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PREFACE

The United States and Japanese counterpart panels on aquaculture were formed in 1969 under the United States-Japan Cooperative Program in Natural Resources (UJNR). The panels currently include specialists drawn from the federal departments most concerned with aquaculture. Charged with exploring and developing bilateral cooperation, the panels have focused their efforts on exchanging information related to aquaculture which could be of benefit to both countries.

The UJNR was started by a proposal made during the Third Cabinet-Level Meeting of the Joint United States-Japan Committee on Trade and Economic Affairs in January 1964. In addition to aquaculture, current subjects in the program are desalination of seawater, toxic microorganisms, air pollution, energy, forage crops, national park management, mycoplasmosis, wind and seismic effects, protein resources, forestry, and several joint panels and committees in marine resources research, development, and utilization.

Accomplishments include: Increased communications and cooperation among technical specialists; exchanges of information, data, and research findings; annual meetings of the panels, a policy coordinative body; administration staff meetings; exchanges of equipment, materials, and samples; several major technical conferences; and beneficial effects on international relations.

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Information on the Culture of Phytoplankton for Aquacultural Needs in Japan

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INTRODUCTION

Aquaculture of useful marine organisms is, at present, relatively advanced in Japan. Artificial mass production of selected species for seeding natural waters is intensively practiced. In many operations involving rearing of seedlings, cultured phytoplankters are utilized directly or indirectly as food organisms and to control environmental conditions in the rearing tank. Additionally, the products of some cultured phytoplankters are used as an ingredient in the preparation of artificial combined foods for aquatic animals. In this report, some information is presented on techniques used in Japan for the mass culture of phytoplankton for rearing aquatic animals.

LARVAL AND JUVENILE FOOD

The species of phytoplankton used in production units or experimentally in rearing larvae and juveniles, and the species of aquatic animals for which they have been used for food, are listed in Table 1 (Hirano 1963; Imai and Shiraishi 1971).

In mass production of marine fish seedlings, *Brachionus plicatilis* (rotifer), *Tigriopus japonicus*, and nauplii of *Artemia salina* (brine shrimp) are used as primary food organisms. *Brachionus plicatilis* and *T. japonicus* are themselves cultured by feeding them on marine *Chlorella* sp. and/or bakers' yeast.

The technique of marine *Chlorella* sp. culture is as follows. The culture tank of plastic or concrete is filled with filtered seawater and placed either indoors or outdoors. Ammonium sulfate at 100 g/kl, calcium superphosphate at 10 g/kl, and urea at 10 g/kl are added to filtered seawater, but the quantities of nutrients added vary with researchers at the various seedling hatcheries. After inoculation with stock *Chlorella* seed, the seawater medium is actively stirred by aeration, or water is circulated by an underwater pump.

For mass culture, marine *Chlorella* is cultured by the above-mentioned method using a large outdoor tank of 100-200 kl capacity. One-half of the *Chlorella* suspension is drawn from the tank for feeding *Brachionus* and *Tigriopus* when the concentration of *Chlorella* has increased to 10-20 $\times$ 10^6 cells/ml. After harvest, the tank is refilled with filtered seawater and the culture is reinitiated. After this process has been repeated two or three times, the seawater in the tank is again fertilized. Within a few days another *Chlorella* bloom occurs and the process is repeated (Fukusho et al. 1971, 1976).

In the early days of artificial rearing of Kuruma prawn, *Penaeus japonicus*, the larvae were fed with cultured *Skeletonema costatum*. In recent years, the larvae of Kuruma prawn and various food organisms are cultured together in a tank in which seawater with such nutrients as potassium nitrate (the level of N:100-200 mg/m^3) and potassium phosphate (the level of P:15 mg/m^3) (Hudinaga and Kittaka 1976) have been added. Quite recently, however, it has been learned that *Chaetoceros* sp. resistant to higher water temperature is suitable for food of Kuruma prawn larvae, and mass culture of this alga is being undertaken.

In the culture of the blue crab, *Neptunus trituberculatus*, the larvae are fed with *B. plicatilis* and *T. japonicus*. To feed these food organisms, marine *Chlorella* is cultured as a part of blue crab culture by methods similar to those used in marine fish culture described previously (Takahashi and Matsui 1972).

Many species of phytoplankton are widely utilized for rearing the larvae of marine molluscs (Imai and Shiraishi 1971; Koganezawa 1975). Pure cultures of phytoplankton such as *Monochrysis lutheri* and *Chaetoceros calcitrans* are used for food of the larvae and juveniles, either mixed or in a single species culture. In general, these phytoplankton species are grown as pure cultures in a vessel of 5-10 liter capacity by the usual culture methods. In large-scale culture of these species, the seawater is purified continuously by a high speed centrifuge (10,000-14,000 rpm) with exposure to ultraviolet light, or by filtration through a ceramic cartridge rather than by sterilization by autoclaving (Imai and Shiraishi 1971; Koganezawa 1975).

Miquel's seawater with vitamin B_{12} and P6-Metal added is a suitable culture solution, but sometimes enriched seawater, as shown in Tables 2 and 3 (Sato and Serikawa 1968), is used in specialized culture.

As an example of large-scale culture of phytoplankton, the culture method of *M. lutheri* for rearing larvae of the pearl oyster, *Pinctada fucata*, is presented. Seawater that has been filtered through a ceramic cartridge (mesh size 5μ) is used to fill a tank of 25 liter capacity and is fertilized with the nutrients shown in Table 2. The culture tank is placed under an intensity of 4,000 lux of illumination in a room kept at a constant temperature of 20 $\pm$ 1 °C. The culture solution is stirred by aeration of 30 liters/min. It is inoculated with *Monochrysis* at a concentration of 2 $\times$ 10^6 cells/ml in the culture solution. A half volume of the *Monochrysis* suspension is taken from the tank for feeding the larvae when the population level exceeds a concentration of 3 $\times$ 10^6 cells/ml, usually after 2 or 3 d. Then more fertilized seawater is added to bring the volume back to 25 liters and the concentration of *Monochrysis* to 3 $\times$ 10^6 cells/ml, and the culture is continued. Numerous harvests from one culture tank produce about 150 liters of *Monochrysis* suspension at the concentration of 4 $\times$ 10^6 cells/ml during about 1 mo (Suguri et al. 1975).

In the culture of abalone, *Haliotis* spp., a peculiar type of collector is used for the purpose of culturing attached diatoms and the creeping abalone larvae on it. The collector is a transparent (or translucent) corrugated plastic plate. Many

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Table 1.--Species of food algae used to rear the larvae and juveniles of aquatic animals. Arrows indicate the direct utilization as food items to rearing species.

Species of algae	Method of utilization	Species reared
Chrysophyceae		
Monas sp.	→	*Crassostrea gigas*
		Anadara broughtnii
		Pteria penguin
		Spisula sachalinensis
		Pinctada fucata
		Haliotis gigantea
		Haliotis discus
Monochrysis lutheri	→	*Anadara broughtnii*
		Atrina pectinata
		Patinopecten yessoensis
		Pinctada fucata
		Pecten albicans
		Chlamys nobilis
		Fulvia mutica
		Spisula sachalinensis
		Schizothaerus keenae
Bacillariophyceae		
Chaetoceros calcitrans	→	*Anadara broughtnii*
		Patinopecten yessoensis
		Pecten albicans
		Chlamys nobilis
		Fulvia mutica
		Meretrix lamarckii
		Spisula sachalinensis
Chaetoceros simplex	→	*Anadara broughtnii*
		Schizothaerus keenae
		Haliotis gigantea
		Haliotis discus
		Pseudocentrotus depressus

Table 1.--Continued.

Species of algae	Method of utilization	Species reared
Chaetoceros gracilis	⟶	*Anadara broughtnii*
Chaetoceros sp.	⟶	*Penaeus japonicus*
Melosira sp.	⟶	*Haliotis gigantea*
		Haliotis discus
Skeletonema costatum	⟶	*Penaeus japonicus*
		Pseudocentrotus depressus
Amphora sp.	⟶	*Haliotis gigantea*
		Haliotis discus
Novicula sp.	⟶	*Haliotis gigantea*
		Haliotis discus
Cocconeis sp.	⟶	*Haliotis gigantea*
		Haliotis discus
Nitzschia closterium	⟶	*Penaeus japonicus*
		Pinctada fucata
		Meretrix lamarckii
		Haliotis gigantea
		Haliotis discus
Phaeodactylum tricornutum	⟶	*Anadara broughtnii*
		Spisula sachalinensis
Cryptophyceae		
Rhodomonas ovalis	⟶	*Anadara broughtnii*
Chlorophyceae		
Chlamydomonas sp.	⟶	*Mytilus edulis*
		Pseudocentrotus depressus
Dunaliella terteolecta	Green water	Marine fishes and shell-fishes
		Pteria pengium
Platymonas sp.	⟶	*Haliotis discus hannai*

Table 1.--Continued.

Species of algae	Method of utilization	Species reared
Chlorella sp. (marine)	— *Brachionus plicatilis* →	*Pagrus major*
or		*Opegnathus fasciotus*
	— *Tigriopus japonicus* →	*Acanthopagrus schlegelii*
		Kareius bicoloratus
		Limanda yokohamae
		Sebastes inermis
		Fugu rubripes
		Lateolabrax japonicus
		Paralichthys olivacus
		Neptunus trituberculatus
	— Green water —	Marine fishes and shellfishes
Chlorella sp. (freshwater)	— *Daphnia pulex* →	Freshwater fishes

Table 2.—Composition of culture solution for *Monochrysis lutheri*.

Seawater	1,000 ml
$NaNO_3$	100 mg
$Na_2HPO \cdot 12H_2O$	14 mg
$NaHCO_3$	12.6 mg
EDTA · 2 Na	18.1 mg
Clewat · 32*	500 mg
Vitamin B_{12}	0.2 μg
Vitamin B_1	100 μg
Biotin	1 μ

*Chemical composition: Fe, 3.8 g; Mn, 7.7 g; Zn, 1.6 g; Cu, 0.07 g; Mo, 6.3 g; B, 24.7 g; Co, 0.17 g; EDTA, a bit.

Table 3.—Composition of culture solution for *Nitzschia closterium*.

Filtered seawater	1,000 ml
$NaNO_3$ (5 g/100 ml)	2 ml
$NaHCO_3$ (16.8 g/l)	10 ml
Na_2SiO_3 (2 g/l)	2 ml
$Na_2HPO_4 \cdot 12H_2O$ (5 g/l)	2 ml
Pl. solution	1 ml
Sterilized at 80°C for 30 min	
Pl. solution	
Na_2EDTA	3.0 g
$FeCl_3 \cdot 6H_20$	0.24 g
$ZnCl_2$	0.03 g
$MnCl_2 \cdot 4H_2O$	0.27 g
$CoCl_2 \cdot 6H_2O$	0.8 mg
$CuSO_4 \cdot 5H_2O$	0.4 mg
H_3BO_3	3.44 g
Distilled water	1,000 ml

sheets of the collectors are hung in a tank filled with seawater and placed under suitable light; subsequently various species of attached diatoms grow on the surface of the plate. These collectors are transferred and hung vertically in the abalone rearing tanks just before the planktonic stages of the larvae transform into the creeping stage (Shibui 1971).

