thomassin, 1971, 1973). In this animal community the same subdivisions as in the Mediterranean *Posidonia* beds may be recognized. On the living leaves one finds a diatom felt, foraminiferans, many hydroids, copepods, amphipods, a great deal of small gastropods, such as *Phasianella*, *Smaragdia* and Cerithidae. There are other groups of animals swimming under the leaf canopy: amphipods,

isopods (*Paracilicaea*, *Synisoma*), carid shrimps, small cephalopods, and fishes. The most important part of the community occurs on the sediment itself, where polychaetes and echinoderms are numerous; among this latter phylum, asteroids of the family Oreasteridae are the most diversified, with species of *Pentaceros*, *Pentaceraster*, *Protoreaster*, the cushionlike *Culcita*, regularia echinoids (*Tripneustes*, *Toxopneustes*, *Astropyga*); holothurioids (*Holothuria*, *Halodeima*, *Synapta*), and endopsammic ophiuroids (*Amphioplus integer*) are also abundant. Among the gastropods, some are detritus- or small algae-eaters, such as species of *Cypraea* and *Strombus*, but others are predators: *Mitra*, *Pusia*, *Vexillum*, *Conus*, *Naticarius*, *Polinices*, *Fasciolaria*, *Murex*, etc. The large crabs such as *Thalamita*, *Portunus*, *Matuta*, and *Calappa* should be mentioned as predators or scavengers. The suspension feeders, mostly represented by pelecypods, may be an exception to the unity of this animal assemblage: Lucinidae (*Codakia*) and Arcidae are predominant in *Syringodium-Thalassodendron ciliatum* meadows, whereas the large Pinnidae (*Pinna*, *Atrina*) are more common in the mixed seagrass beds.

On the inner part of the reef flat, with a water depth of only a few decimeters at low tide, one observes a seagrass bed of predominantly *Thalassia* associated with other phanerogams, namely, *Cymodocea*. Scleractinians are rather rare there; the most abundant taxa are crustaceans (hoplocarids, alpheid shrimps, portunid crabs) and mollusks. Among the molluscan fauna the relative dominance of gastropods is lower than it is in the outer reef flat, pelecypods amounting to 45%, chiefly suspension feeders of the family Lucinidae mixed with some Veeridae. On the fringing reefs of Mahé, Seychelles, J. D. Taylor (1971) described the animal community in the seagrass bed as very similar to that studied in the similar habitat of Great Reef in Tuléar. Echinoids such as *Toxopneustes pileolus* are rather common on sand bottoms in seagrass beds; *Echinoneus cydtomus* is common on seagrass beds in which the bottom is mixed with pebbles.

There is no report on the seasonality and feeding habits of fishes appearing in the seagrass beds. According to the checklist of ichthyofauna in the Tuléar region by Maugé (1967), more than

5

40 species were recorded from "herbiers à Phanérogames" and "herbiers du récif." In addition, many species recorded from the calm water of the lagoon may appear in the seagrass beds. Syngnathidae (*Corytheichthys*, *Hippocampus*, *Syngnathus*, *Syngnathoides*, etc.), various species of Labridae and Gobiidae are common members, and some species of Plotosidae, Serranidae, Gerridae, Lutjanidae, Scorpaenidae, Alteridae, Tetradontidae, etc. were recorded in the seagrass beds.

B. *Thalassodendron ciliatum* Beds on the Eastern Africa Coast

Unlike the fauna of the Mediterranean *Cymodocea nodosa* beds, which must be considered only as a facies of various soft-bottom animal communities, the *T. ciliatum* beds of tropical regions may exhibit a rather particular community; as an example one may cite the beds described by MacNae and Kalk (1958) an Inhaca Island (Mozambique), which also exist on the southwestern coast of Madagascar (Pichon, 1964). These *T. ciliatum* beds are at a rather deep level and are rarely exposed to the air.

