

Seaweeds: Their Productivity and Strategy for Growth

The role of large marine algae in coastal productivity is far more important than has been suspected.

K. H. Mann

The edge of the sea is one of the best habitats for plant growth in temperate latitudes. In favorable circumstances, net primary productivity may be as high as anywhere else on earth—comparable, for example, to a tropical rain forest. Seaweeds, which have successfully colonized this zone, are a unique form of life. They are attached to a hard substrate, not by a root system, but by a holdfast. Instead of relying on a rather localized supply of nutrients in the soil, they take their nutrients from the water that surrounds them. Because this water is kept in perpetual motion by tides and winds, the nutrient supply is virtually inexhaustible. Even if the seaweeds and plankton deplete the nutrients in surface waters, wind-induced or estuarine mixing renews the supply by causing upwelling of deeper water.

The growth of seaweeds below low-tide level, in the sublittoral, is far richer than in the intertidal areas. Before the advent of underwater vehicles and scuba gear, the algae of the intertidal zone were the focus of attention and provided elegant examples of species zonation in relation to gradients of environmental factors, such as degree of exposure to air or amount of wave action (1). While the intertidal zone is inhabited primarily by the fucoids, or rockweeds, the sublittoral is dominated

by laminarians—that is, kelps. In clear water, kelps flourish from low-tide level to a depth of 20 to 30 meters. On gently sloping shores, they may extend 5 to 10 kilometers from the coastline. Several common species of kelp are strap-shaped and may be 2 to 3 m in length. Wave action keeps the blades in constant motion, providing maximum exposure to sunlight and contact with nutrients. Under these conditions, the vegetation may become extremely lush and justify the term “kelp forest,” which is commonly applied. Kelp forests occur on all coasts in temperate latitudes and extend into the tropics where the cool waters of the Peru current extend northward (Fig. 1).

Seaweed Productivity in Nova Scotia

Although standing crops of seaweeds have been documented in various parts of the world (2) and short-term studies of photosynthesis have suggested high rates of production (3), the first year-round study of productivity in the sublittoral was carried out on the east coast of Canada (4). The pioneer work of MacFarlane had shown that in various parts of the Nova Scotian coast standing crops of *Laminaria* had a fresh weight of 20 to 29 kilograms per square meter (5). As part of a multidisciplinary study at St. Margaret's Bay, Nova Scotia, a systematic study of the seaweed zone

along approximately 50 km of the shoreline was carried out with the aid of a research submarine and scuba gear. On 24 transects running at right angles to the shore, it was found that algal zones dominated by *Laminaria* and *Agarum* accounted for over 80 percent of the total biomass of seaweeds in the bay (Table 1) (6). The next step was to investigate the rate at which this biomass was turned over, in order to calculate the annual rate of tissue production.

The method used was basically very simple: 180 plants on five sites with different depths of water and exposure to wave action were identified by numbered tags. There were three species of plants—*Laminaria longicruris*, *L. digitata*, and *Agarum cribrosum*. Small holes were punched at intervals of 10 centimeters along the blades of these plants, and it was demonstrated by the movement of these holes that all growth in length occurred at the junction of the stipe and the blade (Fig. 2). After that, it was only necessary to punch one hole, 10 cm from the base of the blade, and record at intervals of a few weeks how far the hole had moved along the blade. It was found that the rate of movement of the holes was much greater than the net increase in length of the blade—growth at the base was almost balanced by erosion at the tips. The blades resembled moving belts of tissue, and the holes quickly moved from base to tip, “growing off the ends.” Before a hole “grew off,” a new hole was made 10 cm from the base. For 2 years a record was kept of the rate of growth at the bases of the blades of a large number of plants. Although this method was conceptually simple, the practical difficulties of finding and measuring numbered plants in dense kelp forests, in all kinds of sea conditions, and with sea ice as a hazard in winter, should not be underestimated.

Our finding was that all three species completely renewed the tissue in their blades between one and five times a year. Moreover, as the plants grew older they also grew wider and thicker. Plots of length against biomass showed that the increase in biomass was

The author is chairman, department of biology, Dalhousie University, Halifax, Nova Scotia, Canada.

Table 1. Zonation and biomass (fresh weight) of seaweeds in St. Margaret's Bay, Nova Scotia, Canada, averaged from 24 transects.

Zone	Average width (m)	Biomass (kg m ⁻²)	Biomass per meter of shore-line (kg)	Percent of total biomass
<i>Fucus</i> and <i>Ascophyllum</i>	15.5	10.67	124.9	8.7
<i>Chorda</i> and fine browns	87.9	1.08	95.3	6.5
<i>Chondrus crispus</i>	6.0	3.49	20.9	1.4
<i>Zostera marina</i>	4.9	1.02	5.0	0.3
<i>Laminaria digitata</i> and <i>L. longicuris</i>	22.7	16.01	363.5	25.0
<i>L. longicuris</i>	46.5	11.50	534.6	35.8
<i>L. longicuris</i> and <i>Agarum cribrosum</i>	36.7	4.88	179.2	11.6
<i>A. cribrosum</i> and <i>Ptilota serrata</i>	86.3	1.83	158.1	10.7

roughly proportional to the square of the increase in length. Hence, the biomass of new tissue produced annually was up to 20 times the initial biomass of the blade (Table 2). We were particularly surprised to find that growth in length was rapid throughout the winter, and that growth rate reached a peak in late winter or early spring, when the water temperature was close to 0°C (Fig. 3). The ratio of annual production to initial biomass was greatest in young plants and was generally higher for those nearer the surface of the sea. Weighted values of the ratio of production to biomass were calculated for each species, taking into account the relative proportions of young and old plants and the depth at which each species occurred. It was estimated that primary production in the seaweed zone averaged 1750 grams of carbon per square meter per year

(g C m⁻² yr⁻¹) and that in St. Margaret's Bay, with a total area of 138 km², the total production of seaweed was about three times the total production of phytoplankton [191 g C m⁻² yr⁻¹ for phytoplankton (7) against 603 g C m⁻² yr⁻¹ for seaweed, averaged over the entire bay].