In the culture of red sea urchin, *Pseudocentrotus depressus*, phytoplankton species such as *C. simplex* and *S. costatum* are utilized for food of the larvae. These algae are cultured by methods similar to those described for the culture of *Pinctada* larvae (Hirano 1963).

INGREDIENTS OF ARTIFICIAL COMBINED FOODS

Attempts have been made to utilize *Chlorella pyrenoidosa* cultured in freshwater as an ingredient to increase the conversion efficiency of artificial combined food for the creeping larvae of abalone.

Recently, the production of *Spirulina* sp. has reached commercial scale. The mass culture of *S. platensis* and *S. maxima* has been underway since 1974 by an industrial chemical company, through a technical agreement with Institut Français de Pétrole (Nakayama 1975). The company built a culture facility with 5,000 m^2 area at Miyakojima in the Ryukyu Islands. They expect to produce 33 t (dry weight) of *Spirulina* annually. Because of high production costs, *Spirulina* has, in the past, been utilized only for deepening the red body color of goldfish and fancy colored carp by taking advantage of its high carotenoid content (Honma et al. 1974). In recent years, however, *Spirulina* has been utilized as an ingredient in the artificial combined food for Kuruma prawn, as it also has high protein content. In the near future, the demand for *Spirulina* as food for aquatic animals may be substantially increased.

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Recent Problems of Nori (*Porphyra* spp.) Culture in Japan

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INTRODUCTION

Nori culture in Japan began in a primitive form during the Edo Era (late 17th century). However, modern culturing techniques were not developed until the mid-1920's. Before that time a method of culturing, called "soda hibi," using branches inserted vertically into the bottom as the substrate, was employed. In the late 1920's the methods of "sudare hibi" (floating bamboo slats) and "ami hibi" (rope nets) were introduced. The annual yield of nori was greatly increased through use of these new substrates.

In 1949, K. M. Drew discovered the conchocelis phase of *Porphyra umbilicalis,* which stimulated experimentation on artificial conchospore collection in Japan. At the same time, Japanese fishermen began using a floating culture system outside the bays. The combination of experimental effort and expansion of growing areas resulted in a standardization of nori culture methods (1955-60) and in increased annual yields. The annual yield was around 1 billion sheets prior to 1949, increased to 2 billion sheets in 1955, and reached 3 billion in 1962 (Fig. 1).

In 1965, a net-freezing technique was developed at the Aichi Prefectural Fisheries Experimental Station which facilitated storing nori nets for use throughout the season. In addition to this technique, new strains which were developed by fishermen using selective breeding have been employed widely throughout Japan since 1970. These new strains and new methods increased the annual production to over 9 billion sheets of nori in 1973, and the supply became far greater than the demand. Since 1974, in order to protect themselves from the decline in the nori market because of overproduction, the National Federation of Fisheries Cooperatives and the National Federation of Nori and Shellfish Fisheries Cooperatives jointly established a planned production system and have allotted an annual production quota to each prefecture before the beginning of the culture season. In recent years, annual production has been constant at around 7 billion sheets, which is close to the planned production quota.

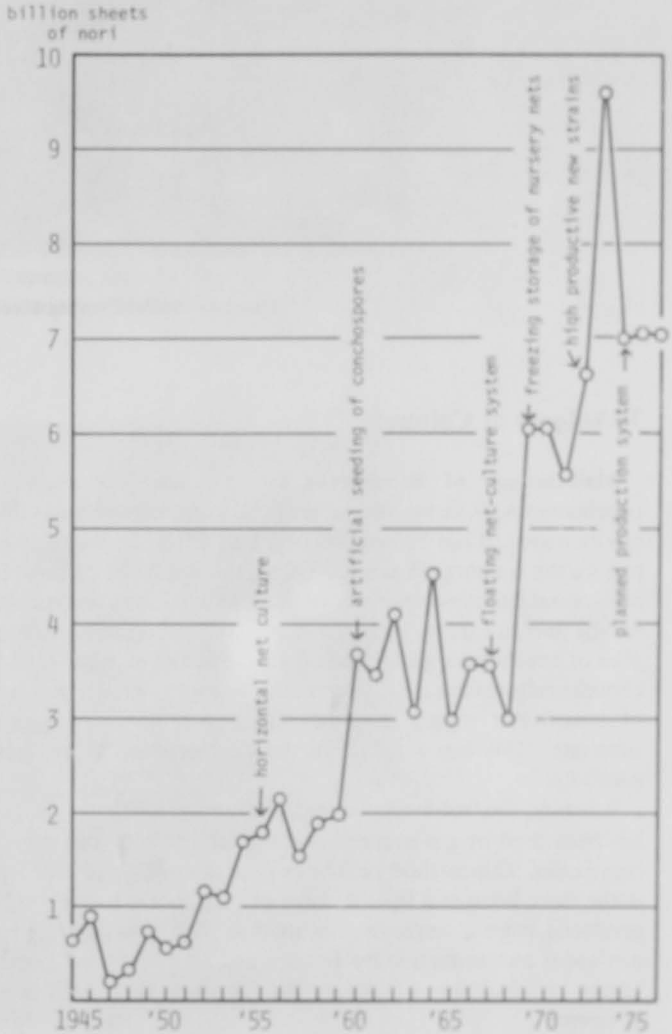

Figure 1.—Changes in methods of nori-sheet production (after Miura 1975).

STATE OF THE ART

Culture Species and Strains

In the early days of nori culture, *P. tenera* was used almost exclusively, but today it has been mostly replaced by the hardier *P. yezoensis,* which has a wider temperature tolerance than *P. tenera.* Other species used less widely in Japan are *P. pseudolinearis, P. kuniedai,* and *P. crispata.*

One of the most active areas of nori research today is the improvement of the quality of the final product. The market qualities of *P. tenera* are higher than *P. yezoensis*; therefore, an attempt to determine which nori traits are desirable and to develop new strains which optimize these traits is being made. Two strains, "ooba-asakusanori" and "narawa-susabinori," are now gaining widespread recognition. Ooba-asakusanori was developed from *P. tenera* and narawa-susabinori from *P. yezoensis* by selective breeding (Miura 1970). The important traits common to both of these strains are abundant release of monospores and late maturity. Production has been greatly improved due to the development and use of these two strains. More study is needed to further improve the quality of the nori products as well as to find more disease-resistant varieties.

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Figure 2.—Artificial seeding of conchospores in the field using conchocelis nets.

Techniques of Culture

Maintenance of conchocelis cultures and collection of conchospores.—As the use of artificial conchospore collection has increased, it has become necessary to artifically maintain or culture the conchocelis stage. At first, the stage was cultured in prefectural fisheries experimental stations and/or other facilities for the nori culturists. Today most culturists raise their own supplies of conchocelis stages; therefore, the actual number of conchocelis cultures has greatly increased, bringing about a problem of insufficient supply of oyster shells suitable for use as a substrate. This has resulted in the development of artificial substrates.

Recently, the free-living method of growing conchocelis stages has been used by government research laboratories and private companies. This method facilitates genetic studies and breeding in the field, because a large number of conchocelis stages can be produced from a single mother thallus. The drawback to this method is contamination by diatoms and other seaweed spores. Direct conchospore collection has not yet been artificially achieved.

Seeding methods commonly used are "zubo" and "han-zubo." In the han-zubo system, tanks (1 m × 20 m × 0.5 m deep) made of heavy gage flexible vinyl are floated on the surface of the sea so that the sides are about 10 cm above the water surface. Each tank contains about 50 "net hibi" and about 500 oyster shells implanted with conchocelis stages. The zubo system is similar, but is completely enclosed (Fig. 2).

Recently, a conchocelis net, the "zubo net" which has been improved from the earlier zubo apparatus and made of small-meshed double nets, is used for artificial seeding. At seeding, a conchocelis net with about 300 shells, which have been previously arranged within it, is set on a framelike simple raft; usually about 50 nori nets to be seeded are spread and staked on the raft. Finally, the raft is covered with a vinyl bag, but inside calm bays the raft is often floated without a cover. The raft is then left about 3 d to achieve good implantation on the nori nets.

To insure success in these methods, suitable and careful maintenance of the conchocelis stage is required; the collection of conchospores must be done within a few days, because of the environmental conditions that are created in a closed system.

Maintenance of juvenile to adult thallus stage.—Net hibi are used universally in Japan today. There are two major support structures:

1) The "kotei shiki" (or fixed method) is used in shallow and calm waters, e.g., within a bay where poles are embedded in the bottom.
2) The "betanagashi" (a floating method) is used offshore and in the open sea where various buoyant objects provide flotation and anchors maintain the position and shape of the system.

There is a third method which is intermediate between the above two methods. It is called "han fudo shiki" (a half floating method) and is used where there is a large tidal fluctuation. This method is used to avoid excessive drying during low tide periods, but keeps the *Porphyra* at the water surface for maximum light.

The most important difference between kotei shiki and betanagashi, as far as *Porphyra* spp. are concerned, is the provision for drying during cultivation. Thalli grown under nondrying conditions are more susceptible to disease, and the nori produced without a drying period are not as high in quality as the nori grown with a drying period. However, to date it has not been scientifically substantiated that drying is the direct cause of the increase in quality.

In the past it was not possible to allow a controlled drying period using the floating raft method. The juveniles were cultured with the fixed method inshore and then transplanted to a floating raft offshore 15-30 d before harvest. Recently M. Inayoshi, a nori culturist, improved the betanagashi method by adding a structure which facilitates raising the nets out of the vater (Ueda 1973). This improved system is becoming increas-ngly popular throughout Japan (Fig. 3).

One of the most important developments that has caused the general upward trend in nori production is the net-freezing technique. This technique makes use of a practical application of a normal physiological characteristic of *Porphyra* spp.—the characteristic being that *Porphyra* has high survival at low temperatures. *Porphyra* is usually grown to about 1-3 cm, but commonly 5-10 cm, on the net hibi. It is then transferred to land and partially dried, and placed in a freezer at −20°C. The net can then be set in place as needed to continue the culture cycle. Placement of the nets is staggered so that culturing can be continued without interruption throughout the season. Nets that have been harvested once or twice, or nets that are defective are replaced with new ones. With the development of this freezing technique, it has become possible to attain rapid growth rates and freedom from some of the diseases which usually plague the plants in late October and early November (Fig. 4).

