28 D.M. John and W. Pople, J. exp. mar. Biol. Ecol. *11,* 81 (1973).
29 D.J. Faulkner, Tetrahedron *33,* 1421 (1977).
30 M. Neushul, in: Contributions to the Systematics of Benthic Marine Algae of the North Pacific, p.47. Ed. I.A. Abbott and M. Kurogi. Jap. Soc. Phycol., Kobe, Japan 1972.
31 B.C. Parker, Can. J. Bot. *47,* 537 (1969).
32 R.H. Whittaker, in: Chemical Ecology, p.43. Ed. E. Sondheimer and J.B. Simone. Academic Press, New York 1970.
33 R.T. Paine and R.L. Vadas, Mar. Biol. *4,* 79 (1969).
34 E.R. Pianka, Am. Nat. *106,* 581 (1972).
35 J.W. Kanwisher, in: Some Contemporary Studies in Marine Science, p.407. Ed. H. Barnes. George Allen Unwin, London 1966.
36 P.S. Dixon, Bot. III. Proc. 5th Mar. Biol. Symp., Gotheburg. 1965, p.67.
37 J.A. West, Br. phycol. J. *7,* 299 (1972).
38 J.H. Connell and R.O. Slatyer, Am. Nat. *112,* 1119 (1977).
39 K.H. Mann, Science *182,* 975 (1973).
40 J.C. Zieman, Estuarine Res. *1,* 541 (1975).
41 D. McKey, Am. Nat. *108,* 305 (1974).
42 R.G. Cates and G.H. Orians, Ecology *56,* 410 (1975).

Marine agriculture: Progress and problems

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Marine agriculture can be defined as the cultivation of domesticated crop plants in the sea. While early agriculturalists domesticated crop plants on land some 10,000 years ago, the domestication of marine crop plants is only about 300 years old[1], and it is within the last 30 years that their cultivation has been achieved on a large scale. 3 marine seaweeds (crop plants) now grown extensively are the red alga *Porphyra,* and the brown algae, *Laminaria* and *Undaria.* Several other seaweeds are utilized, and some others are cultivated, but at present, such efforts are small. Seaweeds harvested for industrial chemicals fall mainly into 3 groups: the alginic acid producing species, the carrageenan producers and the agar producers. Agarophytes are presently harvested from wild populations in 23 countries (Yamada[2]), while carrageenan producers are harvested primarily on the east coast of North America *(Chondrus crispus)* and in the South Pacific (*Eucheuma* spp., Parker[3]).

Marine agriculture in the Orient has centered around *Porphyra, Laminaria* and *Undaria.* By 1975, the Japanese had approximately 67,000 ha of *Porphyra* in production[4]. Fishermen in the People's Republic of China started cultivating *Laminaria* in the early 1950s and, at present, have approximately 13,500 ha devoted to *Laminaria* culture (Tseng, personal communication). Although Western countries are a long way from such extensive farms, the harvest of about 18,500 ha from natural stands of the giant kelp *Macrocystis* from Californian coastal waters is approaching 200,000 wet tons per year (Coon and Ebeling[5], Neushul[6]).

The cultivation of marine plants such as *Porphyra* requires a detailed knowledge of the life history. Before 1948, farmers in Japan placed nets and sticks in the sea in late September each year and *Porphyra* grew on these artificial substrates. In 1948, Drew[7] in England, and a little later, Kurogi[8] and others in Japan worked out the complete life history in the laboratory: *Porphyra* had an alternate life stage, a filamentous form that penetrated and grew within shells on the sea floor. The filamentous form, called *Conchocelis,* produced spores which developed into the thalloid form of *Porphyra.* This knowledge allowed the Japanese to cultivate both life-history phases in the laboratory and to eliminate a large amount of uncertainty in the cultivation of this plant. Further developments such as freezing of the thalloid form (Kurakake[9]), modern mechanized seeding methods and propagation on free-floating nets in the open ocean have further enhanced production (Minura[10]).