Certainly the *T. ciliatum* beds include many species which also inhabit the shallower *C. rotunda* and *C. serrulata* beds, such as the pelecypods of the genus *Atrina*, and many echinoderms (*Holothuria*, *Synaptidae*, *Protoreaster*, *Tripneustes*, *Prionocidaris*, *Temnopleurus*, *Diadema*, etc.). But the *T. ciliatum* community also exhibits three main rather striking peculiarities: (a) the abundance and diversity of gastropods (*Trochus*, *Cypraea*, *Conus*) are higher than in the shallower *Cymodocea* beds and this induces some increase in pagurid abundance; (b) ophiuroids, which are rare in the shallower *Cymodocea* beds, are much more numerous here; (c) *T. ciliatum* green leaves exhibit a rather rich and specific sessile fauna: a species of *Zoanthus*, many characteristic hydroids and bryozoans, the ascidian *Polyandrocarpa*, etc. The fish fauna in this community is insufficiently reported, but a particular assemblage of crustaceans may be observed: *Typhlocarcinodes prioculatus*, *Etisus laevimanus*, *Etisodes electra*, and an unidentified xantid which grazes on the epiphytic felt of the leaves.

C. Seagrass Beds on the Mediterranean and French Atlantic Coasts

Marine phanerogams, like the terrestrial ones, always need a true soil, but the requirements about its granularity and humic substances content differ greatly by species. For instance, in the Mediterranean, *Posidonia oceanica* grows only on muddy sands, the humic substances content of which are rather narrowly defined, whereas *Cymodocea nodosa* may be observed on rather clean sands as well as on putrid muds (Molinier and Deguen, 1961). For the latter species Molinier and Picard (1952) noticed an amazing balance between leaf system and root system and their respective development: on clean sediment with low organic content, rhizomes and roots are poorly developed, but very dense leafage, certainly contributing much more toward fulfilling the metabolic needs of the plant, develops. However, on muddy bottoms where great amounts of organic material, and, consequently, enough nutrient salts occur, leaves are smaller and scarcer, but the rhizomes and roots develop highly. Salinity tolerances of the different seagrass species are also very diverse, both for the interstitial water and for the water washing the leaves.

D. Mediterranean *Posidonia* Meadows

As a good example of a seagrass bed one may take the Mediterranean *Posidonia oceanica* meadow, because this phanerogam forms dense extensive vegetation in bays or open coastal waters of the whole Mediterranean Sea, and it has the greatest influence on sedimentation conditions and exhibits the most complex biotic community (Molinier and Picard, 1952; Pérès and Picard, 1964) Extensive ecological works were carried out on the animal communities of *Posidonia* beds of various localities, mainly by the Endoume school.

Posidonia oceanica is an endemic Mediterranean species; one other species of the same genus grows on the temperate coast of Australia. Before describing the animal communities of fauna, three important peculiarities of this plant must be emphasized. First, at the end of the autumn season the oldest leaves fall down, and decaying

Among decapod crustaceans, most of the permanent residents belong to small sized species; various species of Hippolytidae (*Hippolyte*, *Latreutes*, *Heptacarpus*, *Eualus*), Palaemonidae (*Palaemon*, *Periclimenes*), and Alpheidae (*Alpheus*, *Athanas*). In summer, several species of young penaeid shrimps, *Processa japonica*, *Sclerocrangon angusticauda*, and some portunid crabs appear as seasonal residents. Some species spend their spawning season in the *Zostera* bed, and others spend only their juvenile stage. The small portunid crab *Thalamita sima* is the most dominant crab in the *Zostera* bed of Tomioka Bay; this coincides with the presence of *Thalamita* in some seagrass beds of Madagascar.

