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Handbook of Seagrass Biology: An Ecosystem Perspective

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Applied Aspects of Seagrasses

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Introduction

Since even before some man-ape picked up a rock and hurled it at an enemy, humankind has approached the natural world with a canny eye open for answers to the question, What's in it for me? All animals survey the rest of nature for that which is edible and that which is dangerous; many, like man, change the face of the world as they find it, thus providing themselves a more suitable habitat. The human style has been to add more and more consciousness to that process.

One way to judge the feelings of humankind about an aspect of the environment is to consider another expression of consciousness—how artists have represented it. At least in the culture stemming from Western Europe, seagrass has not the cachet of the spreading chestnut tree nor of waves of wheat. In its natural habitat, seagrass may seem lovely to a scuba diver but none has been driven to composing notable poetry about it. Utilized out of that habitat, seagrass is apparently not inspirational either: there are no songs to the old seagrass-stuffed mattress nor seagrass-thatched roof, though both have been valuable to people at certain times in certain places. Perhaps the homely immediacy of such uses diluted their poetic power.

Consider how seagrasses make their appearance in two highly successful works of recent serious fiction. Based as it is on the life of the men who work the Caribbean turtle fishery, Matthiessens's (1975) *Far Tortuga* could be expected to contain some mention of turtle grass:

> "Well, he might have de luck to snag one comin and goin, cause green turtle out dere in de *day*. Dey out dere grazin on de sponges and de sea grass. But in de twilight dey go up under de reef. Ain't no turtle in de world gone to spend de night out dere amongst de grasses. . . ." The blue boat drifts in the green sea, in twenty feet of water (p. 194).

However, since *I Heard the Owl Call My Name* (Craven, 1973) concerns the life of Canadian coastal Indians, the reference is not so expected.

> "He knew the white fronts that came from Bristol Bay, and watched for the white markings on the dark necks of the Canada geese. He knew the black brants that fed late on the eel grass of Izemberg Bay *(sic)*, passing high over the village like a long whisper, like a sigh, on their way to Baja California. Here every bird and fish knew its course. Every tree had its own place upon this earth. Only man had lost his way" (p. 120).

In both novels seagrass appears as a mere detail, because for both authors the subject is man, but it is man in his environment, formed and forced by a nature into which he is fitted whether he recognizes or accepts it. In acknowledging that sense of earth as one interrelated system, their poetic imagination must give a nod to the distant green substance that is valuable to creatures of value to humankind. The barely mentioned seagrass helps sustain the books' characters indirectly but explicitly, and the characters are shown to acknowledge this.

The less imagination applied, the less value can be seen: this is especially true of economic value. If handfuls of seagrass could be ripped from estuarine muds and applied directly and immediately to some human need, to filling the stewpot or repairing the roof, these more distant effects might be of little interest. But as it is, this apparent digression into the world of fiction underlines the beginnings of our understanding that perhaps the most important applied aspects of seagrass ecology lie in the realm of those subtle connections to other aspects of the natural system that is the earth's biosphere.

Historical uses of Seagrass

Once such a concern with subtleties was more nearly unthinkable. When the world was far more threatening to humans than threatened by them, direct utility had to be the prime concern.

Perhaps merely because of the sources of reports available, eelgrass *(Zostera marina)* as used in northern Europe and North America is the one species with a varied and long record of direct uses, of a range and extent that is nowadays hard to believe. Scagel (1961) noted that both *Zostera* and *Phyllospadix* have been used to some extent by the coastal Indians of western North America for weaving baskets; one of the common names for *Phyllospadix* in the Pacific Northwest is "basket grass." Cottam (1934) reported that eelgrass ash was found at ancient village sites in Denmark; the plants were probably burned for salt and soda, although on islands poor in wood they may have been burned merely for warmth. They provided bedding for the people as stuffing for mattresses and bed ticks, and for their domestic animals, as a substitute for straw. Coastal Danes did use *Zostera* for a tough and long-lasting roof thatch as well; an example of a typical dwelling with such roofing is preserved in the Danish Folk Museum outside Copenhagen (Rasmussen, personal communication). Centuries later eelgrass fibers found use as an upholstery material, as packing, and as a compost for fertilizer. In the first decades of this century the United States even imported eelgrass, at $20–$30 per ton for use in insulation for sound and temperature control. It was sandwiched between layers of kraft, waterproof, or asbestos paper in single, double, or triple array, depending on the intended function of the particular insulation, and quilted to keep the stuffing from shifting. When World War I found Germany short of genuine cotton, eelgrass fiber was substituted for it in the manufacture of nitrocellulose (Cottam, 1934). Scagel (1961) says the harvesters scythed or mowed the plants at low tide, then spread them in the fields to dry partially. Then the harvested plants were soaked for a few days in fresh water, dried thoroughly, and were pressed into bales for shipment to manufacturers of the derivative products.

According to Kireyeva (1964), *Phyllospadix*, *Zostera marina*, and *Z. nana* have been used as stuffing material in the Soviet Union until very recently. Calling it "sea flax," Soviet researchers considered the commercial possibilities of *Phyllospadix* fibers; they noted that the fibers resisted rot and were exceptionally strong. The estimated possible yield of the resource was some 10,000 metric tons dry wt per year in the Vladivostok-south Sakhalin area (Anon., 1967).

Den Hartog and Polderman (1975) indicated the extent of economic interest in *Zostera* historically in the Netherlands as a sidelight to their considerations of the seagrass population changes in the Waddenzee. In 1782 Martinet described harvesting and preparing seagrass and its applications. Nearly a century later, in 1870, the Dutch government still appreciated the importance of the plants and ordered the Oudemans Committee to map the most important seagrass beds in northern Holland.

Through the ages, direct human use of seagrasses has apparently been a matter of employing an available and workable resource, one that was not expensive but not ideal either. The Dutch built sturdy and durable dikes from piles of *Zostera* (den Hartog, personal communication), but not even the plant's prodigiously slow rate of decomposition could make it competitive when brick and concrete became available and economically practical. None of the patients in the Bergen hospital complained when their eelgrass mattresses were replaced with foam rubber (U. Lie, personal communication), and the few thatchers left are not sad that their trade now uses only rushes. The famous Danish eelgrass cigar is an unlamented and unrepeated experiment (T. Fenchel, personal communication). Even the Seri Indians no longer use eelgrass for their children's toys, as Felger and the Mosers note in Chapter 14.

Contemporary Direct Uses of Seagrass

The demands of a burgeoning human population may reverse this wholesale trend away from the use of local resources to some extent and in a limited ecosphere, all may need the opportunism tribesmen once showed. Some of the apparently outmoded as well as some entirely new uses for seagrass may become significant.

NATURAL SYSTEMS

SEWAGE FILTRATION

Since natural seagrass systems serve as traps for sediments and organic material, they may filter effluents. In at least one recorded instance in Australia the efficacy of a *Zostera* meadow to filter raw sewage was established when the removal of the plants led to the poisoning of valuable benthos (McConnaughey, 1974). Researchers at Woods Hole have been interested in experiments incorporating seagrasses into natural effluent purification systems, but reportedly have not yet made concrete efforts in that direction (J. Goering, personal communication).

COASTAL STABILIZATION

Seagrasses, especially those that form dense meadows, affect the physical movement of water and its ability to carry sediment. Further, the powerful roots and rhizomes of most species effectively bind the sediments that may be caught by the baffling effect of the leaves. We discuss these properties at greater length below. Applying this to the capacity for the plants to stabilize the nearshore sea bottom directly to human needs to date has remained speculative. However, the U.S. Army Corps of Engineers is currently considering transplanting seagrasses to stabilize subsurface dredge spoil banks, as well as to revegetate and enhance disturbed areas (Boone and Hoeppel, 1976; Hunt, personal communication).