Other Marine Macrophytes

The productivity of *Laminaria* off Nova Scotia may be paralleled by that of other seaweeds. For example, giant kelp, *Macrocystis*, develops very large biomasses off the coast of California and in the Indian Ocean. The plants have very long stipes, reaching 10 m or more, and the blades form a dense mat near the surface of the sea. Although there may be up to 20 layers of blades, net assimilation cannot in-

crease very much above that of a single layer because of mutual shading. Biomasses up to 22 kg m⁻² (fresh weight) have been reported off California, and 95 to 606 kg m⁻², with an average of 140 kg m⁻², in the Indian Ocean (8). The net annual productivity in California was 400 to 820 g C m⁻² (9). If the ratio of production to biomass in the Indian Ocean were similar to that on the coast of California, production figures would be enormous, but severe self-shading probably prevents such high production. It seems likely that in giant kelp beds in the Indian Ocean there is a net annual production of about 2000 g C m⁻².

Intertidal seaweeds, such as *Fucus* and *Ascophyllum*, may occasionally have rates of production comparable with those of kelps. In Nova Scotia, the fresh weight may be as high as 32 kg m⁻² (5), with an estimated productivity of 640 to 840 g C m⁻² yr⁻¹ (10). It has been shown that *Fucus* and *Ascophyllum* can double their weight in 5 to 10 days, and a natural population was able to fix more than 10 g C m⁻² day⁻¹ (3). Under conditions of rapid removal by wave action or browsing, it is likely that production rates in excess of 1000 g C m⁻² yr⁻¹ are attained. In sheltered areas of the coast, such as the mouths of estuaries and behind barrier beaches, seaweeds are often replaced by angiosperms rooted in the sediments. Common and well-studied species of angiosperms in temperate waters include *Spartina*, which forms salt marshes just below high-water level, and *Zostera*, which is found near and below low-tide level. *Spartina* production ranges from a maximum of 897 g C m⁻² yr⁻¹ in Georgia to less than 200 g C m⁻² yr⁻¹ in Delaware and New Jersey (11). *Zostera* was found to produce 340 g C m⁻² yr⁻¹ in Denmark, but up to 1500 g C m⁻² yr⁻¹ in various parts of the United States (12).

In tropical waters, a variety of sea grasses grow in sheltered, subtidal areas. *Thalassia* in the Caribbean Sea has been studied, and production figures of up to 5.8 g C m⁻² day⁻¹ have been recorded, suggesting an annual productivity on the order of 1000 g C m⁻² (13). At the high-tide level in the tropics, the dominant vegetation type is the mangrove swamp. Species of *Rhizophora* and *Avicenna* are found on the tropical shores of several continents. Silt and organic matter accumulate among the roots and produce anaerobic conditions, but the man-

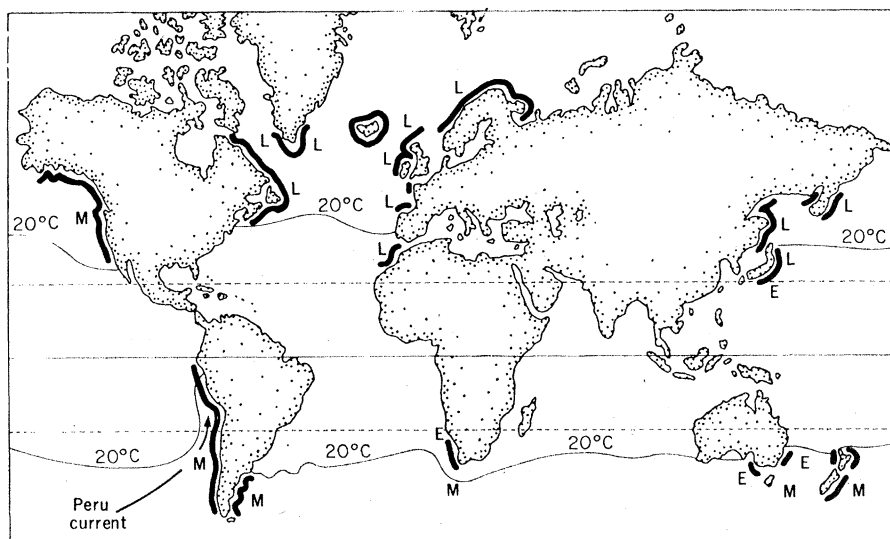


Fig. 1. Occurrence of kelps in quantities sufficient for commercial harvesting (L = *Laminaria*, M = *Macrocystis*, E = *Ecklonia*). The 20°C isotherms are for summer in the Northern and Southern hemispheres, respectively. The distribution of rockweeds (*Fucales*) is approximately the same as that of the kelps. [After Chapman (56)]

groves have aerial roots, which help overcome this difficulty. The conclusion to be drawn from a small number of productivity studies (14, 15) is that gross photosynthesis is high, but net productivity is modest, on the order of 300 to 400 g C m⁻² yr⁻¹.