It is well known that after multiple harvests thalli begin to decelerate in growth. Therefore, by having the capacity to exchange the nets during any given cycle, the viability of culture has been greatly increased. Today, nori culturists set over five times more nets at the time of seeding than before. The extras are frozen for the uses mentioned above. From an economic standpoint, this insures stability in the market and an increase in annual yield (Fig. 5).

PROPOSALS FOR THE FUTURE

Simpler Methods for Conchocelis Maintenance

The work required of fishermen for the maintenance of 5,000 oyster shells bearing conchocelis throughout one-half of the year is demanding, requiring the control of the culture temperature and light intensity, and the protection of the area from contamination by diatoms. Because of these difficulties the alternative, free-living culture of conchocelis stages, should be made suitable for use by fishermen.

Only a few liters of free-living conchocelis culture are necessary for successful transfer to mass culture. The principal difficulties preventing the adoption of the free-living technique by fishermen are contamination by diatoms and other organisms, and the lack of practical methods of conchospore collection. In the laboratory, however, chemicals effective

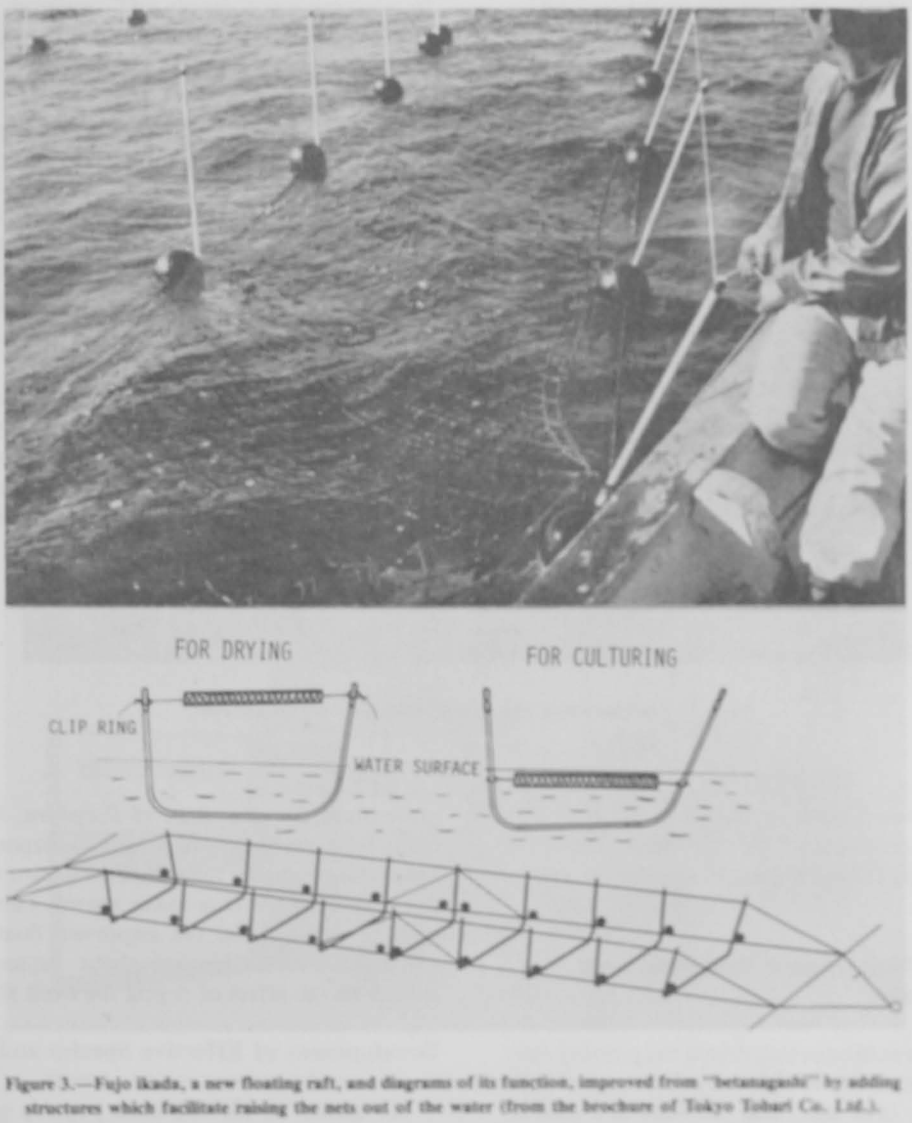

Figure 3.—Fujo ikada, a new floating raft, and diagrams of its function, improved from "betanagashi" by adding structures which facilitate raising the nets out of the water (from the brochure of Tokyo Tobari Co. Ltd.).

Figure 4.—Frozen nori nets stored in −20°C freezer. Nori nets are packed in a vinyl bag after semidrying and then the bags are sealed, since *Porphyra* should be protected from fresh air to minimize their respiration.

Figure 5.—Nori harvesting with a rotary blade, suction-type harvester.

against diatom propagation, such as GeO_2, were discovered (Kirita 1970; Kida and Enomoto 1975). The entire free-living technique is still experimental and requires improvement before transfer to mass culture.

Improvement of the Maintenance Technique from Juvenile to Adult Thalli

It is well known by the cultivator that drying the growing *Porphyra* is an effective way to remove contaminating seaweed such as *Enteromorpha* spp., *Ulva* spp., and diatoms, and also to grow healthy young thalli of *Porphyra*. Moreover, the sheets made from the thalli which have undergone the drying process are of better quality than the ones grown without it. However, the drying results in a lower growth rate of the thalli. Considering these facts, the improved floating raft should be employed extensively throughout Japan, and physiological studies on the effect of drying the thalli should be continued.

Development of Effective Species and Strains

The quality of the two most popular species and their new strains has been compared in terms of their industrial value. *Porphyra tenera* often yields the most expensive product due to the thinness of its thalli; however, this species undergoes decolorization more readily than *P. yezoensis*. *Porphyra yezoensis* has a wider tolerance range to environmental change and to disease than *P. tenera*. The difference in growth rate between the two species is not large, but care must be taken to choose a suitable environment for each.

The two new strains were produced by selective breeding. The object of the effort was to produce algae that have a high growth rate. At present, however, these new strains are not considered to produce good quality sheets. If selective breeding is begun with the objective of producing good sheets, however, the prospect of developing additional useful strains is good. When fishermen deploy the two new strains that have been developed, there is a tendency to overlook the environmental characteristics of their district. Furthermore, these new strains tend to grow thickly and undergo decolorization rapidly. They are especially unsuitable for cultivation in the northern region of Japan. To enable the further expansion of the nori industry, species and strains must be developed for each district. For example, *P. kuniedai*, which occurs mainly in the northern district, might be experimented with in that district.

The most popular method of breeding in general agriculture is crossbreeding. There are many difficulties in applying this method to *Porphyra*, however. The chromosome numbers of *Porphyra* spp. are small, characteristically 3 or 4. If any changes occur on the chromosome level, the phenotypic change may be quite drastic. There are many methods for producing mutants in land plants, but there are none reported in the literature for seaweed. It is therefore necessary to develop an effective artificial technique to produce *Porphyra* mutants.

At present, the most important study required for industrial development of nori is the classification of each species to determine its suitability for quality sheet production. Concurrently, the ability of each species to adapt to the existing conditions of each district must be studied. Until now many species and strains have been employed with little concern for scientific methodology. The major object has been to obtain heavy production. Species have even been imported from foreign countries with little attempt at taxonomic identification. Such efforts should be restricted because of the possible deleterious effects of such introduced species if they spread throughout the culture areas. Organized research work for the preservation of existing strains and the controlled and systematic search for new strains should be established as soon as possible.

Technique for Protection from Disease

The diseases to which nori culture is prone have been classified into two groups: Parasitic and nonparasitic. Of the parasitic diseases the most severe damage today is caused by "red rot" (akagusare), which is caused by the fungus *Pythium porphyrae*. Physiological characteristics of this fungus have been studied in axenic culture. An effective chemical technique for protection from the fungus has not been developed, however, since the use of chemicals in the sea can produce unforseen negative effects on other organisms living in the same area. Because of this, only indirect methods, such as extended drying periods, freezing, or net replacement, have been employed in the nori industry. The same methods are also used in the event of nonparasitic diseases. Because of the possible effects on other species, the application in the field of fungicides and bactericides developed for agriculture should be avoided. It is important that new disease-resistant strains be developed.

Efficient Use of Culture Fields

Overcultivation of culture fields has been restricted in certain districts. Such limitations have not gained general favor throughout the districts, since in the areas where restrictions have been advocated or imposed there has been no consistent scientific policy for insuring efficient yields to replace the former method of overcultivation. In the future the potential productivity of each culture field should be examined and classified, and then the culture field should be used efficiently, according to its potential productivity (Fig. 6).

City sewage and heated discharges of modern civilization can, if applied to the culture field in a controlled manner, have a small positive effect. To date, unfortunately, these wastes have been discharged into the aquatic environment with little regard for their effect upon aquaculture. This attitude must be changed if such material is to be regarded as a nonharmful addition to the sea environment. Aquaculturists must take the initiative to understand the problem and recommend intelligent waste discharge methods. For aquaculture to survive these new poten-

Figure 6.—Modern nori-sheet-making machine. Processing from fresh material through the final goods can be accomplished by one person (from the brochure of Otsubo Tekko Co. Ltd.).

tial dangers, the priority of water quality must be recognized by all concerned.

CONCLUSIONS

Although nori cultivation is almost standardized in Japan, there still remain a few constraints. Nori is marketed as raw sheet nori or processed nori. At present, the demand for raw sheet nori (which is premium nori) is greater than the supply. On the other hand, the supply of processed nori is greater than the demand.

In view of the present situation, the future success of the nori culture industry can be best achieved by encouraging increased consumption. This can be done by maintaining the highest quality in the product and lowering production costs. New technological improvements could influence and insure high quality. Production costs can be lowered by changing or improving existing practices through cooperative efforts similar to those used in agriculture: 1) cooperative cottage industry, 2) modified cooperative unions, and 3) full-scale cooperative union management. An economic evaluation of the industry would also be desirable.

ACKNOWLEDGMENTS

The author expresses deep appreciation to William N. Shaw, chairman of the U.S. Aquaculture Panel of UJNR (United States-Japan Cooperative Program in Natural Resources), and Robert D. Wildman and John B. Glude, NOAA, for their kindness; Tim Ahern, University of Washington, for his kind help and assistance with English; and Shigekatsu Sato and Hisashi Kan-no, Tohoku Regional Fisheries Research Laboratory, for their support.

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The Present Status of Brown Algae Culture in Japan

YUNOSUKE SAITO[1]

INTRODUCTION

Many edible seaweeds are intensively cultivated in Japan. The cultivation of the brown algae *Undaria* (wakame) and *Laminaria* (kombu) is quite popular and advanced.