The same technological story occurred for the brown algae *Laminaria* in China and *Undaria* in Japan. These algae also have alternate life-history phases. The large thalloid form produces spores which are haploid and grow into gametophytes on the sea floor. These gametophytes produce gametes which fuse and form the large thalloid stage. 2 years are normally required for the thalloid form of *Laminaria* to grow large enough for harvesting. Techniques for seeding nets in the laboratory and holding the gametophytes and young sporophytes in the laboratory until they are large enough to compete in the field (Cheng[11]) has shortened the time required to reach maturity. This 'forced' cultivation technique for *Laminaria* developed by Hasegawa in Japan (Kurogi[8]) and by Tseng et al.[12] in China has led to the dramatic increases in *Laminaria* production. Further developments in China include selection of *Laminaria* strains for growth in warm water (Fang et al.[13]). The result of this work in the last 10 years has led to the establishment of *Laminaria* in areas previously felt to be too warm for them to grow (Tseng, personal communication).

Concomitant with increase in size of marine farms in both Japan and China came problems in providing inorganic nutrition and in combating diseases. Development of the *Porphyra* industry in Japan has led to an increase in disease in these crops to such an extent that pathological studies are now of primary importance (Suto et al.[14]). Among *Laminaria* populations, it has been noted that forced cultivation induces malformation in sporophytes and the plants are much more susceptible to encrustation by epiphytic bryozoans (Hasegawa[15]). In China, a number of biotic and abiotic diseases have been noted (Tseng, personal communication).

Certain abiotic diseases of seaweeds appear similar in nature, being found at times of high temperature or low inorganic nutrient levels. Temperature and inorganic nutrient concentrations in coastal seas are seasonally cyclic. High temperature and low inorganic nutrients are generally found during the summer months, while winter temperatures are cooler and the inorganic nutrients in much higher concentrations. The combination of warm surface waters and low nutrients in summer causes weakening and enhances senescence as exemplified by *Macrocystis* forests in southern California (North[16]). Consequently, the plants are predisposed to a variety of fungal, bacterial and viral diseases.

In an effort to alleviate these problems with *Porphyra, Laminaria* and other plants, the Japanese and Chinese have fertilized their oceanic farms. This fertilization has been attempted by placing porous pots containing fertilizer in the water and allowing the fertilizer to diffuse outward (Tseng et al.[17]). Chemical fertilizer has also been sprayed from boats or helicopters over the aquatic crops[18]. A third approach adopted by the Chinese and Japanese is the intermediate application method. Here the plants, while still small enough to be handled, are brought on board small boats and soaked in high concentrations of sodium nitrate, ammonium sulfate and perhaps other nutrients. After 30 min, the plants have absorbed enough to last for 7-10 days (Tseng, personal communication).

The application of vast amounts of inorganic nutrients to ocean seaweed farms is presently uneconomical. In Western countries, mariculture research has focused on the development of pilot projects to use marine algae, which are currently a valuable source of industrial chemicals, in the processing of domestic sewage. These efforts to obtain tertiary treatment of domestic sewage by studies of algal growth in sewage effluent have been made by Ryther[19] and his associates at Woods Hole, Massachusetts. Seaweeds were grown as a final component or 'polishing step' of a water-recycling mariculture system. Such economically important carrageenophytes and agarophytes as *Chondrus crispus, Gracilaria* and *Neoagardhiella* as well as other high production seaweeds such as *Ulva* were employed to assimilate nutrients regenerated by shellfish. The shellfish were fed phytoplankton such as *Dunaliella* grown on a mixture of domestic sewage and seawater. Under these conditions, seaweed production has been found to be very high, but only for short periods of time (Wilson et al.[20]). In other systems, domestic sewage has been diluted and fed directly to seaweeds (Prince[21]). Ryther feels that problems with epiphytes still impede commercially successful tank-farming of seaweeds.