The effects of seagrass on currents and waves is less studied than its effects on sedimentary deposition and binding. There are no reports in the literature of applied experiments in this area. Offshore seagrass beds may be located by the surface slicks that form above them. This characteristic has proved useful to fishermen searching for Dungeness crabs *(Cancer magister)* that harbor in seagrass. Fishermen in southeastern Alaska are frustrated by this smoothing effect, since the calmest water means a bottom surface that nearly guarantees a dragging anchor.

HARVESTED PLANTS

PAPER

Eelgrass has been used in several experimental attempts to provide raw material for papermaking. The most recent of these (Leopold and Marton, 1974) considered only what type of fiber or paper could be made from the plants and what process was most suitable. They indicated that *Zostera* could not be used for making high-grade paper, though Scagel (1961) states that it has been used for this and Burkholder and Doheny (1968) claim that patents to process it for high-grade paper exist. They also claim *Zostera* alone could not be used for making satisfactory cardboard (contrary to the findings of Kizevetter, 1936). They did conclude, however, that both *Zostera* and the freshwater algae *Cladophora* could, by means of an oxygen pulping process, produce low-strength pulps useable as additives to newsprint, corrugated medium, and fiber and particle board. *Zostera* pulp, added to groundwood pulp up to a 20% mix reduced the breaking length but improved the tear factor in the completed paper, as compared to a product made from ground-wood alone. The *Zostera* pulp fibers originated mostly in the plant stems rather than leaves.

Kizevetter (1936) reported that *Phyllospadix* tissue was by structure suitable for paper making, but evidently no one has attempted to apply his findings. The species of surf grass are also difficult to harvest, which may partially explain the lack of applied work with cut *Phyllospadix*.

CHEMICALS

Soviet scientists have been actively investigating *Zostera* as a source of useful chemicals. One of these extracts, zosterin, is especially valued as a strong gelling agent (Paimeeva, 1973). A group from the Vladivostok Institute of Biologically Active Substances has worked on the pectic substances in eelgrass (Ovodova *et al.*, 1968), and have researched the digestive enzymes of creatures that eat *Zostera* (Shibaeva *et al.*, 1970). Lignin analysis, done at Dnepropetrovsk (Malinovskaya *et al.*, 1974), indicates that Black Sea *Zostera* contains on an average 14.8% lignin, while plants from the Sea of Azov contain 23.9%. Dudkin *et al.* (1975), working at Odessa, identified *Zostera* as a potential source of a substance from which to synthesize glycosylurea, a chemical useful as a supplement to feed for ruminants.

FERTILIZER

Van Breedveld (1966) compared seagrass to compost and commercial fertilizer for effect on strawberries and tomatoes. The seagrass, mostly

Syringodium filiforme, was gathered from Florida beaches and placed as a mulch around young plants. No attempt was made to remove salt from the seagrass. Fruit production of both tomatoes and strawberries was greatest with the seagrass mulch; furthermore, the mulch suppressed weeds, the fruits were cleaner and van Breedveld's colleagues judged that they tasted better. The author concluded that seagrasses made a perfectly satisfactory fertilizer. On the island of Malta in the Mediterranean Sea, drift seagrass (mostly *Posidonia*) is collected from the beaches and used as a mulch for planting trees in erosion holes in the island's limestone (S. J. Holt, personal communication).

Herbivory

Superficially it would seem that preparing a list of herbivores for which seagrasses are a regular part of the diet should be a straightforward task. In practice, however, it is not. Some that eat seagrass may not digest it, but rather use the epiflora and fauna growing on the plant leaves (Fenchel, 1972; 1977). Identifying those consumers that actually use the plants themselves is a problem that continues to be studied.

One promising research technique that may help to resolve such questions, and in the process help establish the role of seagrass in marine food webs in general, involves the use of stable carbon isotopes as tracers (McConnaughey and McRoy, 1976). We shall discuss this technique later. Until these techniques have been polished and used to check a wider range of food chains, the best evidence for identifying which animals utilize seagrass in their diets comes from the more traditional sources, field observation and analysis of stomach contents.

TERRESTRIAL HERIBIVORES

DIRECT HUMAN CONSUMPTION

Man the omnivore will try to eat anything, as anthropologists have noted for years, and thus accidental death by poisoning still stands high on actuarial tables. To its credit, seagrass is not known to have killed anyone who ate it; however, it is also not known to have ever generated gourmet joy, either.

The coastal American Indians of the northern Pacific rain forest region reportedly ate *Zostera* shoots: Turner and Bell (1963) noted this for the Vancouver Island area, and University of Alaska workers have encountered some Haida and Tlingit accounts of cooking young portions of the plants. These accounts, however, have not been substantiated, and nowhere has eelgrass figured as a favored food.

The one contemporary example of direct human herbivory of seagrass leaves and stems is the rare use of *Halophila hawaiiensis*, nibbled or added to salads like parsley. The flavor is very mild, akin to bland watercress, but strongly saline.

According to Scholander (1968), *Enhalus* has a submerged plum-sized fruit which Australian aborigines eat. He reported that this fruit also has a slightly salty taste; both pulp and rind were eaten.

Ehrlich and Ehrlich (1970) postulated that world food problems might lead research into developing "high-yield strains of salt-tolerant grasses (such as *Zostura (sic)* and *Phyllospadix*), and raise grains with salt-water irrigation." From the work by Felger and Moser in Mexico (1973), the use of *Zostera marina* seeds as a kind of grain by the Seri Indians has become well known. This research captured the popular imagination, much as the wasting disease made *Zostera* conspicuous by its absence. By December, 1973, the word had even reached *Feminine Fitness* magazine: Its feature column, "A Quickie Look at New Things" included a box headed "Eelgrass: The Answer to the Grain Shortage?" Perhaps caught by the idea of the grain's exceptionally low fat content (about 1.01% with 50.6% carbohydrate and 13.2% protein), the authors seemed to find a positive answer to their headline question. Though scientists are not so positive about that answer, the prognosis is hopeful enough that eelgrass was among the plants considered at a 1974 University of Delaware conference, "Seed-Bearing Halophytes as Food Plants". The working groups considered *Zostera* among the first species on which extensive work should be done. Although the special circumstances apparently leading to the heavy seed production in *Zostera marina* at the southernmost end of its Pacific range do not seem easily transferable to other areas (Felger and McRoy, 1974), at least one group plans to investigate domestication of the plants for agricultural development. In early 1976, Project Seagrain was soliciting technical information for experimental cultivation of eelgrass in northern California (Guenther *et al.*, personal communication). It seems possible indeed—but only possible—that the loaf of *Zostera* grain bread made during Felger's Mexican work will not be the last of its kind.

FODDER

Agriculturalists and chemists have considered many plants for their suitability as food for domestic animals. Seagrasses, since they use zones incapable of sustaining other fodder, have an appealing economic potential. Although there is evidence that historically the plants once were used as fodder and the chemical analyses have seemed promising (e.g. McRoy, 1970; see also Chapter 13) actual feeding experiments have been ambiguous at best. Bauersfeld *et al.* (1969), for example, found that sheep could not survive on a diet composed of 100% *Thalassia*, but when slightly less than 10% of their diet consisted of turtle grass, the sheep had better weight gain than with a normal corn-and-alfalfa ration. The investigators noted as a plus potential size of the resource (an estimated 2.8 tons dry weight of leaves per acre off the west coast of Florida) and as a negative that the leaves had to be washed in fresh water before being fed to the sheep. They did not speculate on the difficulty of harvesting plants commercially.

One of man's domestic animals is reported to eat seagrass; according to M. Robinson, New Guinea pigs swim out to the seagrass beds to eat the plants, probably *Thalassia* (R. C. Phillips, personal communication). However, no agricultural research incorporating seagrass as swine food has been uncovered. Nor have we heard of any research comtemplated as a follow-up to reports of elephants loitering in seagrass beds along the coast of Sri Lanka.