Recently, demand for other brown algae, such as *Nemacystus* (mozuku), *Cladisophon* (okinawamozuku), *Endarchne* (habanori), and *Heterochordaria* (matsumo) have increased gradually because of current popularity of natural foods. At present, *Nemacystus* and *Cladosiphon* are cultivated commercially and *Endarchne* culture techniques are being developed under laboratory conditions. Also, in order to replenish coastal marine resources, attempts in aquatic plant population enhancement with seaweeds belonging to the families Laminariaceae and Sargassaceae have been carried out. One of the important objectives of the fisheries industry in Japan is to further develop the techniques of aquaculture of brown algae.

The purpose of this paper is to describe briefly the present status of aquaculture for Phaeophyceae and also to mention new aquaculture techniques devised recently in Japan.

INTENSIVE CULTURE

Undaria and *Laminaria*

Recent variations in annual production of *Undaria* cultivation are show in Figure 1. In 1975, about 19,000 growers were engaged in intensive cultivation of *Undaria* cultivation grounds about 13,000 ha in area. They produced about 100,000 t (wet weight) (Statistics & Survey Division, Ministry of Agriculture and Forestry, the Japanese Government 1977). The process of *Undaria* cultivation is shown in Figure 2. The alga can be fully controlled artificially through its life cycle and a comprehensive cultivation system has been established for this species (Saito 1975). Recently in Japan, however, increased production of *Undaria* has resulted in an oversupply, and, in addition, the quantity of imported *Undaria* has increased. Consequently, the economics of cultivation are difficult.

Laminaria is mainly cultivated along the coastal waters of Hokkaido and the northeastern region of Honshu. Figure 3 shows recent annual variation in production of *Laminaria*. In 1975, cultivation grounds of *Laminaria* were about 1,200 ha in area, producing about 16,000 t (wet weight) (Statistics & Survey Division, Ministry of Agriculture and Forestry, the Japanese Government 1977). The process of *Laminaria* cultivation is shown in Figure 4; a comprehensive cultivation system has been established (Hasegawa 1976). Special techniques have been developed for cultivation in warm seawaters, such as the Seto Inland Sea, where *Laminaria* does not occur naturally. *Laminaria* cultivation is advancing gradually, but at present its management is difficult.

Figure 1.—Annual variation in production in *Undaria* cultivation.

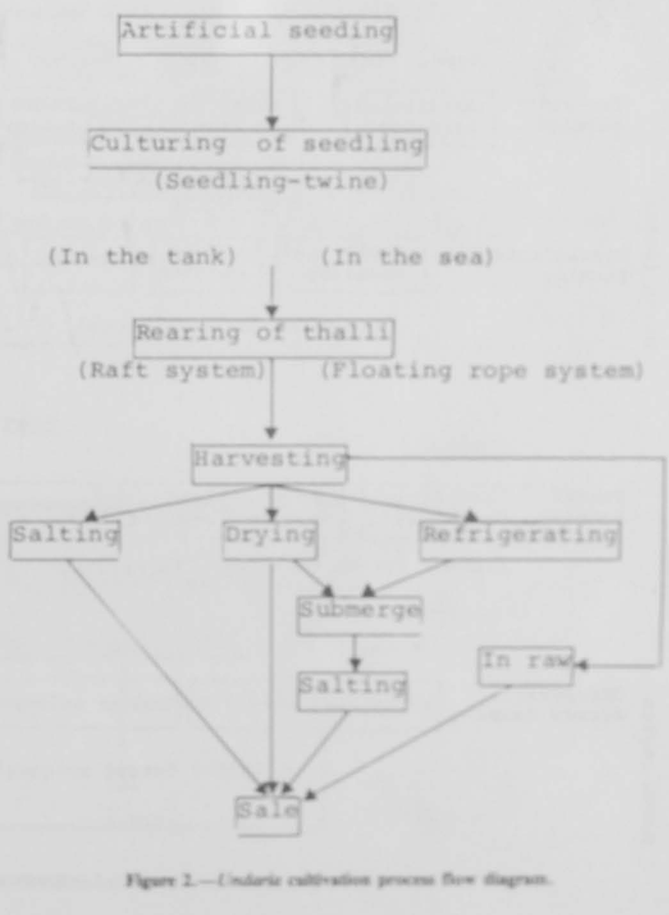

Figure 2.—*Undaria* cultivation process flow diagram.

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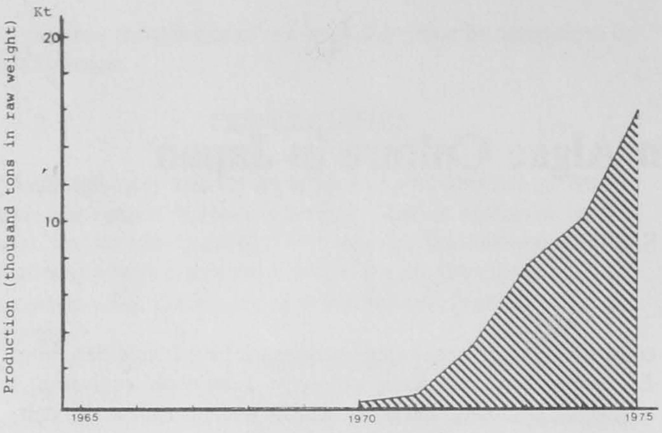

Figure 3.—Annual variation in production in *Laminaria* cultivation.

Under these circumstances, managers of *Undaria* and *Laminaria* culture operations are expected to increase production per cultivating unit and improve the quality of products. To attain these goals, it is necessary 1) to improve techniques to prevent infections and competition from harmful organisms, 2) to have efficient field fertilization, 3) to breed excellent strains, and 4) to culture healthy seedlings.

Nemacystus and *Cladosiphon*

Nemacystus dicipiens grows on sargassaceous algae, especially on branches of *Sargassum patens,* and is distributed on the southern Japanese coast, the west coast of Kyushu, and the northern Japanese coast of Honshu. The annual harvest from natural beds is estimated at several thousand metric tons (wet weight). Its life cycle, ecological characteristics, and cultivation techniques were studied by Migita and Yotsui (1972), Yotsui and Migita (1974), and Yotsui (1975a, b, 1976) (Fig. 5).

Cladosiphon okamurans is found chiefly on the skeletons of dead *Madreporaria* and seaweeds, sometimes on pebbles, cans, shells of dead shellfish, and other hard substrates. Its natural distribution is limited to the Ryukyu Islands. The annual harvest from natural beds is estimated at a few thousand metric tons (wet weight). Its life cycle, ecological characteristics, and cultivation techniques were studied by Shinmura and Yamanaka (1974a, b) and Shinmura (1974, 1975, 1976) (Fig. 6).

The cultivation of these two species involves similar methods, except for the water temperature necessary for spore release, germination, and growth. A characteristic difference between the two groups of cultured algae is that cultivation procedures include the entire life cycle for *Porphyra, Undaria,* and *Laminaria,* and only part of the cycle for *Nemacystus* and *Cladosiphon.* In autumn, the gross sporophytes bearing plurilocular sporangia collected from the field (and also small sporophytes that have been cultured in containers since spring) are placed in tanks under illumination of 2,000 lux with gentle aeration. After a large number of spores have been released into the seawater, culture nets made of synthetic fibers are put inside the tank to collect the zoospores. After the collection of zoospores, the nets are left in the same tank for 1-2 d and then transferred to sea, where they are spread in water of about 0.3 m deep for *Nemacystus* and of about 1 m deep for *Cladosiphon.* The culture nets are supported in the desired water layers by buoys and held by anchors, as shown in Figure 7. A few months after the collection of zoospores, *Nemacystus* grow to 10-30 cm long and *Cladosiphon* to 20-40 cm long under

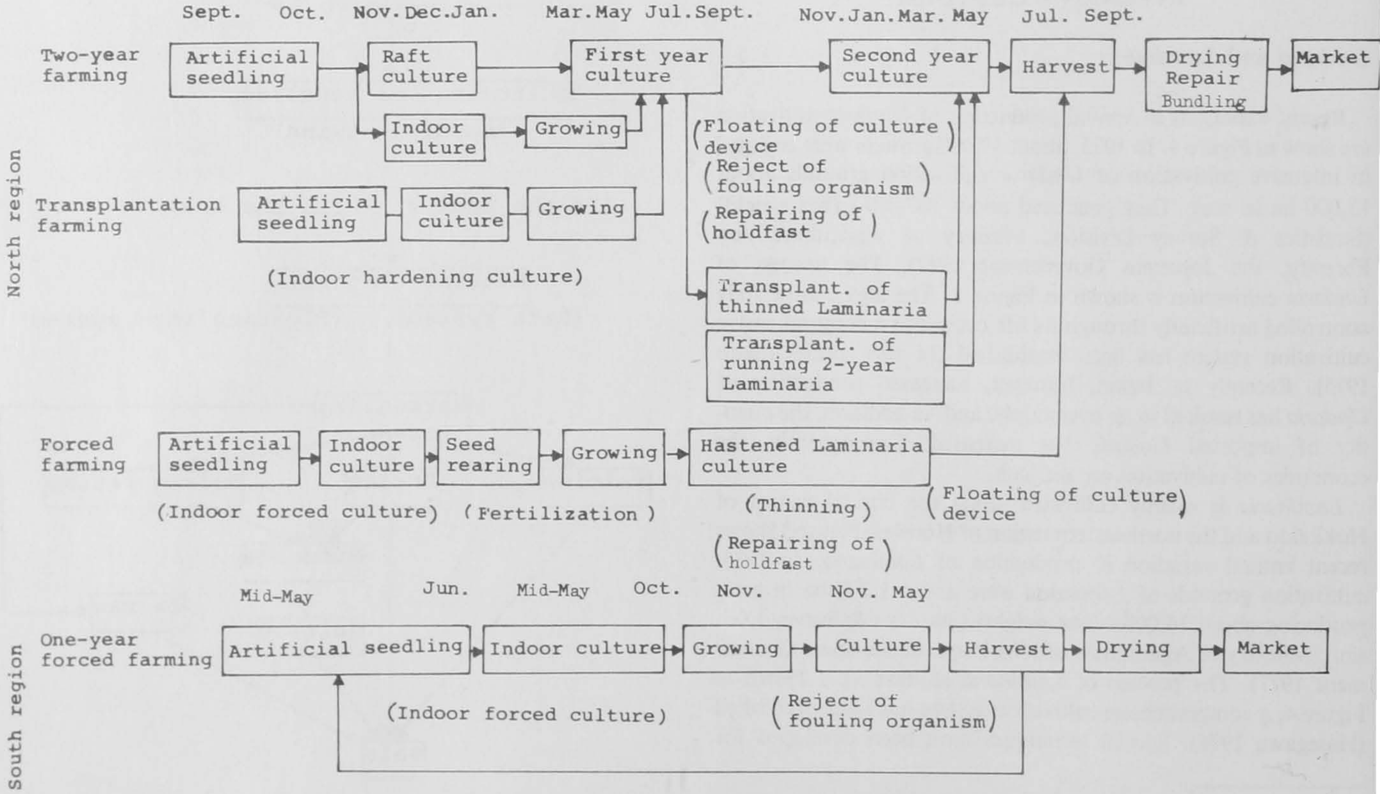

Figure 4.—*Laminaria* cultivation process flow diagram.