A second source of fertilizer for marine farms is artificially upwelled, deep water. Water from depths below the photic zone is rich in inorganic nutrients and can, with wave pumps or other methods, be moved to the surface. Experimental maricultural systems employing deep water as a source of fertilizer have been developed (Roels et al.[22], North[23]). The upwelled water can be used directly to nourish benthic seaweeds (North[23], Haines[24]), or used to nourish diatom cultures which are in turn fed to shellfish and the effluent from the shellfish tanks used to grow benthic algal crops (Haines[24]). Experiments with *Hypnea* (a carrageenophyte) indicate that growth is better when plants are grown in shellfish tank effluent rather than directly in upwelled water. Other experiments (North[23]) in southern California with *Macrocystis* indicate that chelators are required before upwelled water can be used as an effective inorganic nutrient source for benthic algae.

The future of marine agriculture appears quite bright. Oriental progress in the last 30 years has been phenomenal, producing literally thousands of hectares of food farms in near-shore areas. In the West, energy shortages have led to the preliminary phases of an effort to use macroscopic marine algae as collectors of energy in the open ocean. This interest has generated work on an 'open ocean energy farm' (Bryce[25]), in which *Macrocystis* will be grown on a large scale and harvested for its energy value, with a number of commercially valuable by-products.

At present, marine agricultural efforts have experienced problems of providing adequate mineral nutrition, or supplementing the usually insufficient quantities of nutrients in the ocean. But as these farms are increased in size and the cultivated stocks become increasingly homogeneic, problems with biotic diseases will become (and in the Orient, have already become) problems that have to be solved.

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1 Anonymous, Ohmori Porphyra Records, p. 200. Ohmori Regional Educational Committee, Japan 1974, in Japanese.
2 N. Yamada, J. Fish. Res. Bd. Can. *33*, 1024 (1976).
3 H.S. Parker, Aquaculture *3*, 425 (1974).

4 Anonymous, Porphyra Handbook, p. 106. National Federation of Porphyra Fish Cooperatives, Japan 1975, in Japanese.
5 D. Coon and A. W. Ebeling, Investigation of the Effects of Sea Otter Foraging the Subtidal Communities of the Central California Coast. A. Rept Cal. Dept. Fish and Game, Sacramento 1977.
6 M. Neushul, in: Marine Plant Biomass of the Pacific Northwest Coast, p. 163. Ed. R. Krauss. Oregon State University Press, Corvallis 1978.
7 K.M. Drew, Nature *164*, 748 (1949).
8 M. Kurogi, Bull. Tohoku reg. Fish. Lab. *18*, 1 (1961).
9 T. Kurakake, The Manual of Low Temperature Storage of Nursery-Nets in Nori Cultivation, p. 72. Nat. Fed. Porphyra Fish. Cooperatives, Japan 1969, in Japanese.
10 A. Miura, in: Advance of Phycology in Japan, p. 273. Ed. J. Tokida and H. Hirose. Junk Publisher, The Hague 1975.
11 T.H. Cheng, Econ. Bot. *23*, 215 (1969).
12 C.K. Tseng, K.Y. Sun and C.Y. Wu, Acta bot. sin. *4*, 255 (1955), in Chinese with English summary.
13 T.C. Fang, C.Y. Wu, B.Y. Jiang, J.J. Li and K.Z. Ren, Bot. Bull. *10*, 197 (1962), in Chinese with English summary.
14 S. Suto, Y. Saito, K. Akiyama and O. Umebayashi, Textbook of Diseases and Their Symptoms in Porphyra, p. 37. Contribution E18, Tokai Regional Fish. Res. Lab., Japan 1972, in Japanese.
15 Y. Hasegawa, J. Fish. Res. Bd. Can. *33*, 1002 (1976).
16 W.J. North, ed., The Biology of Giant Kelp Beds (Macrocystis) in California, p. 600. J. Cramer, Lehre 1971.
17 C.K. Tseng, K.Y. Sun and C.Y. Wu, Bot. Bull. *4*, 375 (1955), in Chinese with English summary.
18 Anonymous, Nori Cultivation in Pictures and Graphs, p. 145. Nat. Fed. Porphyra Fish. Cooperatives, Japan 1969, in Japanese.
19 J.H. Ryther, in: Preliminary Results with a Pilot Plant Waste Recycling Marine-Aquaculture System, p. 50. WHOI Techn. Rept. 75-41, Woods Hole, Massachusetts 1975.
20 E.H. Wilson, J.C. Goldman and J.H. Ryther, U.S. Dept. Energy Techn. Rept. COO/4000-7701 (1977).
21 J.S. Prince, Aquaculture *4*, 69 (1974).
22 O.A. Roels, K.C. Haines and J.B. Sunderlin, 10th Eur. Symp. mar. Biol. *1*, 381 (1975).
23 W.J. North, unpublished data.
24 K.C. Haines, 10th Eur. Symp. mar. Biol. *1*, 297 (1975).
25 A.J. Bryce, J. Phycol. *13*, suppl., 45 (1977).