Despite the questions remaining and the distance to go before the cultivation of seagrasses as a direct or indirect human food source is possible, research along these lines is likely to continue if only because there is so much salt water and so many hungry people. Every year the concern grows further from the theoretical and closer to the urgent: as Bronowski wrote in 1969, "I guess the single most important biological contribution to world peace will be to produce plants which grow effectively in quite salty water."

OTHER TERRESTRIAL HERBIVORES

Waterfowl are among the most valuable creatures for which seagrasses are an important dietary component. Pintail *(Anas acuta)*, mallard *(Anas platyrhynchos)*, and green-wing teal *(Anas carolinensis)* ducks gorge on eelgrass seeds prior to fall migration when the seeds are available; they also eat epiphytic pelecypods from the plant leaves (R. D. Jones, unpublished manuscript). McRoy (1966) noted that perhaps half the diet of Canada geese, preparing to fly south from Izembek Lagoon on the Alaska coast at fall migration consists of eelgrass vegetation. Most of the diet of the nearly 200,000 emperor geese *(Anser canagica)* that also pass through Izembek in the spring and fall migrations consists of eelgrass (R. D. Jones, unpublished manuscript).

The small sea goose *Branta bernicla* sustains itself mainly on eelgrass. Cottam and Munro (1954) state that 80% of the winter diet of American brant, prior to the wasting disease, was eelgrass. According to Ranwell and Downing (1959), British brant eat *Zostera* rhizomes as well as leaves. The brant on the United States Atlantic coast take *Ruppia* when they are south of the range of eelgrass; on the Pacific they also eat *Phyllospadix* (Cottam *et al.*, 1944). McRoy (1966) estimated that brant in Izembeck consume about 180 g dry wt eelgrass per bird per day. Izembek brant have not been observed to eat rhizomes. Brant are important, popular game birds throughout their range, and in parts of Alaska brant hunting is more than a sport. Einarsen (1965) stated that as much as 10% of the coastal Eskimos' total subsistence waterfowl take consists of brant, and cites statistics suggesting that consumption averages half a brant per person per year for the whole of Alaska's Eskimo population. Steller's eiders *(Polysticta stelleri)* are also an important subsistence resource for the Eskimos and they too are partially dependent on eelgrass. Much of the population of these ducks molts in Izembeck Lagoon, where they feed by scraping the eelgrass leaves through their bills, removing the epiphytes for nourishment (R.D. Jones, personal communication).

Because of the black brant's capacity to utilize eelgrass and because of its tasty flesh, domestication experiments using pelletized dried eelgrass as feed were conducted on this species at the University of Alaska (Morehouse, 1974). The birds tamed adequately but did not thrive on their pellet diet. Insufficient washing of the leaves with fresh water was considered a major contributor to the unpalatability of the diet.

In northern Europe, *B. bernicla* populations have declined markedly since the wasting disease of eelgrass in the early 1930s, according to Salomonsen of the Copenhagen Zoological Museum (Einarsen, 1965). The overwintering population in the Netherlands went from more than 10,000 before the decline of the eelgrass to at most 100 by 1953. Some of this reduction is undoubtedly due to hunting pressure and habitat change, but Salomonsen believed the loss of the *Zostera* was the chief cause.

MARINE HERBIVORES

The millenial day may come when people or their livestock can rely on seagrass as foodstuff directly, but there are already marine creatures on which mankind has relied for years that have in turn relied directly on seagrass for food. These creatures have been converting seagrass into humanly assimilable protein for centuries with no help from humankind; it will only be human eagerness to harvest them or to alter their environment that will stop this.

TURTLES

An adult green sea turtle, *Chelonia mydas,* eats seagrass preferentially as its staple dietary item. Hirth (1971) lists seven seagrass genera in his table of food of mature green turtles. No entirely satisfactory number has yet been applied to the amount of vegetation a turtle will consume nor for the amount of animal matter it will include, but Hirth (1971) reports that six mature turtles collected off the South Yeman coast had stomachs solidly packed with an average of better than 2 kg of seagrass. The juveniles are believed to be chiefly carnivorous (Bustard, 1972).

Some typical examples of human use of this creature, one of the most conspicuous seagrass herbivores, were reported by Bustard (1969) to the First Working Meeting of Marine Turtle Specialists. His report indicated how widespread both the use of turtles and the threat to them is. In beef-rich Australia the green turtle is totally and to date effectively protected from hunting: only the aboriginals in the north may take these animals, and then solely for their own use. Coastal development threatens some nesting beaches. In Fiji, however, turtle meat is considered a delicacy and one for which there is a growing demand. It is even served in hotels and restaurants. Strong conservation legislation does exist, but Bustard has some evidence that it was unevenly enforced. Curiously, since Fijian dugongs have been hunted out of existence and since sea turtles have become scarce, the comparatively unbrowsed seagrasses have come to be considered a local nuisance (Bridges, personal communication). In the British Solomon Islands Protectorate, turtle meat and eggs were part of the native diet, but are not an important one, perhaps in part because in the last decade there were three deaths in the Islands attributed to toxic turtle meat. In Tonga, turtles are a very important part of the native diet and catches have not kept up with demand. Conservation legislation protects the turtles and their eggs during breeding season, but its efficacy in the face of local demand for protein is not known.

Bustard's report chiefly concerned cultures still close to the hunting-gathering phase in the western Pacific, but around the world in the belt of warm ocean, the pattern has been similar: turtles have sustained humans. The Caribbean peoples portrayed by Matthiessen (1975), cited at the start of this chapter, illustrate the ways that sustenance went from subsistence level to marketplace economy. So too the Miskito Indians of Nicaragua are pictured by Ward and Weiss (1973) in their film "The Turtle People." Carr (1954) has written that the green turtles "were a prime factor in the growth of the Caribbean. . . . No other edible creature could be carried away and kept so long alive. Only the turtle could take the place of spoiled kegs of beef and send a ship on for a second year of wandering or marauding. All early activity in the new world tropics—exploration, colonization, buccaneering and the manueverings of naval squadrons—was in some way dependent on the turtle." In this era of freezers and aluminum cans, it is hard to imagine how crucial the turtles must have been, just as it is next to impossible to envision the enormous turtle flotillas that once must have inhabited the seas.

Protein, in the forms of meat, calipee for soup, and eggs, may be the chief economic value of green turtles, but it is not the only one. The shell of this species is not so handsome or so useful as as that of other sea turtles, especially the hawksbill, but it still finds its way into commerce; the leather produced from its hide is valuable, and its oil is in demand by the cosmetics industry (Bustard, 1972).

Currently these chelonians are the subject of some controversial mariculture efforts. Though Bustard (1972) favors this approach, vehement arguments against such endeavors have appeared in the literature (e.g., Ehrenfeld, 1974). Opponents to mariculture, as it has been attempted to date, chiefly stress that commercial ventures further strain a dwindling resource by increasing demand for its products and that they require huge imports of energy for artificial foods and habitats, since turtle "ranching", using natural seagrass impoundments, has so far proved economically unattractive. For discussion of a model turtle ranching program, see Hirth and Hollingworth (1973). Also Bjorndal (personal communication) has noted studies underway on aspects of *C. mydas* ecology on a 7 mi^2 *Thalassia* bed impoundment in the Bahamas, which could be a useful prototype for ranching studies.

SIRENIA

The sirenians, another past and still possible source of meat from the sea, also consume seagrasses and are also endangered for reasons unrelated to the abundance and productivity of their undersea pastures. Again the question is not one of replacing the Hereford steer but of preserving a resource for some people, often ones who cannot afford or do not have access to commercial meats.