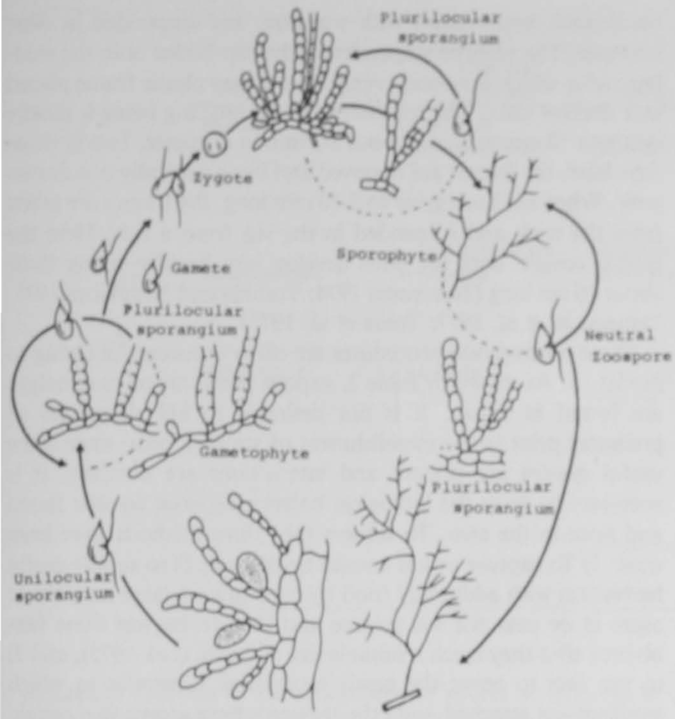

Figure 5.—Life cycle of *Nemacystus decipiens* (Migita and Yotsui 1972).

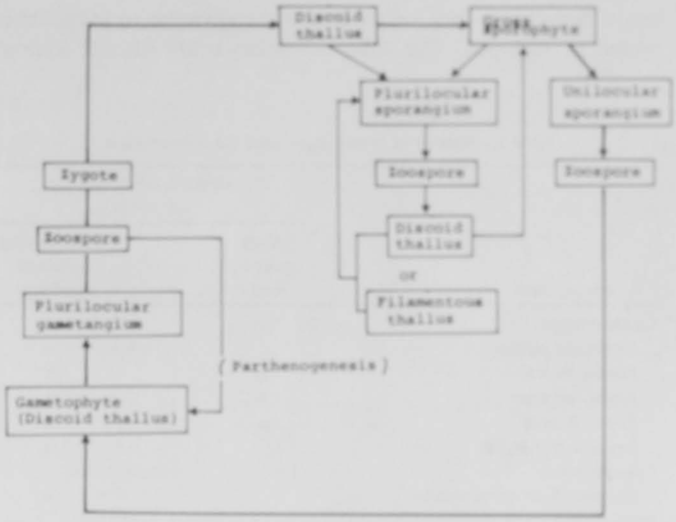

Figure 6.—Life cycle of *Cladosiphon okamuranus* (drawn from Shinmura 1974, 1975).

suitable environmental conditions. The harvest from one sheet of culture net (1.5 × 18.2 m) amounts to 30-60 kg (wet weight) for *Nemacystus* and 80-110 kg for *Cladosiphon*.

For further refinement of cultivation of *Nemacystus* and *Cladosiphon*, it is necessary 1) to define adequate culture conditions on the cultivation grounds, such as water currents, light intensity, and water quality; and 2) to prevent *Ectocarpus* sp. from growing on the culture net in the case of *Cladosiphon*.

EXTENSIVE CULTURE

Several artificial devices for growth of useful seaweeds have been tried, i.e., provision of artificial substrate, reef blasting, weeding and recruitment of seedlings, etc. However, these devices are practiced only with *Laminaria* spp. and *Heterochordaria abientina* in the brown algae, since these are the species in high demand, and with effective cultivation it is easy to achieve a return on the invested capital (Hasegawa 1976).

The combined methods of stone planting and recruiting of seedlings are widely employed for aquatic afforestation with brown algae. Stones or concrete blocks of various forms and sizes are planted on the sea bottom, and then cultured seedlings are transplanted on them by winding the seed twine around them. In another method, spores or embryos naturally attach on such substrates. Species of the families Laminariaceae and Sargassaceae, which are now used for aquatic plant population enchancement, are shown in Table 1. The culture methods of seedlings of algae of the family Laminariaceae are fundamentally similar to those used in intensive culture.

The culture methods for algae of the family Sargassaceae are as follows. Mature fronds are floated in seawater tanks to collect em-

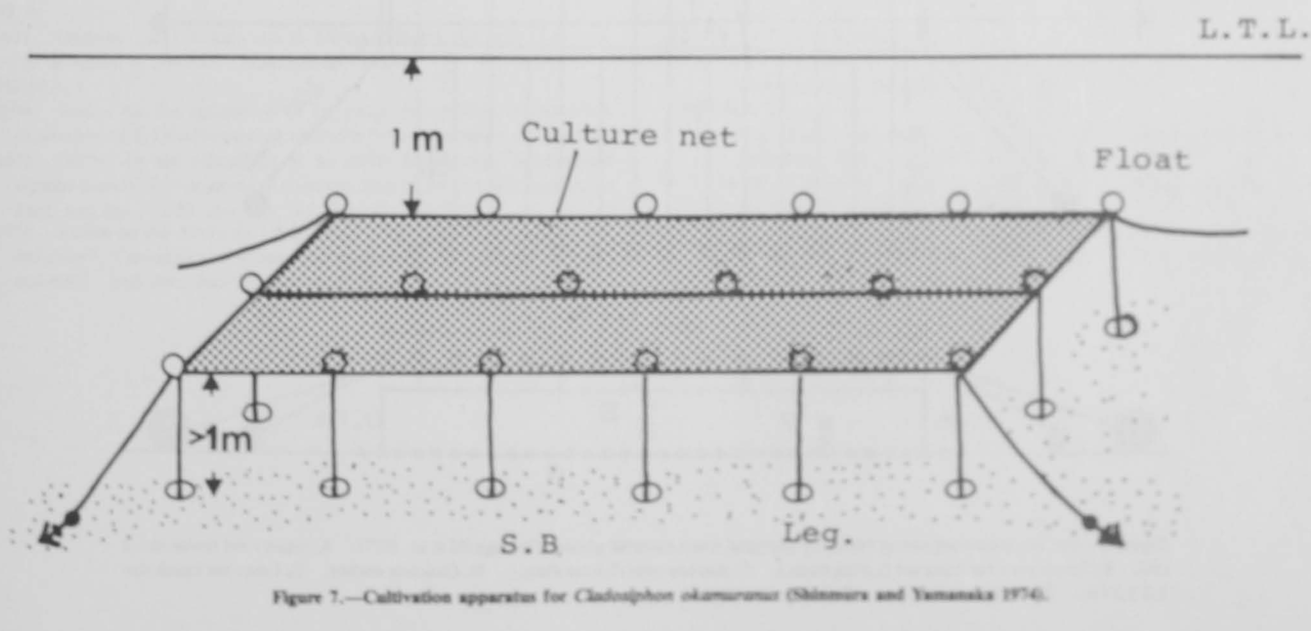

Figure 7.—Cultivation apparatus for *Cladosiphon okamuranus* (Shinmura and Yamanaka 1974).

bryos. Sometimes they are shaken in the seawater to induce the release of embryos. The collected embryos are filtered with a small mesh net, washed with seawater, and suspended in clear seawater. The embryo suspension is then sprinkled onto the seedling twine which is wound evenly on a square plastic frame placed in a shallow tank. The material used for seedling twine is mostly synthetic fiberspun yarn, about 2-3 mm in diameter. Two or three days later, the frames are removed and hung vertically in a deeper tank. When the buds grow to 5-10 mm long, the frames are taken from the tank and suspended in the sea from a raft. Here the frames remain until the buds develop into healthy young thalli about 10 cm long (Tomiyama 1974; Yoshida and Nishikawa 1975; Yamaguchi et al. 1977; Toma et al. 1977).

These propagation procedures are often unsuccessful owing to predators. As shown in Table 2, various predators on macroalgae are found in Japan. It is not desirable to kill all species of predators prior to the establishment of seaweed beds; since some useful species are present and interactions are complex, it is necessary to keep the biological balance between aquatic fauna and flora in the area. To achieve this, three methods have been tried: 1) To capture or kill unused herbivores, 2) to supply useful herbivores with additional food by cultivating a large amount of algae at or near the sea surface and then to harvest these herbivores after they reach a suitable size (Kikuchi et al. 1975), and 3) to use nets to cover the newly established substrates to which seedlings are attached, until the seaweeds have grown to a certain size, as shown in Figure 8 (Yamaguchi et al., 1977).

For the further development of brown algae propagation in the sublittoral zone, it is necessary to: 1) further clarify the

Table 1.—Species of brown algae used for afforestation.