In Fig. 4, the productivity of various marine macrophytes is summarized. It is clear that seaweeds are among the most productive and that their productivity is as high as, or higher than, some of the most productive terrestrial systems. There exists, then, at the edge of the sea a source of intense primary production that helps create the conditions necessary for the abundant growth of organisms which form the food of young fish and that enables the coastal zone to perform its well-known role of nursery for many commercially important stocks of fish. What strategy do seaweeds adopt to enable them to grow so efficiently?

Growth Strategy of Seaweeds

It was shown earlier that *Laminaria* and *Agarum* in eastern Canada perform the surprising feat of growing rapidly throughout the winter, when temperatures are close to 0°C and light intensity is low (4). As Fig. 3 shows, growth rates are increasing at a time of year when temperature and light flux are decreasing. Other species of perennial, subtidal seaweeds have been shown to grow throughout the winter—for example, *Desmarestia aculeata* (16), *Cystoseira granulosa* (17), and *Hijikia fusiforme* (18).

Annual subtidal seaweeds behave

Table 2. Ratio of annual production to initial biomass (P/B) for three species of seaweed in Nova Scotia in two successive years.

Station	Species	Depth (m)	P/B
1968 to 1969			
<i>Laminaria longicuris</i>	Strawberry Island	5	10.66
	Fox Point	5	6.14
		12	3.82
<i>L. digitata</i>	Fox Point	5	20.44
		12	5.50
<i>Agarum cribrosum</i>	Fox Point	12	4.09
1969 to 1970			
<i>L. longicuris</i>	Luke Island	5	14.09
		10	13.24
	Fox Point	5	8.99
		8	7.76
		12	7.54
<i>L. digitata</i>	Fox Point	5	8.39
		8	12.48
		12	9.60
<i>A. cribrosum</i>	Fox Point	12	3.18

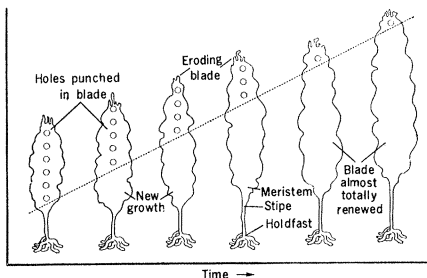


Fig. 2. Movement of punched holes on growing blades of *Laminaria longicuris* (not to scale).

differently. They usually produce the young sporophyte during the spring, grow through the summer, and reproduce during the fall. The spores form microscopic gametophyte stages that survive the winter and give rise to new macroscopic plants in the following spring. Examples are *Chorda filum* (19) and *Saccorhiza polyschides* (20). Hence, it appears that only large, perennial plants grow in the winter, which suggests that stored carbon may be necessary for the process of growth.

Storing food is a function of photosynthesis and respiration. Early work suggested that, with decreasing temperature, respiration fell more rapidly than did photosynthesis, so that, for a given light intensity, the difference between photosynthesis and respiration was greater at low temperatures than at higher temperatures (21). It is now known that, while photosynthesis is nearly temperature-independent at low light intensities, it is strongly influenced by temperature at the high light intensities required to build up a surplus (22). It has also been shown that *Laminaria* is capable of seasonal adaptation of respiration. *Laminaria hyperborea* in Scotland was found to have a respiration rate in August (at 16°C) that was only 40 percent of the rate in May (at 8°C) (23). The rate of respiration of *Laminaria* in northern Labrador was measured at the same temperature in winter and in summer, and the winter rate was lower (3). In this case, the lowering of respiration in winter may be an adaptation in order to survive the long, dark winter without depleting its energy reserves too much. Studies of respiration in a variety of seaweeds, in winter and in summer temperatures, showed summer depression of respiration in *Ascophyllum nodosum* and *Chondrus crispus*, but not in *Ulva*, *Enteromorpha*, or *Ceramium* (3).

Evidence is beginning to show that

the kelps are capable of storage, translocation, and mobilization of carbon reserves. For many years, the kelps were regarded as rather loose aggregations of cells with a limited ability to collaborate physiologically. They have no obvious bundles of vascular tissue comparable to those found in higher plants, but the kelps *Macrocystis* and *Nereocystis* have now been shown to have sieve cells (24), which almost certainly aid translocation. The so-called trumpet cells of *Laminaria* are very similar to sieve cells, except that they are nucleate (25). The dry matter of *Laminaria* varies markedly with season (6, 26). Mannitol reaches a peak in midsummer, and laminarin in

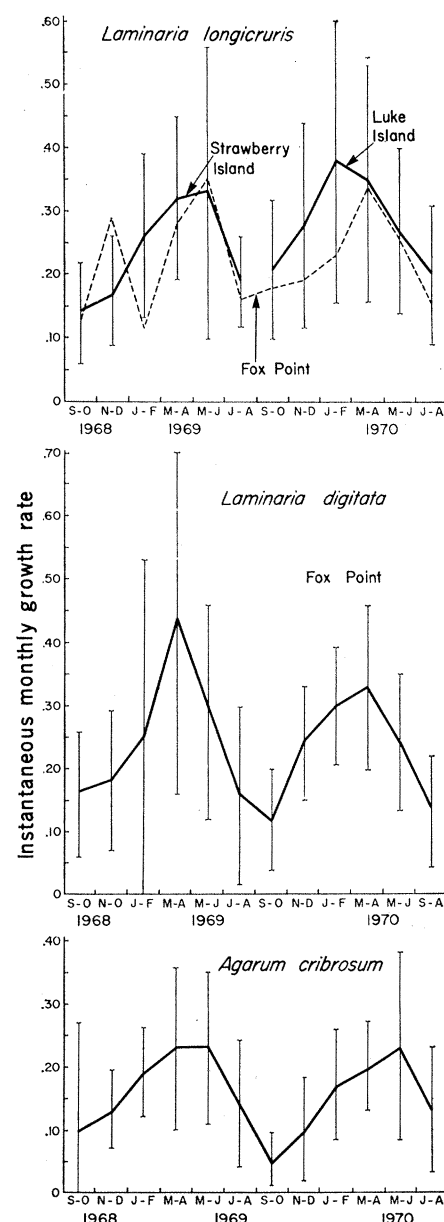


Fig. 3. Seasonal growth patterns of seaweeds in eastern Canada. Vertical lines are standard deviations.