Manatees. There are three specias of manatee still extant: the Caribbean manatee, *Trichechus manatus*; the African manatee, *T. senegalensis*; and the amazonian manatee, *T. inunguis*. In days of their abundance the first two species could be commonly found in estuarine and coastal sea waters. Some populations of Caribbean manatees once migrated seasonally, north from Florida as far as the Carolinas, and to Louisiana with the spring. Apparently some individuals maintain the pattern still, as sightings of manatees off New Orleans and Cape Hatteras in the summer 1975 indicated (Campbell, 1976). The FAO (1974) in an interim document has mentioned manatees eating locally available seagrasses.

Though their gigantic carcasses were once valuable to people for meat, oil, leather, and bone, now manatees are more valuable alive because of their copious appetites. A manatee may weigh as much as 500 kg and may devour up to 20% of its body weight per day in aquatic plants. Thus, these creatures could be invaluable weapons in the continuing battle humans have with aquatic weeds in the tropics (NSRC Guyana, 1974). The proposed manatee research center in Guyana will be attempting to breed manatees in captivity as a first step in domestication.

Dugongs. With the extinction of the algivorous Steller's sea cow, the dugong eats only *Halodule (Diplanthera) uninervis*. According to that marine and truly herbivorous. Gohar (1957) reported that the Red Sea dogong eats only *Halodule (Diplanthera) uninervis*. According to that author, the dugong is not a browser but a harvester: he states that it uproots the plants with its flippers and piles them in heaps, which it later devours. Gohar theorized that this behavior developed so that the sand and mud stirred up by the uprooting could settle out, thus sparing the animals' teeth from being worn down by gritty food and so that mobile fauna associated with the seagrasses could creep away, since not only do dugongs not eat animals but some of the creatures might prove poisonous or harmful to them.

This curious feeding behavior is not substantiated by observers in

Australia or India, as summarized by Husar (1975). She states that the animals grasp the plants with their lip bristles and uproot them with the roughened facial disc. Sand and mud are removed as they shake the food back and forth. The usual feeding pattern leads to completely cleared patches approximately 30×60 cm with these patches together forming a conspicuous feeding trail through seagrass beds. Anderson and Birtles (in preparation) observed dugong behavior in northern Queensland during May, June, and July of 1975 and reported that feeding trails took the form of serpentine gouges in the bottom sediment, apparently dug by snout action. Each trench represented the effort of a single dive; excavation depth averaged 4.5 cm, with widths as great as 26 cm. The length varied according to the density of the seagrasses, from approximately 8 m to less than 3, with the removal of plants reaching almost 80%.

The dugongs Anderson and Birtles watched were in beds of *Zostera capricorni* and *Halophila decipiens* and were evidently eating both species. Though reports are not numerous, the species of seagrasses generally preferred throughout the animals' range seem to be those with thin, relatively non-fibrous leaves and stems: *Halodule uninervis* in the Red Sea (Gohar, 1957); *Cymodocea* spp, off India (Jonklass, 1961) and Africa (Jarman, 1966); *Halodule uninervis, H. pinifolia, Cymodocea serrulata,* and *C. rotundata* off Queensland, Australia (Heinsohn and Birch, 1972); *Halophila ovalis* and *Halodule uninervis,* 98.8% and 1.2% respectively of the ailmentary canal contents of one dugong drowned off Townsville, Queensland, Australia (Murray *et al.*, 1976). Jones (1967) reported that two dugongs, successfully kept captive at Mandapan Camp in south India for more than six years were hand-fed 50-60 kg of cut seagrass per day. Barnett and Johns (1976) observed a lone female dugong during three months of the Australian winter: although *Halophila ovalis* and *Thalassia hemprichii* were also available to her, she ate only *Halodule uninervis* and *Cymodocea rotundata* —which the observers determined "by literally pulling the grasses which the dugong had uprooted out of her grasp. (Surprisingly, she did not flee.)" This dugong fed in seagrass patches, sparse to luxuriant in density, uprooting plants as described by Husar (1975) but not making conspicuous trails in the process. The dugongs' habit of uprooting the seagrasses on which they feed should encourage the continued growth of the favored plants, which are often pioneering species capable of colonizing disturbed substrate (den Hartog, 1970). When seagrasses are unavailable, dugongs will eat algae (Heinsohn and Spain, 1974).

Bertram and Bertram (1973) have discussed the economic importance once held by dugong meat and oil, which has always been great for local human populations exploiting the seacows as a protein resource. Commercial exploitation was heavy only in Australia during the nineteenth century. The oil was considered medicinally valuable; some 8–10 gal could

could be extracted from a large female caught in wintertime. The bones were esteemed for making "the best charcoal for sugar refining" but the carcasses were usually given to the Aboriginal harpooners. The same authors (1968) have noted, "Dugong meat, like that of manatees, has always been highly prized, both for its flavour and for the fact that it is surprisingly slow to putrefy." Implicitly, one reason for the intensive native hunting of dugongs is the meat's reputed aphrodisiac properties.

Australia has recently considered a study project on the coastal Aboriginals' use of dugongs (Nietschmann, unpublished mss.) but we have encountered no other reports of ethnologic investigations into native use of these mammals. Nor have we heard of any attempts to farm or ranch them, though Heinsohn and Spain (1974) have called for domestication efforts. Dugongs' natural rate of increase would pose a problem for such efforts: Heinsohn *et al.* (1976) estimate calf recruitment at one every three years.

Competition between dugongs and turtles. Most works that touch on the foods of either of these creatures note at least in passing that the other is the only probable large competitor for the production of the undersea pastures. Most then go on to point out that the question is academic since stocks of both are so depleted. If it is ever not to be academic, surely further impoundment studies with both species captive in the same meadow are called for.

Implicit in the reports to date, however, is that the competition under at least naturally occurring conditions would not be crucial to either. Turtles crop seagrasses by biting off leaves, and though they do indeed take *Halodule uninervis* when it is available, they also eat the tough seagrasses like *Posidonia* and *Thalassia*. Dugongs uproot their food, and the tough rhizomes and root systems of the latter two species (and *Zostera marina*, which turtles also graze [Babcock, 1937; Felger and Moser, 1973] when it impinges their range) would not be conducive to this feeding style. Dugongs apparently avoid rock and coral reefs, whereas turtles are often close to such underwater constructions; further, as Husar (1975) reports, dugongs graze out a patch and move on, leaving a feeding trail but not a denuded bed. There are reports from the few areas where both animals still exist of neutral or no interactions: in the Gulf of Aden, local fishermen claim to have seen dugongs feeding along with turtles (Hirth and Carr, 1970); in Queensland, Andersen and Birtles (in preparation) reported turtles surfacing within two meters of dugongs, with no evident problem for either species. Heinsohn (1976) supported the view that green turtles and sirenians would not be important competitors for this resource, but noted that grazing animals, such as dugongs, do divert productivity away from detritus food chains. If the grazing were heavy enough, the value of the seagrass beds for nurseries and shelter for other species could be reduced.

OTHER MARINE HERBIVORES

One scientific myth that has long permeated seagrass research is that few animals eat the plants. Like most such pervasive items of long standing, this proves not to be true. The following admittedly incomplete list of 154 species of direct, seagrass herbivores, both marine and terrestrial, is its own refutation of this truism (Table 1).

The reasonable question is, Why did this view gain such a foothold? One can only speculate on which answer or answers are most nearly true. A scan of the table for geography shows, as might be expected, that most of the undersea herbivores are warm-water creatures, but most scientists have not lived by warm coasts. So there has been the problem of bringing the observer to that which is to be observed. Further there has been the problem of bringing the observations together, since they have appeared everywhere from wildlife management journals to economic treatises on agriculture in the developing countries.