Taxonomic composition of fishes and decapod crustaceans and their seasonal trends give a proof of striking similarity or parallelism between them and those of the Mediterranean *Posidonia* beds and *Zostera* beds of the Atlantic coast. The trophic network analyzed by Kikuchi also exhibits a very striking similarity to that existing in the *Posidonia* beds; among the benthic invertebrates, seagrass grazers are very scarce and most of the species feed upon epiphytic microalgae, diatoms, and detritus on the *Zostera* leaves and bottom surface. Most fishes in the *Zostera* beds feed upon moving epifauna, especially small crustacea, and there are few piscivores. Diurnal rhythms of feeding of fishes were studied by Kitamori and Kobayashi (1958); Fuse (1962) and Kikuchi (1966) described seasonal changes of trophic network influenced by population fluctuations of both predator and prey species and the changeover of prey items accompanied by development of fish predators. Though none of them tried to calculate biological production and energy flow in the *Zostera* beds, Hatanaka and Iizuka (1962c) estimated production and conversion efficiency (amount of growth/amount of consumption of crustacean food) of *Sebastes inermis*, one of the dominant species in the *Zostera* beds.

I. *Zostera marina* Beds of the Pacific Coast of North America

Although there are many papers on the ecology and physiology of seagrass in the United States and Canada, quantitative descriptions of

animal communities are few. A general description of fauna in the *Zostera* beds is found in "Between Pacific Tides" by Ricketts and Calvin (revised by Hedgpeth, 1968). Here we encounter a fauna similar to that in the other geographic regions. Recently, studies on both *Zostera* itself and consumer components have been carried out on Izembek Lagoon by the staff of the University of Alaska. Tack (unpublished) studied fish fauna, their distribution and standing stock in the *Zostera* beds, and recorded 25 species belonging to 11 families.

J. *Thalassia* Beds in the Gulf of Mexico and Caribbean Sea

Thalassia testudinum beds are able to entrap suspended mineral particles and create terraces as high as 1 m above the level of surrounding bottom. They are often mixed with chlorophytes such as *Penicillus*, *Udotea*, *Avrainvillea*, etc., but the only common epiphytes are species of the genus *Fosliella*.

G. N. Voss and N. A. Voss (1960) have described at Bimini Island, Bahamas, turtle grass beds where *Thalassia testudinum* is mixed with *Halodule beaudettei* and *Syringodium filiforme*, whereas the channels between the beds are covered by *Halimeda*. The fauna is rather similar to that briefly studied by Rodriguez (1959) at Margarita Island, Venezuela, and exhibits three subassemblages; (a) on green leaves some epiphytic algae; (b) on and in the shallowest sediment some pelecypods (*Codakia orbiculata*, *Modiolus tulipus*), gastropods (*Cantharus*, *Nitidella*) and a holothurian of the genus *Thyone*; (c) in the deeper zone (0.5 to 2 m) a very rich fauna of large-sized gastropods (*Strombus gigas*, *Murex brevifrons*, *Fasciolaria tulipa*, *Aplysia protea*) together with some echinoderms, such as the asteroid *Oreaster reticulata* and the echinoid *Lytechinus variegatus*. In fact, it is not quite certain that the latter subassemblage is really linked with the turtle grass.

In the United States, O'Gower and Wacasey (1967) studied benthic communities in the *Syringodium* bed, *Thalassia* bed, and sand bottom in Key Biscayne and Virginia Key, Florida. As the sampling was carried out during low tide when the seagrass bed was exposed to air, the main

objects are infaunal animals. In polychaetous annelids, *Onuphis magna* and *Loimia medusa* were dominants and *Nothria*, *Notomastus*, *Semiodera*, *Terebellides*, etc. are commonly found in both seagrass beds. For bivalves, *Codakia orbicularis*, *Cardita floridana*, and *Chione cancellata* appeared frequently, and a bay scallop *Aequipecten irradians* moved among the seagrass rhizomes. As gastropods, *Columbella*, *Bittium*, *Nassarius*, *Prunum*, etc. are recorded. The authors analyzed the effects of water movement and shading on the occurrence of main component species by statistical methods.