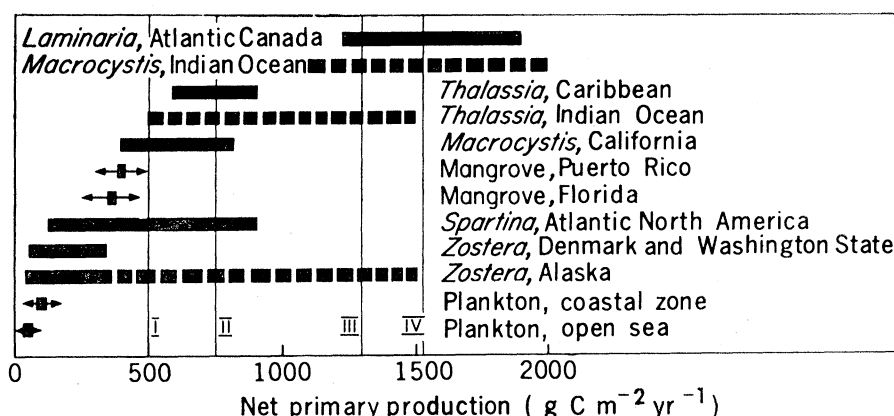


Fig. 4. The productivity of various marine macrophytes, compared with some terrestrial communities [I = medium-aged oak-pine forest, New York; II = young pine plantation, England; III = mature rain forest, Puerto Rico; IV = alfalfa field (an intensively managed system), United States]. Calculated as kilocalories $\times$ 0.1. [Source: E. P. Odum, *Fundamentals of Ecology* (Saunders, Philadelphia, ed. 3, 1971).] Broken lines are estimates based on biomass data.

late autumn. In *L. hyperborea*, laminarin may account for 36 percent of the total dry matter, with the highest figures occurring in plants from sheltered locations. In fucoids, the seasonal fluctuations in storage is much less marked than it is in kelps. In *A. nodosum*, laminarin reaches a maximum of 5 percent of dry weight in November and a minimum of 1 percent in May. Mannitol varies from about 10 percent in September to about 7 percent in February (27). This difference is associated with a difference in seasonal growth patterns, the kelps growing in winter and the fucoids growing entirely during the summer period of active photosynthesis.

Evidence of translocation of stored food has been obtained from experiments with *L. hyperborea* (22, 28). The normal plant develops each year a new frond that is clearly distinguishable from the frond of the previous year (Fig. 5, a and b). Plants kept in complete darkness from January to June were able to grow a new frond, presumably by using translocated material. Plants from which most of the previous year's frond had been amputated at the end of winter, but which were given normal light conditions, produced a new frond only half the size of that produced by the control plants. Plants that had begun to produce a new frond were cut into three pieces: stipe, new frond, and old frond. Growth of the new frond, in normal light conditions, was only one-tenth as much as that of the new fronds of intact plants (Fig. 5c) (22, 28). All this suggests that material

stored in the previous year's frond is translocated and used to produce a new frond in the winter and spring.

More direct evidence of translocation has been obtained by attaching a small, transparent container of radioactive sodium bicarbonate to the surface of a photosynthesizing kelp. Some hours later, an autoradiograph revealed a stream of radiocarbon products moving toward the base of the blade (29).

How Canadian Seaweeds Differ

The work on translocation in *L. hyperborea* does not explain the winter growth of the species observed in eastern Canada. In *L. hyperborea*, winter growth is confined to the production of a new frond, with the old frond still attached, and Luning's work has clearly shown that translocation from the old to the new takes place. In *L. longicruris* and *L. digitata*, however, the fronds are completely replaced at least once in the course of the winter, as evidenced by the growth of punched holes from base to tip and off the end. While it is probable that reserves of laminarin accumulated in the summer are mobilized to begin winter growth, it is inconceivable that they can be used to maintain it through several cycles of blade renewal. The alternative hypothesis, which has not been tested so far, is that these kelps are able to photosynthesize enough under winter conditions to provide the raw material for growth. It has been suggested that in high latitudes, where

winter conditions are particularly severe and prolonged, it is very unlikely that sufficient light energy reaches the plants to enable them to survive autotrophically. They must therefore practice heterotrophy, deriving their energy from the uptake of organic compounds from solution (30).

Whatever the basis for winter growth, one may ask what advantage accrues to the plants by reversing the seasonal pattern found in temperate latitudes. In part, it may compensate for the erosion that takes place at the tips of the blades as a result of wave action. On the open Atlantic Coast, wave action is felt at all depths at which kelp grows. While the severity of erosion varies according to weather conditions, it was found that winter growth generally makes up for the erosion and increases the size of the blades. In addition, the expansion of photosynthetic surface was most rapid when the concentrations of nutrients in surface waters were at their annual maximum; in this way, the plants were able to grow most rapidly before the phytoplankton bloomed and depleted the concentrations of nutrients.