But perhaps the most reasonable answer is another question: to which of these species is seagrass a vital dietary component? Even the green sea turtle can shift to *Sargassum* if seagrass is unavailable (Heinsohn and Spain, 1974), and the black brant also devours *Ulva* and other algae (Einarsen, 1965). The blue crab is one of the most valuable commercial species listed in Table 1, but fishermen use meat and fish scraps to bait these animals. Van Westernhagen's (1973) study of the Philippine rabbitfishes confirms that they eat the tough leaves of *Enhalus* and *Thalassia*, but if the fish are given the opportunity, they prefer to eat more tender algae, just as does the widely cultivated milkfish. Numbers gleaned for the list usually show seagrass as only a percentage, often a low percentage, of the diet of the herbivores that have been observed to eat it. Seagrasses are potentially nourishing to herbivores (e.g., McRoy, 1970; Bauersfeld *et al.*, 1969) although not all agree on the extent of that nourishment potential (e.g., Tenore, 1975). The way in which nutrients are packaged may make them inaccessible to creatures without specialized digestive tracts (Murray *et al.*, 1976).

Despite the hours spent preparing the list, we believe its most significant feature is its incompleteness. We still do not know all species of herbivores nor all special of seagrasses consumed by them; we have scant idea of the percentages of diet, weights, areas, and values. In the realm of applied ecology, this is certainly one that calls for more research and for greater communication of research results.

Detrital Food Chains

No other single topic in the applied ecology of seagrasses is so frustrating to deal with as the indirect contribution of seagrasses to marine food chains through detritus.

The great bulk of material present in any seagrass meadow, in any single seagrass plant, at any time is destined for detritus. Recent intensive studies (J. Ogden, 1976) have indicated that at least in tropical areas primary herbivory accounts for a greater loss of seagrass biomass than had hitherto been believed; even in the *Thalassia* beds studied, however, tons of shed and bitten-off leaves drift away to enter the detrital system, eventually to sink to the oceanic abyss (Menzies *et al.*, 1967; Wolff, 1976; and Chapter 11).

Dead seagrass generally decomposes through the action of physical breakup and bacteria. The thronging bacteria are cropped by protozoan grazers, which are in turn eaten by carnivorous microzoa, that become the prey of yet larger fauna. Incrementally the predators grow larger, and we are as certain as we are of anything in the oceans, that these chains that begin with the dead seagrass end on the dinner table. Carr and Adams (1973), for example, found that detritus consumers were of major importance in at least one feeding stage of 15 out of the 21 species of juvenile marine fishes they studied.

Klug (Chapter 12) has reviewed decomposition processes of seagrass. For food chains it seems that these processes do not make seagrass detritus more digestible or palatable, but do make it an improved breeding ground to nourish bacteria (Fenchel, 1970). Continuing studies on different detritivores have emphasized that it is seagrass as a bacterial substrate, not as a food item, that is important for the nourishment of these creatures. Tenore's (1975) study of detrital utilization by the polychaete *Capitella capitata* provides what appear to be typical findings: at first the worms incorporated finer particles of eelgrass detritus, but the older the detritus, the larger the particles they consumed. This correlates well with the observation that initially the smaller particle sizes favor microbial development. And Tenore, like Fenchel before him, notes that the long decay period of seagrasses might be a very important factor in prolonging the term of available food for coastal detritivores.

Imai *et al*, (1951) illustrated an economically important facet of an eelgrass detrital food chain. Mangoku-ura inlet is the second largest source of the Japanese seed oyster industry; over 80% of its 1800-acre area is densely covered with *Zostera marina*. The late summer decay of some 2000 tons of shed eelgrass leaves lead to a prodigious bloom of bacteriophagous flagellates (identified as *Monas* sp.), which in turn provide food for oyster larvae. Aquaculturists along the inlet produce some 6 billion seed oysters per year.

Though documentation tying detrital seagrass directly to an economically valuable resource, such as Imai has provided, is rare, work currently underway may help quantify the extent to which seagrasses in natural systems become transformed into food for people via either detritus or direct herbivore food webs. Seagrasses have $^{13}C/^{12}C$ ratios significantly different from phytoplankton (Parker and Calder, 1970). The ratios of these naturally occurring, stable carbon isotopes are conservative enough to be followed through detritus and the tissues of animal levels away from direct herbivory. For example, McConnaughey and McRoy (1976) have speculated that the proportion of eelgrass-derived carbon present in the brown bears of the Alaska Peninsula might be calculated by this method. With such natural tracer techniques it would be possible to follow seagrass contributions in the sea qualitatively, by species composition, and quantitatively, by the amount of seagrass-derived carbon to be found in creatures along the food chain.

Nursery and Shelter

In this important realm, the worth of seagrass ecosystems is often well hidden beneath the water. In some cases the value of the undersea meadows as vital habitats has been discovered only when the population of some species important to humans has declined following the disappearance or removal of the seagrasses (e.g., Dexter, 1944); in others it is implicit from the presence of important species during certain life phases or seasons (e.g., Kikuchi and Pérès, 1977).

"Nursery" is as yet ill-defined in terms of ecological implications. An area can be a nursery because adult breeders congregate there for spawning, because larvae or juveniles concentrate there, or because of specific conditions necessary for a developmental stage, for example, eelgrass for attached bay scallop postveligers (Thayer and Stuart, 1974). "Shelter" seems more straightforward, but holds the implicit questions of Shelter from what? or Shelter for what? In the case of benthic vegetation, the answer can be anything from hiding places for highly edible fauna to protection from currents that could sweep weak swimmers away. After the wasting disease destroyed the eelgrass near Cape Ann, Massachusetts, spawn of the softshell clam *Mya arenaria* was swept out to the open ocean and a local commercial fishery closed as a result (Dester, 1944). Where Australian swans denuded seagrass beds, shrimp, oysters, scallops, and crabs died off, perhaps from the effects of the raw sewage that the plants had previously filtered (McConnaughey, 1974).

We know that there are many reasons for the presence of animals in seagrass beds: the environment is more stable, since seagrasses hold sediments, baffle currents, provide shade and concomitant temperature modification. Also, there is as much as 20 times more surface area for small sessile flora and fauna as compared to unvegetated areas. There are more hiding places for prey and thus more prey for predators to eat (McRoy, 1973). We also know that research is needed to identify and then quantify the exact reasons for and importance of seagrasses as nursery and shelter areas for a diverse fauna and flora.

Field work described by Ward and Wyman (1975) is exemplary for the kind of observation needed. They studied the behavior of two cichlid fish of Sri Lanka, the green chromide *(Etroplus suratensis)* and the orange chromide *(E. maculatus)*, in the Negombo Lagoon near the city of Colombo. The tiny (8 cm at maturity) orange chromide is known to European and American hobbyists as an aquarium fish, but in Sri Lanka it is caught for food by children. The larger (25 cm, 700 g) green chromide is an important local protein source; the authors estimated that 17,000 tons of these fish are caught from the one lagoon annually. The fishing method used for generations has involved the construction of an artificial mangrove habitat; a brush pile of cut mangroves is demolished once a month and virtually the entire resident finned population is netted.

Their underwater observations showed, however, that the brush-pile residents were fish that had lost out in the competition for preferred habitat; both chromide species first attempt to establish territories to live and breed in the seagrass beds surrounding the brush piles. For spawning, the green chromide clears a sandy patch in a stand of *Halodule* and lays adhesive eggs on the plant roots exposed at the borders of the excavation. The eggs almost perfectly mimic the nodular galls on the roots produced by the fungus *Plasmodiophora diplantherae*. Young green chromides when alarmed take up positions next to leaves of another seagrass, *Halophila*, which they mimic closely in size, color, and shape. Orange chromides, although they would also spawn on twigs and algal mats, often attached their eggs to the blades of *Halophila* edging the smaller patch they cleared, and lived by preference in the meadows.