Species name	Methods of recruitment of seedlings: Setting mother fronds	Transplanting cultured seedlings
Laminariaceae		
Laminaria japonica		o
Eisenia bicyclis	o	o
Eisenia arborea	o	o
Ecklonia cava	o	o
Undaria pinnatifida		o
Cystoseiraceae		
Cystophyllum sisymbrioides		o
Sargassaceae		
Sargassum piluriferum		o
Sargassum patens	o	o
Sargassum pinnatifidum	o	
Sargassum horneri	o	o
Sargassum serratifolium		o
Sargassum tortile		o
Sargassum fulvellum		o
Sargassum ringgoldianum		o
Sargassum thunbergii		o
Sargassum assimile	o	
Sargassum siliquosum	o	

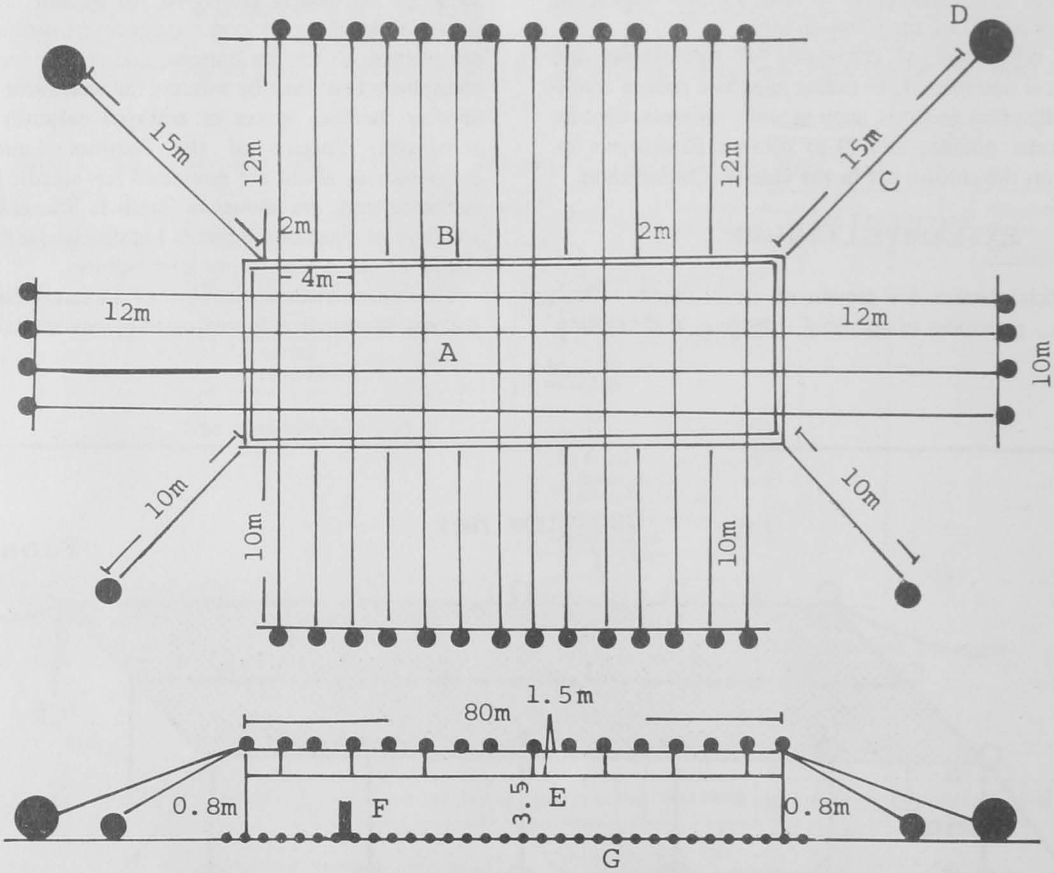

Figure 8.—Net for protecting young buds, for example, from harmful grazers (Yamaguchi et al. 1977). A. Square net (mesh size 2 cm). B. Frame rope for fence net (2.4 cm diam.). C. Anchor rope (1.8 cm diam.). D. Concrete anchor. E. Fence net (mesh size 1.2-1.5 cm). F. Underwater zipper. G. Lead chain sinker.

Table 2.—Predator fauna for macroalgae in Japan.

Phylum	Class and subclass	Order	Family	Genus
Mollusca	Gastropoda			
	Prosobranchia	Archaeogastropoda	Haliotidae	*Haliotis*
			Acmaeidae	*Cellana*
			Trochidae	*Omphalius*
			Turbinidae	*Turbo*
	Opisthobranchia	Anaspidea	Aplysiidae	*Aplysia*
Echinodermata	Echinoidea	Echinoida	Toxopneustidae	*Pseudocentrotus*
			Strongylocentrotidae	*Hemicentrotus*
				Strongylocentrotus
			Echinometridae	*Anthocidaris*
Vertebrata	Osteichthyes			
	Teleostomi	Percida	Girellidae	*Girella*
			Embiotocidae	*Ditrema*
			Labridae	*Halichores*
			Chaetodontidae	*Chaetodon*
			Scaridae	*Leptoscarus*
			Siganidae	*Siganus*
		Tretaodontida	Monacanthidae	*Stephanolepis*
				Navodon
		Cottida	Hexagrammidae	*Hexagrammos*

mechanisms involved in the attachment of spores or embryos in relation to environmental conditions, such as current and wave action, and to develop techniques which can improve these environmental conditions; and 2) study the mechanisms of succession of fauna and flora in the propagation grounds and to develop techniques to control the succession.

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The Use of Phytoplankton for Aquaculture Needs—a Status Report

WILLIAM N. SHAW[1]

INTRODUCTION

The important role of phytoplankton or algae as a food source in aquaculture is sometimes overlooked since there is a natural tendency to emphasize the commercially cultured species. Phytoplankton as food for cultured species, at some or all life history stages, is a critical element of production systems. In some instances, the culture of algae is the most expensive part of the total system, requiring the most space and labor to maintain. If the algae die, the total culture system fails. The purpose of this paper is to give several examples of the key role phytoplankton plays in aquaculture.

MOLLUSK CULTURE

One of the most widely recognized uses of phytoplankton is in shellfish hatcheries. Here algae are utilized to culture shellfish larvae to metamorphosis and for a short period of time thereafter, until the shellfish are placed in the natural environment. There are two accepted methods for culturing phytoplankton for hatchery use—the "Loosanoff Method" and the "Glancy Method."

The Loosanoff Method employs cultures of single species of known genera utilizing sterile containers and water. The usual method is to start off with a small quantity of inoculant (Fig. 1) and, through a series of progressive changes, to build up to large volumes of algae. These cultures in turn are fed directly to the shellfish larvae. In the past, the most acceptable species have been *Monochrysis lutheri* and *Isochrysis galbana* (Ukeles 1976). In more recent studies, Dupuy et al. (1977[2]) have utilized a combination of three algae—*Pyramimonas virginica* (Va-17), *Pseudoisochrysis paradoxa* (Va-12), and *Chlorella* sp. (Va.-52). They have reared larvae to the "eyed" stage in 9-11 d using these three algae.

In the Glancy Method, seawater is passed through nylon bag filters or through a centrifuge. The effluent is piped into large containers which are illuminated by sunlight (Fig. 2). The filtering or centrifuging of the water removes large particles and organisms, and only small cells such as diatoms, flagellates, and nannoplankters pass through. A bloom occurs within 24 h. No fertilization or inoculation is necessary to attain the bloom. The bloom, usually of mixed and unknown species, is fed to the shellfish larvae (Fig. 3). This method has worked successfully with hard clam, *Mercenaria mercenaria*, and bay scallop larvae, *Argopecten irradians*, particularly on the eastern shore of Virginia (Castagna 1975).

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[2]Dupuy, J. L., N. T. Windsor, and C. E. Sutton. 1977. Manual for design and operation of an oyster seed hatchery for the American oyster, *Crassostrea virginica*. The VIMS/Sea Grant Program Spec. Rep. No. 142, 111 p.

Figure 1.—Stock solutions of phytoplankton.

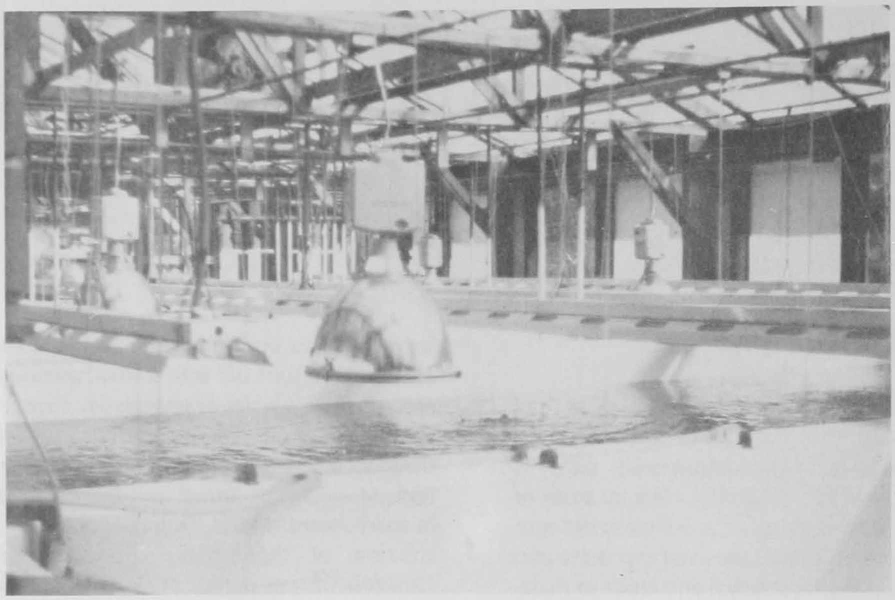

Figure 2.—Phytoplankton tanks at a commercial shellfish hatchery on Long Island, N.Y.

Phytoplankton production plays a key role in the success or failure of a shellfish hatchery. It is one of the most expensive items associated with a hatchery and takes a large amount of space. Recognizing these factors, studies are underway in several laboratories to replace phytoplankton with artificial diets.

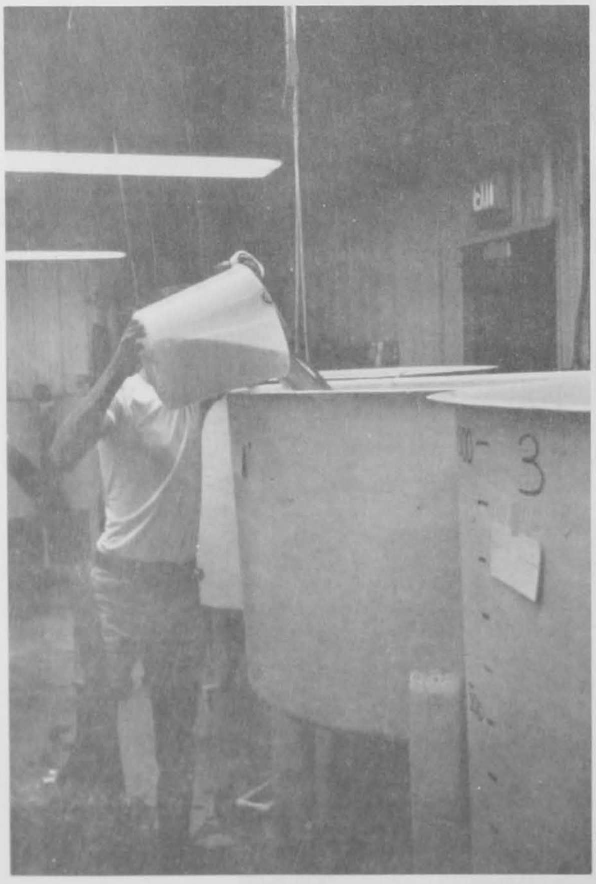

Figure 3.—Phytoplankton being poured into shellfish larvae grow-out tanks.