The strategy adopted by these perennial sublittoral macrophytes is unique and appears to be highly successful. Their productivity is as high as that of many intensively managed crops. It is made possible by their constant immersion in a nutrient-containing medium and by their protection from freezing. In this respect, they have a great advantage over intertidal forms. *Ascophyllum*, in the intertidal zone, is intermittently subjected to freezing temperatures and accumulations of ice and snow. It has limited food reserves and, under these conditions, can do little more than minimize its respiratory losses and endure until conditions improve. Other species of seaweed adopt the strategy of passing the winter in the microscopic stage.

The marsh grasses, such as *Spartina alterniflora*, behave much like terrestrial grasses in this climate, translocating stored material to underground organs and allowing the aerial shoots to die and decompose. Such plants are unable to perform significant amounts of photosynthesis in Nova Scotia between November and May. The strategy of *Zostera* varies according to location. In subtidal situations it may remain green and apparently capable of photosynthesis throughout the winter, while plants exposed at low tide

are damaged considerably by the frost.

Evidence now being obtained indicates that the anaerobic mud surrounding the roots of marsh grasses and sea grasses is the site of fixation of large amounts of atmospheric nitrogen (31). This renders the plants independent of supplies of dissolved nitrogen, which appear to limit primary production in many coastal areas. There is also evidence that salt marshes play an important role in overall coastal productivity. In a study of Petpeswick Inlet, Nova Scotia, which contains large areas of salt marsh, it was found that a great deal of dissolved nitrogen was exported on the ebb tide (32). These nutrients are made available for uptake by coastal algae, including the seaweeds.

The Fate of Seaweed Production

In St. Margaret's Bay, the main herbivores of the seaweed zone are the sea urchin, *Strongylocentrotus droebachiensis*, and the periwinkle, *Littorina littorea* (33). An energy budget was constructed for the sea urchin population (34), and rough calculations were made for the periwinkles (33). It was shown that the herbivores did not consume more than 10 percent of the net production of the seaweeds. The remaining 90 percent entered various detritus food chains, as particulate or dissolved organic matter.

Sieburth and Jensen, working in the United States and Norway, and Khailov and Burlakova, working in the Soviet Union, found that seaweeds in the laboratory release up to 40 percent of the products of gross photosynthesis in soluble form (35). Brylinsky measured in the field the photosynthesis, respiration, and production of dissolved organic matter by five species of marine macrophyte and found that none released more than 4 percent of the assimilated carbon (36). It is therefore possible that the high levels of production of organic matter observed by the other workers were induced by the experimental conditions.

Even if actively growing, healthy plants do not release soluble organic matter in large quantities, there is little doubt that senescent and dying plants do (37). In the case of the *Laminaria* discussed earlier, it is probable that release of dissolved organic matter takes place almost continuously, since

erosion at the tips is a continuous process and more than half the dry weight of the blades consists of soluble carbohydrates and ash (26).

There are two main routes by which dissolved organic matter may enter the particulate phase—uptake by microorganisms or physiochemical change. High concentrations of bacteria have been reported from the surfaces of seaweeds (38), and *Leucothrix*, a common algal epiphyte, has been shown to take up radioactive thymidine from the surrounding water (39). It seems probable that most dissolved organic material released by macrophytes is rapidly taken up by the bacteria on their surfaces or in the surrounding water. Dissolved organic matter that is free in the water is readily converted to particulate form at air-water interfaces (such as bubbles or the sea surface) or by adsorption on inorganic particles (40). Both microorganisms

and particulate organic matter are normal constituents of that diverse but ecologically important material known as detritus.

To summarize to this point, it is known that the kelps which occur commonly on the shores of the world's oceans in temperate climates are among the more productive plant systems known to man. It is estimated that less than 10 percent of this production normally enters grazing food chains and that the remainder enters detritus food chains, having been released as particulate or dissolved organic matter.

The subsequent fate of this material has yet to be investigated, but work on other forms of detritus give an idea of what to expect. Odum and de la Cruz have reported on the fate of *Spartina* leaves (41). The ash-free dry matter from fresh leaves was about 10 percent protein. That from dead leaves newly dropped was about 6 percent; as the leaves became broken up into successively finer particles, their protein content rose to about 24 percent. The change was attributed to a buildup of microorganisms on the leaf particles. Similar results were obtained in a study of the fate of mangrove leaves (15).

Detritus in this form is a highly nutritious food for planktonic and benthic invertebrates, and even for some kinds of fish (42). Snails and amphipods have been shown to strip the microorganisms from the detritus they consumed, releasing feces with a much reduced nitrogen content (43). Within a few days of liberation, the nitrogen in the fecal pellets had risen again, presumably because the pellets had been recolonized by microorganisms. In this way, even compounds that are refractory to the digestive systems of invertebrates may be progressively consumed by microorganisms and passed on to plankton or benthos.

Interactions with Other Organisms

Sea urchins graze on kelps and other seaweeds and have a major influence on their distribution. Within the *Laminaria* zone in St. Margaret's Bay are to be found various-sized patches of almost bare rock that are characterized by the presence of high densities of sea urchins (*S. droebachiensis*) (6). In the kelp forest, the average biomass density of sea urchins is 150 g m⁻², while in the bare patches it is 1200 g