Two species of sea urchin, *Lytechinus variegatus* and *Tripneustes*, range the whole area of the seagrass beds and graze the seagrass and algae. Moore et al. (1963a,b) estimated the consumption rate of *Thalassia* by two species of sea urchins. Size specific consumption rates were determined in laboratory experiments, size compositions and density of the urchins were surveyed in the field, and consumption rates were estimated per area basis per month. At the place of highest density, seagrass leaves consumed by *Lytechinus* reached 120 to 140 g dry wt/30 days, and this figure corresponds to maximal values of *Thalassia* production within the same period. Ogden et al. (1973) have shown that nocturnal migrations of the echinoid *Diadema antillarum* Philippi from patch reefs into surrounding beds of seagrass (mixed bed of *Thalassia testudinum* and *Syringodium filiforme*) occur in the areas of the Virgin Islands that were investigated. Grazing by the sea urchins on the seagrass during nocturnal excursions is responsible for the formation of halos of denuded seagrass beds around the reefs. Greenway (1973) has studied the grazing of *Thalassia testudinum* by the echinoid *Lytechinus variegatus* (Lamarck) in Kingston Harbor, Jamaica. Urchins were found to consume 24.0 dry wt/m^2-week of a mean gross production of 53.8 g dry wt/m^2-week. A minute fraction (0.06 g dry wt/m^2-week) was consumed by fishes, chiefly the scarid *Sparisoma radians*. Randall (1965) pointed out the importance of grazing by parrot fishes (Scaridae) and surgeon fishes (Acanthuridae) on seagrass in the Caribbean. Randall (1967) found 13 species of fishes (Scaridae and Acanthuridae) which has seagrasses (*Thalassia*

testudinum and *Syringodium filiforme*) in their gut contents. One of these, *Sparisoma radians*, averaged 88% (five specimens examined) of the gut contents as *Thalassia*.

In the *Thalassia* beds of Texas lagoons, seasonality of fishes and larger invertebrates was studied by Hellier (1958, 1962) and Hoese and Jones (1963). As the common fish fauna in the *Thalassia* bed, the following species were noted; several species of Syngnathiidae, *Gerres cinereus*, *Lagodon rhomboides*, *Gobiosoma robustum*, *Archosargus probatocephalus*, etc.

Finally, it must be pointed out that the present knowledge of fauna of *Thalassia* beds is quite insufficient, especially mobile phytal fauna, as well as sessile and sedentary fauna.

III. SEAGRASS BED SIGNIFICANCE FOR ASSOCIATED FLORA AND FAUNA

After reviewing the present knowledge of the animal communities in the seagrass beds of the world, we have to consider some general features of them, and point out the problems to be solved.

A. As a Structural Habitat or Shelter

1. The seagrass makes a dense submerged vegetation, and it increases the available substrate surface for epiphytic algae and associated fauna. For example, the leaf area index (leaf area/bottom area on which seagrass grows) in the *Zostera marina* bed in Southwest Japan is about 2 to 2.7 in winter and reaches about 4 to 5 in the full growing season (June). Therefore, epiphytic algae and benthic diatoms growing on the seagrass leaves also play an important role as primary producers. Differentiation of the plant body into leaves, stems, and rhizomes increases the diversity of microhabitats and results in an increase of ecological niches for associated biota.
2. Dense vegetation softens the water movement by currents and waves, and offers calm underwater space within it.
3. Depending on hydrodynamic conditions, suspended silt and other colloidal substances form sediments in the seagrass bed. Though this sediment trapping action is one of the general features of seagrass beds, the effectiveness of the activity is different by species, by growth forms and

topographical situations. The most significant case is the Mediterranean *Posidonia oceanica* beds. As is described in Sec. I, this species has upright growing rhizomes covered with paintbursh-like fiber. The sediment trapping action of this species is so effective that the *Posidonia* bed has to counteract its sinking into the ground by an upward growth of rhizomes, and the process leads to the building up of underwater terraces. In sheltered small bays, the wave action is not sufficient to prevent the rising of the terrace; then the terrace is able to reach near the water surface, and the terrace and floating leaves give the effect of a kind of breakwater at some distance from the shoreline. Inside this terrace water movement becomes very calm and fine sediment deposits there. Though it is not described in detail, *Thalassia testudinum* in the Gulf of Mexico and Caribbean Sea forms raised terraces. This *Thalassia* bed seems to be the climax form of succession in the submerged vegetation, like the *Posidonia* bed. In the case of *Zostera marina*, the most dominant seagrass in the northern hemisphere, rhizomes grow only horizontally, and sediment trapping ability is rather low.