Most knowledge of which species shelter in seagrass beds has come from the sampling net rather than the diver's eye, however, and so the kind of detail gathered by the foregoing work is rare in the literature. It is known that one reason blue crabs *(Callinectes sapidus)* may be found in eelgrass beds is that they eat molluscs that harbor there (Orth, 1975). It is known that Dungeness crabs *(Cancer magister)* are so likely to be found in eelgrass that one of the plant's common names in southeastern Alaska and British Columbia is "crab-grass" (personal observation), but why they are there is not known. Similarly the association of spiny lobsters with seagrasses has often reached the popular press: National Geographic magazine shows juvenile lobsters marching through a meadow (Herrkind, 1975) and Skin Diver magazine states, "Any bug-snatching skin diver knows that crawfish hide in the reefs during the day and feed in the grass beds at night" (Barada, 1973). Earle (1971) reported that carnivorous reef fish leave the coral for the seagrass at night because the hunting is good there, but Ogden (1976) found that the herbivorous reef fishes he studied made only occasional and brief forays to the seagrass beds. On the Gulf of Mexico coast, pink shrimp harbor in seagrass beds (Hoese and Jones, 1963) before they are recruited to the valuable commercial fishery. This has been shown in Florida waters as well, when dredging of seagrass beds reduced the shrimp (den Hartog, 1977). Off New England sport fishermen search out cunner *(Tautogolabrus adspersus)* in the eelgrass beds (Shumway and Stickney, 1975). Tabb (1966) documented the importance of seagrasses as habitats for the valuable seatrout, and with coworkers (1962) for stone crab. An important food item for the spotted seatrout is the pinfish, *Lagodon rhomboides*, which is not only found in the beds but eats the seagrasses in summer (Odum and Heald, 1972).

Juvenile sheepshed *(Archosargus probatocephalus)* live in seagrass beds (Springer and Woodburn, 1960), as do juvenile black sea bass (Briggs, 1973); both species are important game fish when adult. Young soft clams in Chesapeake Bay find eelgrass an ideal substrate on which to set for the two weeks before they burrow into the bottom, matured and dug in, they are protected from predators like blue crabs by the root mat of *Zostera* (Briggs, 1973). Eels *(Anguilla rostrata)* are found in Chesapeake eelgrass also—and sometimes are reported to eat it (Hildebrand and Schroeder, 1928).

Single significant species thus are often associated with seagrass, but the relationship of the faunal community in seagrasses to their habitat and to their potential impact on human needs has not been sufficiently investigated. One report which exploited the natural experiment of the wasting disease for such considerations is that of Stauffer (1937): he reported the loss of one-third of the species in the faunal community of the North West Gutter lagoons in Massachusetts following the disappearance of the eelgrass, including scallops, mussels, and shrimp species. Losses were heaviest among the epiphytic community and least among the burrowers, with swimmers suffering more than bottom-surface inhabitants. In New Zealand, the varied *Zostera* community includes not only snapping prawns *(Alpheus)*, mullet, flounder, and scallops *(Pecten novaezelandiae)* of direct interest to people, but also small bivalves, gastropods, and an "extremely rich" fauna of burrowing worms, food for varied and valuable carnivores (Morton and Miller, 1968). The small wading birds of New Zealand, particularly turnstones, prefer to forage in *Zostera* areas.

Other chapters in this book go into greater detail on animal communities of temperate and tropical seagrass beds. Some of these creatures are primary food sources for humans, but far more have indirect relevance. Kikuchi (1974) has noted that resident and transient fishes in eelgrass beds eat organisms that live in the beds, and that a greater number of such edible organisms live in the beds than in adjacent unvegetated areas. The Japanese work he reviews has emphasized the importance of the seagrass habitat to juveniles and subadults of commercial fishery species; a significant reason for that, he indicates, is the combination of suitable sizes and numbers of prey for young fish.

For whatever reason, typically though not universally (Rasmussen, 1977), a seagrass meadow is the habitat for a more diverse and dense fauna than are surrounding unvegetated areas. Research documenting this has been reviewed by Kikuchi and Pérès (1977), and by Kikuchi and Ogden in this volume (Chapters 9 and 10). Orth's (1973) findings, for example, illustrate the usual pattern: in Chesapeake Bay, the highest densities of infauna occur in the most dense *Zostera* meadows. When the local population of cownose rays *(Rhinoptera bonasus)* increased explosively and destroyed some of the Chesapeake eelgrass beds, he reported (1975) that not only was the diverse, dense epifaunal community of the leaves destroyed, but also that there were twice as many species and more individuals of infauna per sampling core prior to the plant destruction than after.

Seagrasses and the Face of the Earth

Like the true grasses that cover dry land, so too do the seagrasses both preserve and alter the terrain they cover. When tons of the Great Plains' topsoil blew away after it had been denuded of its tough sod covering, people immediately observed the devastation; they could not observe or predict the effects to follow the nearly contemporaneous destruction of the North Atlantic eelgrass beds. Some of these effects on the attendant fauna have been covered by Cottam (1934). Rasmussen (1973; 1977) considered the long-term faunal effects and patterns of recovery accompanying the return of the *Zostera* and discussed the effects of the plants' disappearance on the land, both the adjacent shores and the subsea floor of the fjord he studied. The differences were indeed large.

Why should this be so? Like the prairie turf, meadowforming seagrasses possess strong root systems capable of binding and holding the substrate from which the plants draw nourishment and maintain anchorage. The substances which seagrasses hold are soft and fine, a soil which would quickly succumb to the scouring action of waves and currents were it not for the plants. Thus, Rasmussen (1977) found that in the Isefjord, the benthic plants replacing the eelgrass were seaweeds attached to the now-scoured rocky bottom. They would only hold to the stones but not hold them down, for the shore after storms was littered with rocky rubble, its seaweed still attached, tossed there by waves.

Seagrasses not only hold substrate but build it. The dead plant material is trapped by the living, as the peatlike "mattes" of the Mediterranean illustrate (Molinier and Picard, 1952). For thousands of years *Posidonia oceanica* has constructed its own reefs, its rhizomes growing vertically to prevent the plants' being smothered by their own exuberance in trapping material. Scoffin (1970) quantified the current-slowing effects of a dense *Thalassia* bed in the Bahamas and found that flows as high as 40 cm/sec as measured immediately above the submerged leaf tips slowed to zero as measured at the sediment-water interface beneath the leaves. Under such circumstances sediment carried by the moving water would naturally fall out. Epiphytes often cover mature seagrass blades, making the leaf surfaces more sticky. Adhering particles are added to the substrate when the coating degrades (Burrell and Schubel, 1977).

This propensity of seagrass beds to collect materials has been applied by geologists to locate ancient seagrass sites. Not only are the sediment particle sizes finer within the beds, but the sediments also contain foraminiferal tests from species particularly associated with seagrasses. Because of the variety of habitats within seagrass meadows, there is also a greater variety of foraminifera species (Brasier, 1975). In warm waters, seagrasses have carbonate accumulation potentials comparable to those of coral reef communities: Davies (1970) credits seagrass with the development of an enormous, fringing bank 80 miles long, 5 miles wide, and 25 to 30 feet thick in Shark Bay, West Australia.

Davies' observations in Australia also provided further documentation for the seagrass meadows' soothing effects on troubled water. He reported (1970) that dense meadows flatten waves, and the beds were generally backed by calm water. Violent wave action can damage seagrass beds (e.g., Thomas et al., 1961) but the propensity of the beds to mute the effects of storm waves in shallow water can be of enormous value to people. Burrell and Schubel (1977) report computer studies estimating the considerable effect of seagrasses in reducing surge height during a Florida hurricane. Seagrasses and storms have been discussed by Thomas *et al.*, (1961) on the U.S. Gulf Coast, but we have encountered no specific discussions of storms vs. seagrass in north temperate waters.