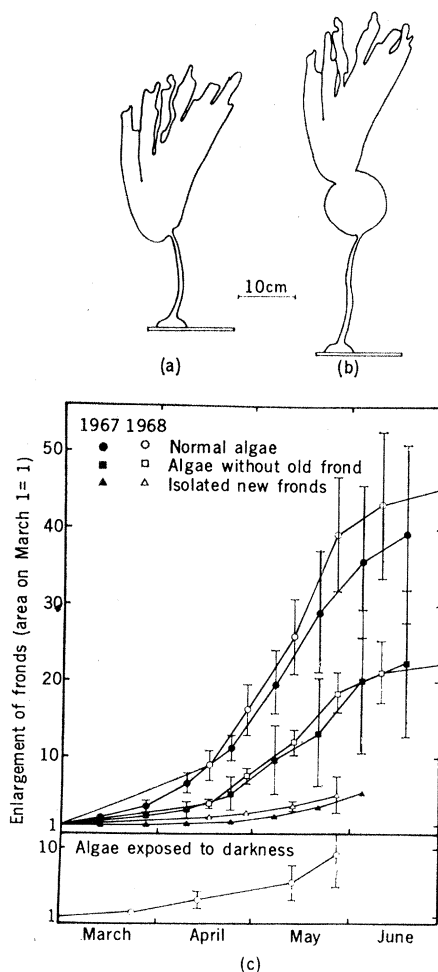


Fig. 5. *Laminaria hyperborea* (a) before and (b) after being kept in darkness from January to June; (c) relative growth of new season's frond under various experimental conditions. [From K. Luning (22, 28)]

m⁻² (37). I have observed numerous instances of populations of sea urchins advancing the boundary of the cleared areas, at a rate of several meters per annum, by biting through the bases of the stipes and moving forward en masse. *Laminaria* is a preferred food of sea urchins (44), and sea urchins grow well in the laboratory when this is the sole source of food (34). Hence, there is little doubt that the sea urchins are responsible for the gaps in *Laminaria* cover. Bare areas from which all sea urchins are removed are rapidly recolonized by seaweeds (45).

Similar results have been obtained after removing other kinds of sea urchins in other areas: namely, *Strongylocentrotus purpuratus* and *S. franciscanus* (46), *Paracentrotus lividus* (47), and *Echinus esculentus* (48). The damage that *Strongylocentrotus* spp. inflict on beds of giant kelp (*Macrocystis*) along the coast of California is a matter of economic concern and has been extensively studied (49). The sea urchins have been controlled with quicklime, and *Macrocystis* has re-established itself. There have also been observed natural cycles in which the sea urchin populations declined, presumably because they had overeaten their food supply. However, sewer outfalls appear to modify the interaction by providing nourishment for sea urchin populations in the absence of kelp, thus preventing the seaweed from returning to the area (50).

It is probable that outbreaks of high population density in sea urchins are triggered by reductions in the population density of their predators. The outbreaks in California have been attributed to a decline in the number of sea otters (*Enhydra lutris nereis*) as a result of hunting. A reversal of this trend in California was followed by a sharp decline in the population of sea urchins and expansion of kelp beds (49, 51). The starfish *Pycnopodia* was shown to be a key factor in the control of sea urchin populations near Seattle (46). In the case of the sea urchin populations of eastern Canada, the lobster *Homarus americanus* may well be the key predator. When lobsters are placed in cages on the sea floor and given their choice of several kinds of food, sea urchins are high on the list of preferred species (45). In the laboratory, two lobsters consumed 131 sea urchins, weighing a total of 342 g, in 7 months (44). Rock crabs are also

active predators on sea urchins, but they eat smaller sizes and they eat less. Since lobsters are also predators of rock crabs, lobsters appear to be the controlling influence.

Human predation on lobsters is intense (52), and it is probable that the reduced population of lobsters on the east coast of Canada and the United States has permitted population explosions of sea urchins, with consequent overgrazing of the seaweed beds. An analogous situation would be the hunting of carnivores: on the Kaibab Plateau of Arizona (53), for example, such overhunting allowed deer populations to expand and overgraze their food supply. If my conclusions about the relationship of man, lobsters, sea urchins, and seaweed are correct, this is probably the first documented example of such a four-level interaction in the sea.

The zonation of seaweeds seems to be determined partly by the gradients of environmental factors (light, temperature, wave action, and so forth) encountered as one proceeds from high-tide level to the maximum depth of seaweed distribution and partly by competitive interactions. For example, *Agarum* in the San Juan islands is confined to the lower sublittoral, while *Nereocystis* and *Laminaria* dominate in shallower water. The zonation is achieved, in part, as a result of the grazing of sea urchins, which show a clear preference for *Nereocystis* and *Laminaria*. It appears that, in shallow water, these species can grow fast enough to offset both the grazing of the sea urchins and competition from *Agarum*, but in deeper water, where light is less intense, the *Laminaria* and *Nereocystis* succumb to the sea urchins and *Agarum* takes over (54). A similar explanation may account for part of the zonation observed on the east coast of Canada (6). In parts of Newfoundland, *Laminaria* spp. are confined to the very turbulent zone just below the level of low tide, while the remainder of the sublittoral carries dense populations of sea urchins, along with coralline algae, *Agarum*, and *Ptilota*. It is postulated that only in the turbulent sublittoral fringe are the activities of sea urchins sufficiently impeded to allow *Laminaria* to persist (55). It would be interesting to try to control the sea urchin populations by protecting and adding to the number of lobsters.