4. By photosynthetic activity seagrasses produce oxygen and consume CO_2 dissolved in the water during the daytime. High O_2 concentration in the seagrass bed can support high densities of various animal forms. On the other hand, much oxygen is consumed by these plants and animals and by bacterial decomposition of organic debris in the seagrass bed at night. There are significant seasonal and diurnal fluctuations of O_2 concentration, CO_2 and pH, and other water quality factors accompanying the change of photosynthetic activity of grasses (Ledoyer, 1969f; Imai et al., 1950). Ledoyer (1964b) described nocturnal vertical migration of moving epifauna and suggested the migration was caused by the decreasing of dissolved O_2 at the bottom layer.

5. Excessive illumination in the daytime is diminished by the leaf canopy, protecting the bottom from insolation and permitting a shaded microenvironment to develop at the base of the vegetation. When the intertidal seagrass bed is exposed to the air, leaves cover the bottom surface and protect their inhabitants against strong sunlight and minimize the fluctuation of temperature and salinity. This shading effect will differ by species and growth form.

The interaction of several or sometimes all of the factors mentioned above is responsible for the seagrass bed function as spawning site or nursery ground of fishes and other mobile animals, even for species usually living in other habitats.

B. As Food Resources

So far as it has been reported, there are few invertebrates feeding on living seagrass leaves. Some omnivorous animals occasionally graze green leaves, but this grazing effect seems to be negligible. Large opisthobranchs such as *Aplysia* spp. and strombid snails are herbivorous, but their main food is not seagrass but the algae with it. Kristensen (1972), who examined distribution and activity of digesting enzymes of various marine invertebrates, reported that most marine invertebrates cannot digest structural polysaccharides because they lack adequate digestive enzymes. The only significant grazers are sea urchins. As was described in Sec. I, sea urchins are one of the most important components of seagrass bed communities in the world. However, both on the tropical coast of the Indian Ocean and in all temperate regions, sea urchins feed mainly upon algae and rotten seagrass leaves, and no evidence of green seagrass grazing was reported. On the other hand, in the Caribbean Sea several species of sea urchins actively graze on living seagrass, *Thalassia* (Moore et al., 1963a,b; Randall, 1964b; Ogden et al., 1973; Greenway, 1973). In the same region, Randall (1965, 1967) pointed out the importance of seagrass grazing by parrot fishes. Parrot fishes (Scaridae) and surgeon fish (Acanthuridae) are very common reef fish in all tropical shallow seas and are known as active grazers; however, most of them are algivores and coral grazers and do not graze significantly on seagrass except in the Caribbean Sea. Local difference of food habitats among the same taxonomical groups raises many questions to be solved. Further detailed studies are needed to ascertain the real facts of seagrass grazing in different geographical regions (ecological situations of seagrass and available alternative food, habits of grazers, presence or absence of digestive enzymes in grazers, possibility of existence of cellulose-decomposing symbionts, etc.).

Marine turtles and sirenians (manatees) are probably the only big vertebrate grazers on seagrasses. According to the compiled data

of Hirth (1971), breeding and feeding sites of the green turtle *Chelonia mydas* are spread through the whole area of tropical and subtropical regions. Various species of seagrasses were recorded as food for the turtle. However, both the sea turtle and sirenian populations have decreased in recent years, and their grazing effect on seagrass beds may not be so important. In the northern country, some species of geese and ducks feed upon seagrasses in the intertidal and shallow waters during low tide (Ranwell and Downing, 1959).

Most of the small invertebrates feed on algal felt. As epiphytic small algae, *Hypnea*, *Polysiphonia*, *Cladophora*, *Enteromorpha*, etc., are commonly recorded from different geographical regions. A considerable quantity of benthic diatoms grow on the leaves and fine sediments, including rich organic substances, deposit on them. In addition, micro- and meiofauna living in the algal felt are preyed on by macrograzers accompanying the algae. Small gastropods (Trochidae, Cerithiidae, Rissoidae, etc.) are all algal felt feeders. Many amphipods, isopods, and tanaids also feed on the mixture of microflora and detritus. Some of them which have strong mouth parts (*Cymodoce*, *Idotea*, *Amphithoe*, etc.) feed on the algae or rotten seagrass. Some of the phytal crustacea cling on the seagrass or on the epiphytic algae, waving their antennae in the water and collecting the suspended organic particles.