Abuse of the Resource

Human perturbations of the environment become pollution when they have an unintended deleterious effect on those species and systems with which we share the biosphere as well as upon ourselves directly. Seagrasses too sometimes lose in the battle with the byproducts of human effort to alter the world.

THERMAL POLLUTION

If current hypotheses about the wasting disease of eelgrass prove correct (McRoy, 1966; Rasmussen, 1973, 1977; McRoy and Bridges, 1974), then *Zostera marina* may well be very susceptible to the chronic elevated water temperatures produced by electrical generation plants. Studies accompanying the operation of the Turkey Point generation facility in Florida showed that both *Thalassia* and *Halodule* were adversely affected and were killed immediately adjacent to the discharge canal by the hot water effluent (Zieman, 1970). Roessler (1971) showed *Thalassia* was affected where water temperatures were 3°C or more above the natural ambient. Decline in the *Thalassia* biomass near the thermal plume of a power generating plant in Quayanilla Bay, Puerto Rico, has been documented by Kohlemainen *et al.* (1975) but the authors caution that scouring as well as the water temperature had increased. Evidence is mounting that different seagrass populations within a given species have normal temperature tolerance limits appropriate to the normal climatic conditions of their geographic position, and that such local populations are very likely to be affected by alterations in their customary temperature regime (Thayer *et al*, 1975). Phillips (1974) has pointed out that the reproductive phenology of *Zostera* is probably temperature-dependent, and he cautioned that discharge of heated water could disrupt the plants' cycles.

SEDIMENTATION AND TURBIDITY

Many human activities increase the sediment load of the water column above seagrass beds. Among them are farming techniques upstream that increase the turbidity of entering river waters to outright dredge and fill operations that leave the seagrass meadows buried under meters of upturned mud. From whatever source the excessive sediment comes, different seagrass species seem to have different capacities to cope with it.

Phillips, in observations made early in 1976 (unpublished manuscript), noted that Texas *Thalassia* and *Halodule* transplants survived 10–20 cm of new sediments from dredging in the Port Aransas area. In the same area, Odum (1963) found *Thalassia* was killed by the deposition of approximately twice as much (30 cm) dredged sediment. Heinsohn (1976) reported several seagrass beds important to dugongs in Australia, damaged or destroyed by human-caused sedimentation, a factor now also threatening Mexican seagrasses (Lot, 1977).

Smothered beds may have difficulty reestablishing themselves even if enough sufficiently clear water remains above the new bottom level; Wood (1959) found that bottom sediment denuded of *Zostera* became oxidized, and he believed this might be one reason why the plants were slow to recover their former territory. Zieman (1976) reported a similar nonrecovery during 2 to 5 years of observation of *Thalassia* flats gouged by motor boat propellers. He believed the key may have been the plants' intolerance for the changed redox potential of the disturbed sediments.

In some instances dredging has not proved to be an unmixed curse for the affected seagrasses. Odum (1963) reported that seagrasses not smothered by the dredging in his study area actually gained in productivity and chlorophyll content, as compared to their undisturbed state, during the growing season following the one in which the dredging took place. While the dredging was going on, turbidity had lowered light penetration; productivity and chlorophyll content of the plants was also lowered. Odum thought the growth surge during the year following might be due to increased nutrients available from the redistributed dredge spoil.

Zieman (1975) reported that when dredging physically removed plants and rhizomes of *Thalassia testudinum* in tne Caribbean, the beds did not recover for many years. Boca Ciega Bay, Florida, was dredged and filled, reducing its area by 20% and altering many of its bottom characteristics, including the extent of its *Thalassia* beds. Taylor and Saloman (1968) estimated the cost of the bayfill operation at $1.4 million per year in lost fisheries and water sports.

Heck (1973) believed that the reduction in seagrass beds and the attendant reduction in fauna at the mouth of the polluted Fenholloway River in Florida stemmed from the increased turbidity and siltation caused by an upstream pulp mill rather than from any toxic substances in the mill effluent. Van Eepoel *et al.* (1971) and Grigg *et al.* (1971) have documented the death of deeper Caribbean seagrass beds and the thinning of shallower ones in waters made turbid by dredging. Phillips (1960) has noted *Thalassia* sensitivity to excessive turbidity.

TOXIC SUBSTANCES

Seagrasses seem relatively resistant to substances which can poison other forms of marine life. Chesher (1971) studied the effects of copper-contaminated (up to 6700 ppb) discharge from a desalination plant at Key West, Florida. The sediments in a *Thalassia* flat receiving the effluent showed high copper content and the echinoids inhabiting the flat were killed off, but the plants themselves seemed not to suffer during the three years they were under observation. Attempts to transplant the *Thalassia* into particular effluent regimes failed when the plants were not protected from local herbivores that ate the leaves and kept them cropped to the roots, but accompanying laboratory studies indicated that the photosynthetic activity of turtlegrass was depressed by 50% during 24-hr exposure to a 12% effluent. Seagrasses have been shown to concentrate cobalt, manganese, iron (Parker *et al.*, 1963), zinc (Parker, 1962), and probably copper (Barsdate and Nebert, 1971). The plants apparently store these elements without damage, at least to the levels so far investigated, but they may thereby make excess metals available for movement up the food chain (Zieman, 1975). A possible transfer of manganese and iron from *Thalassia* to sea urchins has been documented by Stevenson and Ufret (1966).

Zobell (1963) has pointed out seagrass susceptibility to oil pollution. The Santa Barbara oil spill of 1969 devastated the *Phyllospadix* beds on adjacent shores; Foster *et al.* (1971) reported that surfgrass readily takes up and holds oil, unlike the macroalagae that seem to resist oil adhesion. Up to 100% of the exposed blades were killed. Fully subtidal plants were undamaged, however. Rosenthal (personal communication) reported that by 1972 the *Phyllospadix* had not yet recovered. Dalby (1968) found that seagrasses along the English coast shed their leaves after being contaminated by crude oil but were able to regenerate new blades from protected roots and shoots.

Too much of a good thing can be toxic; for example, nutrient concentrations from sewage outfall. Zieman (1975) pointed out that since seagrasses can take in nutrients through the leaves as well as through the roots, moderate amounts of extra nutrients could well enhance growth. This was apparently true for the *Thalassia* bed he observed just inshore from the Miami sewage plant on Virginia Key, Florida, where the growth of both the seagrasses and their epiphytes was extraordinarily luxurient. He also noted, however, that the algal blooms often accompanying nutrient excess can cut light penetration so much that seagrass may suffer or be completely overgrown (e.g., Dong *et al.*, 1972). McNulty (1970) found *Halophila decipiens* and *Halodule beaudettei* perceptibly more resistant to effluents in Biscayne Bay than was *Thalassia testudinum,* since the former two species could exist in low quantities within 1 km of the outfall whereas *Thalassia* grew sparsely only outside that limit. Barada (1972) has observed and reported an extreme case of sewage pollution off White's Point, California, where the outfall for the city of Los Angeles deposited more than 25 cm of heavy sludge, not only smothering eelgrass and macroalgae, but turning the bay floor into a biological desert.

In general, seagrasses, especially the more eurybiontic pioneer species, seem fairly resistant to human tinkering. But that does not mean that all important constituents of seagrass ecosystems are equally well defended. The eelgrass that grows lushly beneath the fuel dock at Sitka, Alaska, seems to thrive in water chronically contaminated with petroleum, but Dungeness crabs no longer harbor among the plants (personal observation).

Realm of Uncertainty

At a meeting in early 1973, a scientist beginning work on seagrass ecosystems listened for some hours to a handful of experts in the field discussing the current state of seagrass research. "Fascinating," he finally commented. "Apparently we don't even know what it is that we don't know."