References and Notes

1. T. A. Stephenson and A. Stephenson, *J. Ecol.* **37**, 289 (1949).
2. G. Michanek, *F.A.O. Fish. Circ.* **128**, 37 (1971).
3. J. W. Kanwischer, in *Some Contemporary Studies in Marine Science*, H. Barnes, Ed. (Allen & Unwin, London, 1966), pp. 407-420.
4. K. H. Mann, *Mar. Biol. (Berl.)* **14**, 199 (1972).
5. C. MacFarlane, *Can. J. Bot.* **30**, 78 (1952).
6. K. H. Mann, *Mar. Biol. (Berl.)* **12**, 1 (1972).
7. T. Platt, *J. Cons. Cons. Int. Explor. Mer.* **33**, 324 (1971).
8. W. J. North, Ed. *Nova Hedwigia* **32** (Suppl.) 1 (1971); P. Grua, *Terre Vie* **2**, 215 (1964).
9. K. A. Clendenning, *Nova Hedwigia* **32** (Suppl.) 259 (1971).
10. D. F. Westlake, *Biol. Rev.* **38**, 385 (1963).
11. J. M. Teal, *Ecology* **43**, 614 (1962); R. B. Williams, "Proceedings of the Atlantic Estuarine Research Society Meeting, Hampton, Virginia" (mimeographed, 1965); M. H. Morgan, unpublished data.
12. C. J. G. Petersen, *Rep. Dan. Biol. Sta.* **25**, 1 (1918); P. R. Burkholder and G. H. Bornside, *Bull. Torrey Bot. Club* **84**, 366 (1957); K. H. Mann, *Mem. Ist. Ital. Idrobiol. Dott. Marco De Marchi Pallanza Italy* **29**, 353 (1972).
13. H. T. Odum, P. R. Burkholder, J. A. Rivero, *Univ. Texas Inst. Mar. Sci. Publ.* **9**, 404 (1959); J. A. Jones, thesis, University of Miami (1968); M. Brylinsky, unpublished data.
14. F. Golley, H. T. Odum, R. F. Wilson, *Ecology* **43**, 9 (1962).
15. E. J. Heald, thesis, University of Miami (1969).
16. A. R. O. Chapman, *Phycologia* **10**, 63 (1971).
17. —, unpublished manuscript.
18. S. Suto, *Bull. Jap. Soc. Sci. Fish.* **17**, 13 (1951).
19. G. R. South and E. M. Burrows, *Br. Phycol. Bull.* **3**, 379 (1967).
20. T. A. Norton and E. M. Burrows, *Br. Phycol. J.* **4**, 19 (1969).
21. H. Kneip, *Int. Rev. Gesamten Hydrobiol. Hydrogr.* **7**, 1 (1914); R. Harder, *Jahrb. Wiss. Bot.* **56**, 254 (1915).
22. K. Luning, in *Proceedings of the Fourth European Marine Biology Symposium*, D. J. Crisp, Ed. (Cambridge Univ. Press, Cambridge, England, 1971), pp. 347-361.
23. W. A. P. Black, *J. Soc. Chem. Ind. (Lond.)* **69**, 161 (1950).
24. N. L. Nicholson, *J. Phycol.* **6**, 177 (1970).
25. B. C. Parker and J. Huber, *ibid.* **1**, 172 (1965); H. Ziegler and I. Ruck, *Pflanz. 73*, 72 (1967).
26. W. A. P. Black, *Nature (Lond.)* **161**, 174 (1948); *J. Soc. Chem. Ind. (Lond.)* **67**, 169 (1948); *ibid.*, p. 172; *ibid.* **69**, 161 (1950); *J. Mar. Biol. Ass. U.K.* **29**, 45 (1950); *ibid.* **33**, 49 (1954).
27. A. Jensen, *Rep. Norw. Inst. Seaweed Res.* **24**, 23 (1960).
28. K. Luning, *Mar. Biol. (Berl.)* **2**, 218 (1969).
29. K. Schmitz, K. Luning, J. Willenbrink, *Z. Pflanzenphysiol.* **67**, 418 (1972).
30. R. T. Wilce, *Bot. Mar.* **10**, 185 (1967).
31. D. G. Patriquin, *Mar. Biol. (Berl.)* **15**, 35 (1972); — and R. Knowles, *ibid.* **16**, 49 (1972).
32. W. H. Sutcliffe, Jr., personal communication.
33. R. J. Miller, K. H. Mann, D. J. Scarratt, *J. Fish. Res. Board Can.* **28**, 1733 (1971).
34. R. J. Miller and K. H. Mann, *Mar. Biol. (Berl.)* **18**, 99 (1973).
35. J. McN. Sieburth and A. Jensen, *J. Exp. Mar. Biol. Ecol.* **3**, 290 (1969); K. M. Khailov and Z. P. Burlakova, *Limnol. Oceanogr.* **14**, 521 (1969).
36. M. Brylinsky, thesis, University of Georgia (1971).
37. R. E. Johannes, *Advan. Microbiol. Sea* **1**, 203 (1968).
38. E. C. S. Chan and E. A. McManus, *Can. J. Microbiol.* **15**, 409 (1969).
39. T. D. Brock, *Science* **155**, 81 (1967).
40. E. R. Baylor and W. H. Sutcliffe, *Limnol. Oceanogr.* **8**, 369 (1963); G. A. Riley, *Advan. Mar. Biol.* **8**, 1 (1970).
41. E. P. Odum and A. A. de La Cruz, in *Estuaries*, G. H. Lauff, Ed. (American Association for the Advancement of Science, Washington, D.C., 1967), pp. 383-388.
42. W. E. Odum, in *Marine Food Chains*, J. H. Steele, Ed. (Univ. of California Press, Berkeley, 1970), pp. 222-240.