As there are few seagrass grazers, most of the plant materials are utilized by animals as semidecomposed organic substances on or in the substratum. Different stages of decay may correspond to different consumers. For example, some sea urchins or crustaceans feed on rather big pieces of dead leaves; deposit-feeding mollusks and polychaeta feed on much-degraded organic matter. The process of decomposition and successive change of food value for animals is an important subject to be analyzed. The role and importance of microorganisms in detritus food chains will be discussed in Sec. V.

IV. GENERAL FEATURES OF THE FLORA AND FAUNA

A. Ecological Subdivision of the Seagrass Bed Community

As is elaborately described for the Mediterranean *Posidonia* beds and the *Zostera* beds in Japan, the animal community in a seagrass bed can be subdivided into several subunits by microhabitat structure and mode of life of the animals. The first category is the biota on the green leaves. This consists of: (a) epiphytic felt flora and micro- and meiofauna living in it (many protozoans--ciliates, flagellates, foraminifers--free living nematodes, minute polychaetes, rotifers, tardigrades, copepods, and ostracods are included in this subcommunity); (b) sessile fauna (Hydrozoa, actinians, Bryozoa, tube-building polychaetes, and compound ascidians); (c) moving epifauna creeping and walking on the leaves such as gastropods, polychaetes, turbellarians, nemertini, crustaceans, and some echinoderms; (d) as a variation of moving epifauna, there is a group of swimming animals which are able to rest on leaves--mysids, hydromedusae, *Spadella*, small squids, and special fishes (*Lepadogaster*, syngnathid fishes) must be mentioned in this category.

The second category is the biota attached to stems and rhizomes. Some nest-building polychaeta and amphipoda (*Erichthonius*, *Corophium*, etc.), as well as some kinds of sessile fauna are commonly found in this layer. In the case of terrace-forming seagrasses, a special fauna develops in that layer.

The third category is mobile species living under the leaf canopy: decapod crustaceans, cephalopods, and fishes. This highly mobile fauna must be subdivided into several categories according to the residence period in the seagrass bed: (a) permanent residents, (b) seasonal residents, (c) temporal visitors which forage a wider area than the seagrass bed, and (d) occasional migrants. Generally speaking, permanent residents are smaller in size and mobility, while

The problem of detritus food chains is one of the most important studies in shallow-water ecosystems.

The assimilation of detritus and its associated bacteria by three species of macrofauna which are abundant in *Zostera* beds was investigated by Adams and Angelovic (1970) using radioactive tracer techniques. The amount of $^{14}CO_2$ respired per milligram of dry body weight by animals that fed on different types of labeled food was compared to determine the relative amount of assimilation of a particular food. Animals were fed sterilized and unsterilized detritus labeled with ^{14}C to determine if they assimilated either the detritus per se or its associated bacteria as food. All three species ingested and assimilated detritus. After 3 days of feeding, a small gastropod, *Bittium varium*, had ingested and assimilated more detritus per milligram of body weight than either the grass shrimp, *Palaemonetes pugio*, or the polychaete, *Glycera dibranchiata*. Both *Palaemonetes* and *Bittium* assimilated ^{14}C from labeled bacteria associated with the detritus as well as from the labeled detritus. In the case of *Bittium*, assimilation efficiency of sterilized and unsterilized detritus is almost the same (46.3% and 48.6%, respectively).