Sometimes that point is still disputed, even in the realms of applied ecology. We have already commented on the frustrations of not knowing exact and quantifiable relationships, for example, in the detrital foodwebs that begin with dead seagrass and conclude with humans. Nonetheless, evidence abounds that such relationships exist and are significant, even if they are not quite so vital as once was believed (Petersen, 1918). Such uncertainties regarding the real value of seagrass ecosystems are still pervasive and can take many forms.

One area where the uncertainty can baffle coastal managers is the apparent struggle between seagrass and shellfish. The bay scallop, *Argopecten irradians,* is one such valuable shellfish species. Marshall and Lukas (1970) found that the effects of *Zostera* and its attendant epibiota included lowering dissolved oxygen content and current flow, both undesirable for maximum scallop growth. Earlier work by Marshall (1947, 1960) had also indicated that scallops did better in an environment without eelgrass. Much of this work was done along the Rhode Island and adjacent coasts. Recently, just across the border in Connecticut, the East Lyme-Waterford Shellfish Commission placed a raft in the Niantic River that was designed to scour the bottom, removing the eelgrass and retarding its regrowth so that the scallops could become more plentiful. Thayer and Stuart (1974), however, found that eelgrass was an important substrate for bay scallop larvae. Scallop harvest methods such as dredging, which disturbed the plants, quickly led to a fall in the catch of mature scallops. The work was based at the National Marine Fisheries Service laboratory at Beaufort; the State of North Carolina has established the eelgrass beds of the Newport River estuary as a state-federal research preserve, thus saving the habitat for scallop spat.

The processes of science require that experiments be repeated and results checked. Surely, with such a valuable animal under consideration, someone will find it appropriate to study the oxygen content of the water above the eelgrass in the Newport River and the numbers of larval scallops on the Niantic River plants, as well as examining the direction of catch statistics for both areas. Meanwhile fishermen will pursue the scallops in the seagrass, some perhaps trying to kill the plants as they do so to preserve their resource while others try not to damage them for the same reason. The problem with oysters parallels that of scallops. From Japanese studies we know that eelgrass provides the base for the food chain that sustains larval oysters (Imai *et al.*, 1951), but any oyster fisherman knows that oysters need a hard substrate on which to mature and that they are smothered by the sediment caught by seagrasses.

There are some situations in which seagrasses are of definite use but of uncertain value for creatures of value to people. For example, herring along the northeastern Pacific coast *(Clupea pallasii)* spawn on both benthic algae and eelgrass (Outram, 1961). Clearly *Zostera* is not a necessary substrate for herring eggs, but it is not known if it is preferred by the herring, preferred (or even necessary) for some populations of herring, or not preferred by any. Perhaps a forest of mops would be as acceptable to the fish as a bed of *Zostera*. We can only reason that at the least, since eelgrass and macroalgae of the region inhabit different substrates, eelgrass extends the possible surface available for herring spawn.

Warner (1976) spends many pages detailing the reasons why eelgrass beds are a highly favored habitat for blue crabs in Chesapeake Bay. The poor catch there in 1976 has been blamed on the local decline of *Zostera* meadows (Anon., 1976). Yet somehow the blue crab populations of the United States' Atlantic coast sustained themselves throughout the years of the wasting disease. In the Chesapeake the total blue crab catch was approximately 5% less in 1939 than 1929 (Fiedler, 1931; 1942). Again, we can reason that life is better for blue crabs when they live in eelgrass; thus we have more of them to eat. It remains a difficult judgement to verify, much less quantify.

There are other situations in which seagrasses are clearly valuable to other organisms that are of unknown direct value to humankind. For example, Harlin (1975; Chapter 8) notes that seagrasses are crucial to over 100 species of epiphytic algae. We do not know which if any of these are essential in important food webs. At a more arcane level, we can only guess that none contains a potentially valuable antibiotic or other compound.

Throughout the foregoing pages we have touched on many points of uncertainty in the applied ecology of seagrass ecosystems. These have ranged from questions whose answers may be urgent, such as those concerned with sources of human food, through those of potential great importance, for example, the effect of seagrass beds in protecting shorelines from storm waves, on to those whose answers are interesting, such as, When did seagrasses colonize the Caribbean? For many of these questions, the answers come with appropriate price tags attached, or at least eventually attached. The real cost to the Japanese seed oyster farmer for the loss of *Zostera* in his inlet, for example, could be computed in fairly exact monetary terms, as could the spreading cost of such a loss to the Japanese national economy.

However, one of the areas in the realm of uncertainty is extraordinarily difficult to price. For want of a better term, we can call it esthetics. The beauty of an undersea meadow is not apparent to everyone, even to those who can meet it on its own terms beneath the water. Some observers may be delighted with the diversity of life harbored in a seagrass bed, while others might get gooseflesh at the sight of creepy wrigglers. That range of reaction is appropriate to our species, for diversity is also a human characteristic. As human activity has begun to threaten the diversity of the natural world, so we have come to value that diversity. When a river is threatened by a proposed dam, often now people who have never even seen the river will give money for its defense. What is the monetary value of diversity? What is the worth of a river, a forest, a lake, a seagrass bed, in itself? That is the most uncertain area of all.

Conclusions

Once upon a time humankind made use of every resource close at hand. Now we have television and the Teamsters; that portion of the world which calls itself modern has become monolithically dependent on a handful of resources, of which petroleum is currently the most prominent.

The two fictional works quoted at the beginning of this chapter had one more point in common: they were both elegies for ways of life in their dimming twilight. They portray people living close to their resource base in a manner nearly gone from the western world and rapidly vanishing elsewhere. The more the turtle fishers of the Caribbean and the Indians of British Columbia come to buy their food at the supermarket, the more their lives will depend on the same resource base as do the clerks in Japan and the street sweepers in Belgium.

Perhaps it is the supermarkets that need changing. Sophisticated economists and agronomists are calling for a reversal of the ever narrowing trend: we are too big, too numerous to balance on a tiny base. It is unimaginable that *Zostera* grain, produced in a few Mexican bays could feed as many people as do the Alberta wheat fields. But a drought in Alberta will matter far less to the people living on those Mexican shores if they can utilize the seagrass cereal as a ready resource. With the best management possible, the Caribbean turtle fishery could not supply the meat that the Argentine pampas can, but a revolution in Argentina need not threaten the protein supply for Antigua if the local *Thalassia* pastures are feeding many green turtles.

There are ways to credit dollar amounts to the value of seagrasses in practical applications: bay scallops sold in the neighborhood market in Fairbanks were recently selling for $4 per pound, and one could calculate the value of a dugong landed by an aboriginal harpooner in Darwin by comparing it to the cost of beef in the same city. Most evaluations of seagrass ecosystem contributions to human needs are not so tidy.

We can perhaps better gauge those contributions by looking at the problem from the other side: What of value is lost if seagrass ecosystems go? The wasting disease provided a natural experiment in partial answer to this question—partial since the systems were gone for a comparatively brief time, during much of which their slow decomposition could have been sustaining many creatures and processes. Even so, documentation of loss and alteration for the affected areas is extensive.

The summing up, then, of the value of seagrass meadows to humankind must be a further set of questions. We cannot yet quantify, much less define, most of the contributions of seagrass ecosystems to food webs involving humans; we can not yet manage human activities in concert with ecological principles, and consequently development of the coastal zone is a persistent threat to the diversity of marine ecosystems. We do not yet know enough to make sound judgments about the implications of enhancing one type of marine ecosystem at the expense of another, and this is particularly true for seagrasses.

But we know enough to understand in general what we would lose if catastrophe took seagrass ecosystems from the world ocean. We would lose options. More than ever, that is a loss beyond affording.

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