Studies are also underway to utilize phytoplankton, not only for the hatchery aspects of bivalve culture, but also for growing mollusks to marketable size. The University of Delaware is growing large volumes of algae, principally *Thalassiosira pseudonana,* as part of their attempt to develop a controlled environment for shellfish mariculture. Initially, the algae were grown indoors, utilizing artificial lighting (Fig. 4). The high costs for artificial lights needed to produce large volumes of algae caused the researchers to switch to an outdoor greenhouse system (Fig. 5). In recent studies (Pruder et al. 1978), cell counts in 9,000 liter containers have been increased from less than 2×10^6/ml to over 10×10^6/ml [a 5-fold increase] by bubbling N_2 and CO_2 gas mixture. The addition of gases controls the pH and dissolved oxygen levels which in turn favor algal growth. The main difficulty is finding suitable algal species that can withstand high temperatures and also promote shellfish growth. In earlier experiments with two species of algae, *T. pseudonana* and *I. galbana,* oysters have been grown to market size in 9 mo. Unfortunately, the latter algae cannot be grown under greenhouse temperatures. Recently, another species of *Isochrysis* from Tahiti has been grown successfully in the controlled environment and appears to be an excellent food for bivalve mollusks.

In St. Croix, Virgin Islands, a unique culture method is being tested, using nutrient-enriched water pumped from 800 m depths to grow phytoplankton. Deep water is pumped into two 50,000 liter pools (Fig. 6) that have been inoculated with *Chaetoceros curvisetus* (Fig. 7). The water is then pumped continuously to raceways containing the clam *Tapes japonica.* This system has produced excellent growth and a high quality product. The economics of the system, plus final testing of raceway design, are now being examined.

In Woods Hole, Mass., studies are underway using the effluent from secondary sewage treatment, which is mixed with seawater to grow a single-celled marine alga in 120,000 liter ponds (Fig. 8). The seawater containing the bloom of

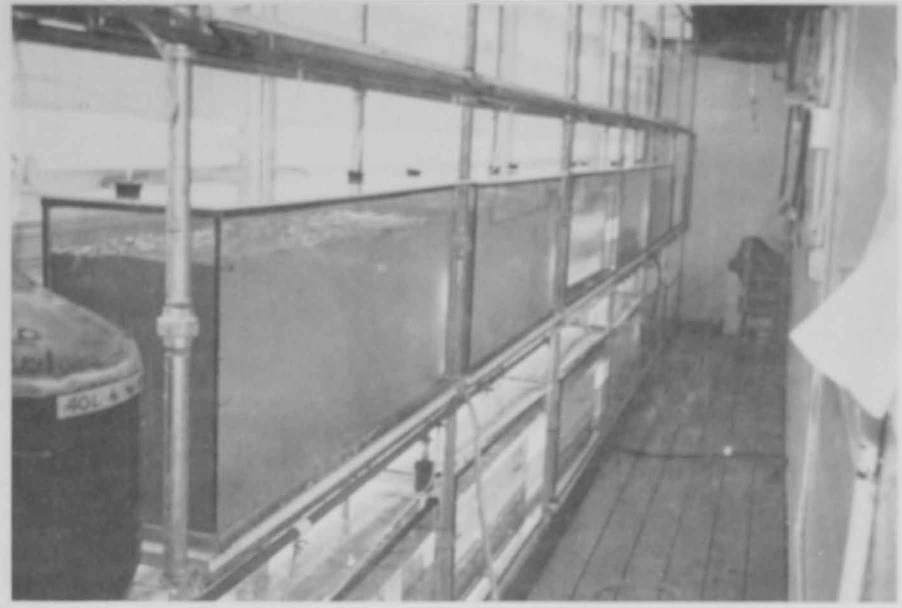

Figure 4.—Phytoplankton aquariums, University of Delaware, Lewes, Del.

Figure 5.—Special cylinders used to grow phytoplankton at the University of Delaware's controlled shellfish grow-out system.

phytoplankton is continuously fed to shellfish. In turn, the effluent from the shellfish culture is passed into containers holding seaweeds, such as *Graciliaris foliifer* and *Agardhiella tenera*. These seaweeds remove nutrients not initially assimilated by the phytoplankton and the shellfish (Ryther 1977).

Principal species of algae grown in the system have been *Skeletonema costatum* in the winter (0°-9 °C) and *Phaeodactylum tricornutum* in the summer (10°-25 °C). One of the biggest problems is maintaining a favorable temperature for shellfish growth. With temperatures fluctuating from 0° to 25 °C, it is difficult to correlate shellfish growth with food supply. Presently, the facility is not able to heat or cool large volumes of water to the desired temperature to maximize shellfish growth. Another problem to be faced is the certification (by the U.S. Food and Drug Administration) of shellfish that are grown in such a system.

In Hawaii, two private companies, Aquatic Farms, Ltd. and Kahuku Seafood Plantation, are growing oysters on land-based facilities. Phytoplankton ponds, as large as 0.405 ha, are being used to provide the necessary food for tray-grown oysters.

Figure 6.—Phytoplankton pools, St. Croix, Virgin Islands.

CRUSTACEAN CULTURE

Phytoplankton plays an important role in the nutrition of shrimp larvae. There are two methods used to obtain the necessary amount of phytoplankton: Fertilizing the larval tank to obtain the necessary bloom, or growing the phytoplankton separately and adding it to the culture tank. The principal species cultured is *Skeletonema* sp., although other species, such as *Tetraselmis* sp. and *Thalassiosira* sp., have also been used successfully (Yang 1975). Recently, a private firm has been culturing and freeze-drying *Skeletonema*. This product has been used successfully in culturing shrimp larvae in Texas. Mock (1974) has successfully concentrated *Skeletonema* by centrifuging, refrigerating or freezing, and then using it at a later date to feed shrimp larvae.

Figure 7.—Cylinders of phytoplankton used to inoculate pools, St. Croix, Virgin Islands.

Considerable interest has developed in the use of phytoplankton in culturing several species of *Macrobrachium* larvae, particularly *M. rosenbergii*. Fujimura (1966) stressed the value of growing *Macrobrachium* larvae in "green water." He claimed that algal supplements increased larval survival and shortened the time to stockable postlarvae. Studies by Maddox and Manzi (1976) concluded that algal supplements increased larval survival and the production of postlarvae while decreasing the length of time required for metamorphosis. In the above experiments, the larval tanks were inoculated with algae to produce cell counts ranging from 400,000 to 1,300,000/ml. However, a commercial company in Puerto Rico successfully rears *Macrobrachium* larvae without algal supplement. Therefore, the question of the need for algae for rearing freshwater prawn larvae still remains unresolved.

Algae play another interesting role in the culturing of *Macrobrachium* in ponds. The Puerto Rican company mentioned above has run into serious problems with aquatic weeds. In an attempt to control the growth of weeds, fertilizers have been added to the ponds to create an algal bloom. The bloom in turn acts as a shadow which cuts the sun's rays; thus, the aquatic weeds cannot grow. The greatest problem encountered with this method is maintaining a stable bloom.

FINFISH CULTURE

Experiments have been carried out in Alaska to test the feasibility of using artificial upwelling to enhance primary

Figure 8.—Phytoplankton ponds, Woods Hole, Mass. Photograph by D. Cheney.

productivity in Alaskan impoundments (Nevé et al. 1976[1]). Deep, nutrient-rich water was pumped into an experimental pond. Primary productivity was five times greater in the pond receiving upwelling than in a pond supplied with surface water. Hopes were to use this increased productivity for growing clams, oysters, and abalone, and the increased phytoplankton biomass would also be utilized by zooplankton, a major food for growing pink and chum salmon fry.

In Arcata, Calif., researchers from Humboldt State University have been rearing Pacific salmon in saltwater ponds fertilized with domestic wastewater (Allen 1976). Nutrient-rich wastewater was added to these ponds (Fig. 9). The nutrients stimulated a phytoplankton bloom. The bloom was in turn fed upon by zooplankton; coho and chinook salmon fry then fed on the zooplankton. The general concept of this experiment was to reduce hatchery feed costs by augmentation of the production of natural feeds with domestic wastes.

Algae are a necessary component in the culture of many marine finfish larvae. In most cases, algae are used as food for zooplankton, such as *Artemia* sp. and rotifers. The zooplanktons are then utilized by the larval fishes. For example, in the culturing of the southern sea bass, *Centropristis melana*

[1]Nevé, R. A., R. C. Clasby, J. J. Goering, and D. W. Wood. 1976. Enhancement of primary productivity by artificial upwelling. Univ. Alaska Sea Grant Program Rep. 76-8, 22 p.

Figure 9.—Arcata oxidation pond, North Humboldt Bay, northern California.

(Roberts et al. 1976), thread herring, *Opisthonema oglinum* (Richards and Palko 1969), scaled sardine, *Harengula pensacolae* (Houde and Palko 1970), and Florida pompano, *Trachiontus carolinus* (Hoff et al. 1978), this procedure is used. Roberts et al. (1976) also found that *Dunaliella* or *Nannochloris* algae maintained water quality when culturing *C. melana*.

SUMMARY

I have briefly outlined examples of the key roles that phytoplankton plays in aquaculture. It is, in some cases, one of the major costs in an aquaculture facility. For example, in a shellfish hatchery in Maryland, over 200 liters of algae are used daily to culture oyster larvae. The manager stated that this represented 40% of his total production costs (Krantz[4]). To reduce these costs, programs like the one in Delaware are using sunlight and gases to increase cell counts. In other cases, like the one now being carried out at the Virginia Institute of Marine Science, artificial diets are being developed to replace the algae. Yet, it is obvious that phytoplankton will continue to be important in many aquaculture programs. A substitute is still in the distant future.

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Seaweed Cultivation: A Review[1]

ARTHUR C. MATHIESON[2]

ABSTRACT

A synopsis of information regarding technical, biological, and sociological problems associated with seaweed cultivation is given. The biology, ecology, and resource management of 12 economically important seaweeds (*Chondrus crispus, Eucheuma, Gelidium, Gracilaria, Hypnea, Iridaea, Palmaria palmata, Porphyra, Pterocladia, Laminaria,* and *Macrocystis*) in North America, the United States' possessions, the Trust Territories of the Pacific Islands, and the Philippines are extensively reviewed. The needs for enhanced energy production (e.g., methane), waste recycling, and increased food production have stimulated many seaweed cultivation activities dealing with polyculture, artificial upwelling, and marine biomass. The growth and potential benefits of seaweed populations in association with these programs are reviewed. It is suggested that a coordinated knowledge of the biology, ecology, physiology, biochemistry, and population genetics of economic seaweeds is fundamental for their future husbandry, management, and conservation. Equally important is a thorough consideration of engineering and economic principles for the sustained utilization and mariculture of these seaweeds. Several recommendations for the further advancement of seaweed mariculture programs in North America are given.