43. R. Newell, *Proc. Zool. Soc. Lond.* **144**, 25 (1965).
44. J. H. Himmelman and D. H. Steele, *Mar. Biol. (Berl.)* **9**, 315 (1971).
45. P. A. Breen, unpublished data.
46. R. T. Paine and R. L. Vadas, *Limnol. Oceanogr.* **14**, 710 (1969).
47. J. A. Kitching and F. J. Ebling, *J. Anim. Ecol.* **30**, 373 (1961).
48. J. M. Kain and N. S. Jones, in *Proceedings of the Fifth International Seaweed Symposium*, E. G. Young and J. L. McLachlan, Eds. (Pergamon, Oxford, 1966), pp. 139-140; N. S. Jones and J. M. Kain, *Helgol. Wiss. Meeresunters.* **15**, 460 (1967).
49. W. J. North, Ed., *Kelp Habitat Improvement Project, Annual Report 1964-65* (California Institute of Technology, Pasadena, 1965); *Kelp Habitat Improvement Project, Annual Report 1968-69* (California Institute of Technology, Pasadena, 1969).
50. J. S. Pearse, M. E. Clark, D. L. Leighton, C. T. Mitchell, W. J. North, *Kelp Habitat Improvement Project, Annual Report 1969-70*, W. J. North, Ed. (California Institute of Technology, Pasadena, 1970), appendix, pp. 1-93; M. E. Clark, in *Kelp Habitat Improvement Project, Annual Report 1968-69*, W. J. North, Ed. (California Institute of Technology, Pasadena, 1969), pp. 70-93.
51. J. H. McLean, *Biol. Bull. (Woods Hole)* **122**, 95 (1962).
52. D. G. Wilder, *Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer.* **156**, 21 (1965).
53. A. Leopold, *Wisc. Conserv. Dep. Publ.* **321**, 3 (1943); G. Caughley, *Ecology* **51**, 53 (1970).
54. R. L. Vadas, thesis, University of Washington (1968).
55. J. H. Himmelman, unpublished data.
56. V. J. Chapman, *Salt Marshes and Salt Deserts of the World* (Interscience, New York, 1960).
57. I thank those who have assisted this investigation and review, by advice or loan of material, particularly A. R. O. Chapman, J. S. Craigie, A. C. Neish, R. L. Vadas, and J. H. Himmelman. Figures 1 and 4 are reproduced, with permission, from *Mem. Ist. Ital. Idrobiol. Dott. Marco De Marchi Pallenza Italy*, **29**, 353 (1972); Fig. 3 from *Mar. Biol. (Berl.)* **14** (1972), p. 205; Fig. 5 from *ibid.* **2** (1969), pp. 221-222.

Human Impact of the Managua Earthquake

Transitional societies are peculiarly vulnerable to
natural disasters.

Robert W. Kates, J. Eugene Haas, Daniel J. Amaral,
Robert A. Olson, Reyes Ramos, and Richard Olson

... [T]he framers of the existing constitution of the State, in view of the rivalry and jealousy which exist between the cities of Granada and León, and in order to relieve the Legislative Assembly from the overawing political influence of the latter, designated the city of Managua as the place of its meeting. The choice was in many respects a good one; Managua is not only central as regards position, but its inhabitants are distinguished for their attachment to "law and order," and their deference to constituted government.

When the men of Granada and the men of León made a compromise decision in 1855 to locate the capital of Nicaragua on the shores of Lake Xolotlán (1), they made a political accommodation and a geophysical blunder. No other city of similar size has had a more recurrent record of destruction than Managua. It has experienced severe shaking in 1885, destruction in 1931, severe but localized damage in 1968, and enormous destruction in 1972. Thus it is not surprising that, in the days and weeks following the 23 December 1972 disaster, at least 39

groups of geologists, seismologists, and engineers from seven different countries converged on Managua to examine in detail this latest experience, for each such major geologic event provides field data for earthquake science and engineering.

Less common was the mission that we, as geographers, sociologists, and political scientists specializing in natural hazard and disaster preparation, prevention, and research, undertook. Of some 40 major earthquakes in the last 25 years for which detailed scientific and engineering reports are available,

only four have been seriously studied and reported upon by social scientists. Reasons for this discrepancy lie partly in the organization of science: earthquake study is a well-organized component of the disciplinary structure of the physical sciences and of engineering, but comparable organization is only beginning to emerge in the social sciences. Underlying such organization is the view that the measurement and observation of earthquakes and their physical impacts is the proper activity of the physical sciences and engineering; the measurement and observation of human impact and response is in the purview of journalists, relief organizations, and governments.

But the extraordinary quality of the 23 December earthquake in Managua cannot lie in its magnitude, physical mechanisms, impact on the crustal structure, or assemblage of seismic observations. An estimated 1000 shocks of equal or greater magnitude occur each year, the fault traces and mechanisms are unexceptional, and the seismic record is sparse. What brought at least 114 geophysicists, seismologists, and engineers to Managua in the month following the earthquake was the extraordinary destruction wrought by this earthquake, the potential for recurrence, and the hope of gaining from the Managua experience insights that would reduce earthquake loss elsewhere in the world. We share this hope and consider this article complementary to the extensive geophysical, scientific, and engineering documentation that will surely appear. But we also place our brief and hurried observation of human response (2) in the context of the major questions of natural hazard and disaster research: How do men survive and even prosper in environmental settings of high risk and recurrent loss? What is the nature of human response to catastrophe?

Dr. Kates is professor of geography and Mr. Amaral is a Ph.D. candidate, Graduate School of Geography, Clark University, Worcester, Massachusetts 01610. Dr. Haas is professor of sociology and head, Program on Technology, Environment and Man, Institute of Behavioral Science, University of Colorado, Boulder 80302. Robert Olson is assistant director, Metropolitan Transportation Commission, Berkeley, California 94705. Dr. Ramos is assistant professor, Department of Sociology, University of California (San Diego), La Jolla 92110. Richard Olson is a Ph.D. candidate, Department of Political Science, University of Oregon, Eugene 97403.