D. Seasonality of the Seagrass Life Cycle and That of Animal Components in the Community

Seasonal variations of animal populations must be investigated by adequate quantitative sampling methods and continuous efforts. The analysis of relationships between the seasonality of seagrass and that of animals in the seagrass beds will suggest that detritus-feeding animals and filler-feeding animals increase in the decaying season of seagrass; on the other hand, herbivorous mobile fauna increases in the growing season of seagrass and decreases in the decaying season (some of them may change their microhabitat to the bottom surface). In a well-protected inlet in north Japan, Imai et al. (1950) studied the seasonality of the *Zostera marina* beds which densely cover the main part of the inlet, the animal populations living in them, and some physicochemical factors of seawater.

They observed a cyclic exchange of nutrient elements between seawater and *Zostera*; dissolved phosphates and inorganic nitrogen compounds decrease during the growing season of *Zostera*, and increased again during the decaying period. Dissolved oxygen concentration and pH values also showed clear seasonal variation. In the decaying season (summer), dissolved oxygen concentration markedly decreased by reduction of photosynthesis and increase of microbial activity. A large number of minute *Monas* sp. (flagellates) appeared in seawater and were consumed by larger filter-feeding benthos and their planktonic larvae. The breeding season of oysters and other macroinvertebrates coincides with this mass appearance of flagellates. The authors considered that microbial populations first increase in the course of seagrass decomposition, and then the flagellates increase, consuming the bacteria. The seasonal cycle of the seagrass bed community must be different under various climates and other ecological conditions.

E. Implication of Seagrass Bed Production to Other Coastal Ecosystems

Here we consider energy exports from the seagrass system to surrounding biotopes via floating plants and migration of animals. After the fruiting season, old seagrass leaves die off and fall down; even green leaves are often split off from their rhizomes by wave action in stormy weather. Some of them immediately sink down and deposit in the seagrass beds, but others are carried away by currents and waves. A considerable portion of the detached seagrass leaves are stranded and make heaps on the shoreline, and decomposition and consumption are carried out in the heaps. The fauna in the heaps of dead seagrass leaves consists of both terrestrial and marine origin. Talitridae (Amphipoda), Tylidae (Isopoda), some gastropods, oligochaetes, some halophilous insects such as special groups of Collembola and staphylinid Coleoptera, and millepedes are common members of this community. In some Danish lagoons where a large quantity of dead seagrass leaves deposit, there has been found to be a reduction of

dissolved oxygen and production of H_2S, and a special sulfide system develops (Fenchel and Riedl, 1971; Rasmussen, 1973).

Another portion of the floating leaves is transported to other marine biotopes of the continental shelf; it deposits on the sea bottom and this supply of organic matter may enrich the biotopes there. There is scant advance in respect to quantitative evaluation of this lateral transport of materials since the pioneer work of Petersen and Boysen-Jensen (1911) and Boysen-Jensen (1914). Boysen-Jensen tried to evaluate the distribution of *Zostera*-derived detritus by the existence of pentosan, which is the intermediate decomposition product of structural carbohydrates. He followed the seagrass-derived material to the baymouth and downward. Recently, Poizat (1969) studied the distribution of organic detritus derived from *Posidonia oceanica* outside the bay where *Posidonia* grows. In his study areas near Marseille, there are large deposits of decaying plants near the baymouth which gradually lessen with distance and depth offshore. The particle size of this plant debris is largest at the baymouth, and it becomes finer accompanying the increase of distance from the living seagrass beds. He recognized a positive correlation between the total density of macrobenthos and the abundance of this biogenic detritus. Menzies et al. (1967) reported the presence of transported turtle grass leaves in the abyssal sediments off North Carolina and suggested that seagrass-derived detritus may play a role in organic enrichment of abyssal waters. However, there is no quantitative information on this aspect at present.

Another form of energy or material transport from seagrass beds to the surrounding environment is the migration of animals which graze or forage in the seagrass beds. For instance, a good example of the interconnection of *Thalassia* beds and coral reef communities in the West Indies is the nocturnal migration of thousands of grunts (Pomadasyidae) which move from reefs to seagrass beds to feed on invertebrates inhabiting the beds. It has been suggested that the fecal material of the fishes deposited on the reefs may constitute a significant energy import to the coral reef community (Ogden et al., 1972).

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