Abiotic disease in seaweeds: thermal effluents as causal agents

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Extreme environmental conditions acting alone may induce changes in plants which, if prolonged, constitute abiotic disease. Representative of this broad category of causal agents is thermal pollution which may act on seaweeds more or less severely: in the former instance, the result is immediate damage or death; in the latter, various syndromes develop that are analogous to sun scalds or heat cankers of terrestrial plants (Andrews[1]).

With the proliferation of electric generating stations (EGS), the need for cooling water, supplied in abundance by the ocean, has risen precipitously. Thermal pollution is potentially a major hazard to nearshore benthic marine organisms. Seaweeds are especially vulnerable because they have neither the option of emigrating nor that of adjusting behaviorally to heated waters. Unlike higher plants, which are exposed to a wide range of temperatures (~ 90 °C), seaweeds generally exist in a much narrower spectrum (~ 30 °C) (Gessner[2]). With the exception of bluegreen algae (Brock[3]), the thermal tolerances of most algae and seagrasses are relatively narrow compared to terrestrial plants.

This discussion will not be limited to thermal effects on seaweeds per se but will include seagrasses, salt marsh grasses and, to a limited extent, mangroves. Salt marshes and mangroves border most low energy coastlines in temperate and tropical regions respectively, and both contribute significantly to the structure and energy flow of nearshore marine ecosystems. Where appropriate, laboratory data or research on freshwater plants will be cited to support or clarify field studies. The natural temperature ranges of marine waters depend primarily on latitude, ocean currents and season. Surface tropical water masses typically range from 24 to 30 °C except where upwellings of colder bottom water occur. Summer water temperatures in temperate-boreal regions range from 12 to 20 °C. The presence of lagoons, bays, rivers and local circulation patterns markedly alter these broad regimes. Temperature increases at older EGS range from 5 to 15 °C and from 5 to 8 °C at newer plants (Mihursky et al.[4]). Thus, the present pattern of concentrated thermal effluents will eventually be replaced by thermally lower and more diffuse plumes.

Thermal tolerances (heat resistance) of seaweeds are remarkably uniform for species occupying similar habitats (e.g. Schwartz and Almodovar[5]). Similar to terrestrial plants, algae from relatively benign environments have narrower tolerance ranges than species from physically or seasonally variable habitats. Temperate-boreal algae, for example, have broader tolerances to temperature, especially heat, than tropical species. Likewise, seaweeds growing in shallow subtidal waters (2–5 m) have higher heat tolerance than species growing at 12–15 m (Gessner[2]). This inverse relationship between depth and tolerance continues also throughout the intertidal region, culminating with the most resistant species at the highest intertidal levels.

There is little published information on the direct effects of thermal effluents on algal thalli. Symptoms