INTRODUCTION

Seaweeds or benthonic macroscopic marine algae are presently employed as a source of phycocolloids (naturally occurring storage products), as foods, for the removal of inorganic nutrients, and as potential solar energy collectors (Mathieson 1969, 1975; Michanek 1975; Ryther 1975; Naylor 1976; Jackson 1980; Rao et al. 1980) and for a variety of other uses (Kiran et al. 1980). In addition, they form a very productive fringe to the ocean, which provides a nursery area for many commercially important species of fish and invertebrates (Mann and Chapman 1975). The present paper is an update of an earlier paper (Mathieson 1975), which summarizes information on the cultivation, biology, ecology, and resource management of the major economically important seaweeds in North America, the United States' possessions, the Trust Territories of the Pacific Islands, and the Philippines. An understanding of such information is necessary for the maintenance and continued utilization of these valuable resources.

The first section, Seaweed Mariculture—An Overview, discusses several biological, technical, and sociological problems associated with seaweed cultivation, and reviews recent conclusions dealing with the potentials of seaweed mariculture. The second section, Mariculture and Ecology of Several Seaweeds, summarizes current mariculture activities of 12 major economically important seaweeds: 10 red algae and 2 brown algae, commonly called kelps. Except for *Palmaria palmata* and *Porphyra,* all of the species contain the phycocolloids agar, carrageenan, or algin, which are the basis (or potential basis) of major industrial utilizations of seaweeds (Mathieson 1969, 1975). The third section, Selected Mariculture Programs, describes the growth of seaweeds in association with the artificial upwelling system in St. Croix, U.S. Virgin Islands, as well as the marine biomass and several polyculture waste-recycling programs.

SEAWEED MARICULTURE—AN OVERVIEW

Several individuals have recently summarized the potentials of seaweed mariculture (Krishnamurthy 1967; Suto 1974; Huguenin 1975, 1976, 1977; Mathieson 1975; Bonotto 1976; Neish 1976a, b, 1979; Saito 1976; Wheeler et al. 1979; Abbott et al. 1980). Some major conclusions from these studies are reviewed in order to give a better perspective for the needs, opportunities, and problems associated with seaweed cultivation.

Three basic approaches to the mass culturing of seaweeds have been described (Huguenin 1975, 1976, 1977): 1) Lagoon or pondlike enclosures, 2) open-ocean upwelling, and 3) intensive raceway. Lagoon culture methods employ natural areas such as estuaries, bays, and ponds which are dependent upon natural flushing; such methods are presently employed in Japan for a variety of seaweeds (Saito 1976), in China with *Laminaria* (Cheng 1969), in Taiwan with *Gracilaria* (Shang 1976; Lin et al. 1979), and in the southwest Pacific with *Eucheuma* (Doty 1973a, b; Parker 1974). The open-ocean upwelling system is presently being developed (Beleau et al. 1975; Wilcox 1975a, b, 1976a, b, 1977) to produce 40,500 ha open-ocean seaweed farms of the giant kelp, *Macrocystis pyrifera,* based on artificially upwelled nutrients. Many of the efforts to date in North America have employed unattached vegetative mass culturing of seaweeds in manmade raceways, with either a V-shaped cross section or a perpendicular wall with a single sloping bottom and aeration, pumping, or paddle agitation. In addition, oval-shaped tanks have been used with the water being circulated either by pumps or paddles. Huguenin (1977) suggested a fourth system, intensive rotary culture, which would be similar to a spray irrigation or sewage trickling filter system. Such a system would periodically wet and rotate seaweeds, which are uniformly distributed in large, shallow, circular basins that contain only a small amount of water. For each of these approaches, potential performance, costs, risks, and relative advantages are compared.

The future potentials of large-scale seaweed culture systems have been evaluated (Huguenin 1976), based upon a case study approach, taking into account such factors as scale and size, species selection, nutrient distribution, flow control, harvesting,

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and economics. According to Huguenin (1976), the major problems and uncertainties regarding intensive seaweed cultivation are those of scale, hydraulics, residence time, nutrient supplies, monitoring and control of the facility, control of epiphytes, seaweed physiology, and species selection. Basically an interdependent knowledge of seaweed biology, engineering, economics, and operating policies will be required for any successful seaweed culturing system.

Harvesting from closely managed natural stocks is becoming increasingly expensive (e.g., with *Chondrus crispus*), and it may not provide sufficient material for the projected needs of commercial marine plant industries. Hence, mariculture techniques are being developed in Canada. Neish (1976a, b, 1979) gave a comprehensive review of the Canadian seaweed mariculture industries, which are in an early stage of development. Seven strategies are being examined in order to enhance control over raw material: 1) Management of natural stocks, 2) addition of substrata and habitat improvement, 3) live storage of harvested plants, 4) vegetative propagation of wild stocks, 5) vegetative propagation of selected clones, 6) grow-out of hatchery seed, 7) grow-out of hatchery seed from selected seed.

The simplest form of plant mariculture in Canada consists of providing suitable growing conditions (i.e., substrata) for commercially desirable species. Habitats may also be "improved" by the removal of undesirable species and by fertilization of natural beds. To date, neither of these strategies is used extensively in Canadian mariculture programs. Live storage of harvested plants has been practiced for a number of years in the dulse, *Palmaria palmata*; rockweed, *Ascophyllum* and *Fucus*; and Irish moss industries. This may vary from simply holding harvested plants in bags in the sea for a few days until suitable drying weather occurs to a complex form of holding living material in large tanks with agitation by compressed air. In such tanks, dulse can be kept alive and growing for 4-6 mo. The vegetative propagation of suspended cultures of seaweeds was first initiated in Canada with *C. crispus* (Neish and Fox 1971; Neish and Shacklock 1971; Shacklock, Robson, Forsyth and Neish 1973; Shacklock, Robson, and Simpson 1973) at the Sandy Cove field station of the National Research Council of Canada. Several companies (Marine Colloids, Inc. and Genu Products Canada, Ltd.) have recently initiated cultivation programs of Irish moss based on this technology, as well as the selection of fast-growing strains of *C. crispus*, to increase yields and growth rates[1]. As several seaweeds cannot be propagated vegetatively, grow-out techniques must be initiated, particularly with annual species or species with an annual frond and a perennial holdfast.

Several characteritics of an intensive marine plant mariculture system have been described (Neish 1976a, 1979), including the efficient use of natural energy and materials, investment capital, operating expenses, enhancement of applied biology programs to develop crop control and management techniques, biosynthesis of desired end products (e.g., phycocolloids), monitoring of crop and culture conditions, control of harvesting, integration of sales and supply, and maximum efficiency or profitability by control of all levels of the system. Several technical problems have arisen since the initiation of an active Canadian mariculture program in 1950 (Neish 1976b). Some of the areas that will require particular attention are pests and diseases, improved techniques for seed stock and selection, increased knowledge of algal physiology, and correlation and utilization of existing knowledge.

Density and tank agitation are interacting parameters associated with propagation of detached seaweeds and have profound effects on yield, crop cleanliness, production cost, and other economically critical variables (Neish and Knutson 1979). According to the same investigators, the maximum sustained yields per unit of pond area occur at densities of 1.0-2.5 kg of live algae/m^2. At lower densities, fast growth rates were observed but area yields diminished and epiphytization became a problem. Agitation by mechanical, pneumatic, or hydraulic means reduced epiphytization by mixing the crop and by physically disrupting epiphytes. Agitation was also important from the standpoint of mixing nutrients, exposing all fronds to light, and contributing to the general homogeneity of culture conditions. An optimization of pond agitation, which requires energy, and density-yield relationships will obviously determine the capital intensity of a culture system.

A general review of the principles and perspectives of seaweed cultivation in enclosed systems has also been summarized (Neish 1979). The main features of closed systems are discussed in relation to several research and development projects in the United States, Canada, and elsewhere; i.e., instances where seaweeds are being employed in polyculture systems, as well as for food and fodder, as feedstock for chemical industries, as effectors of tertiary effluent treatment, as recovery vectors for valuable compounds, and for removal of deleterious compounds are enumerated. Overall, Neish characterized closed-system seaweed cultivation as a high-investment, high-technology business requiring a firm foundation of scientifically verified facts. An opportunity brief describing many of the technical, economic, and biological factors associated with closed-cycle aquaculture was recently summarized (Anonymous 1977d).

The seaweed cultivation program at the University of California, Santa Barbara, was recently summarized by Neushul et al. (1976), Neushul et al. (1977), and Charters and Neushul (1979). They emphasized that many of the problems of creating a suitable environment for the growth and reproduction of large seaweeds were yet to be solved. Successful experimental cultivation depends on having large volumes of seawater, the temperature and chemistry of which must be held within prescribed limits. Contaminants and epiphytes must also be controlled (Polne et al. 1980). The requirement of water motion is particularly important for many seaweeds (Charters et al. 1972, 1973). The Santa Barbara cultivation system consists of an outdoor greenhouse with aquaria, which is combined with an indoor cultivation room, having controlled light intensity and photoperiod. The greenhouse was designed to permit the sustained growth of large kelps, several of which have been grown for over a year in a continuously healthy state. Other plants have been grown from germlings, transplanted to the ocean, and periodically returned to the greenhouse for measurement and study.

Several other descriptions of experimental culture facilities were given at the international symposium "The Cultivation of Marine Organisms and Its Importance to Marine Biology" (Kinne and Bulnheim 1970). For example, South (1970) described an experimental culture facility for the growth of kelps, which consisted of a tank system supplied with filtered, free-flowing seawater and artificial illumination. He was able to obtain sporophytes of *Alaria esculenta* 30 cm long in 6 mo, starting from zoospores. The papers by Kornmann (1970), Jones and Dent (1970), Simonetti et al. (1970), and Smith and Jones (1970) from the same symposium should also be consulted as they give

[1]Marine Colloids, Inc. is now a subsidiary of FMC Corporation, Rockland, ME 04841.

a variety of details regarding cultivation techniques. Chapman (1973c) summarized several other seaweed cultivation methods, including a spray culture system perfected by L. A. Hanic that showed excellent potential. In addition, an automatic culture system for growing and testing the effects of pollution on seaweeds has been described by Markham et al. (1979). Various outplanting techniques were reviewed by Neushul and Powell (1964) and Hanic and Pringle (1978a, b).

A detailed account of engineering principles and their role in aquaculture was summarized by Wheaton (1977). Two major areas were addressed: The influence and importance of physical and biological parameters on aquatic organisms; and engineering considerations in aquaculture, including culture system design, water supply flow and level instrumentation, pump requirements, impoundment structures, filtration, disinfection, and aeration. Much of this information should be consulted as it is particularly relevant to future seaweed cultivation programs.

According to Krishnamurthy (1967) there are six major problems restricting enhanced seaweed cultivation: 1) Selection of a suitable environment for growth, 2) engineering of the seashore for farming, 3) protection of the crop from physical and biotic effects, 4) probable pests and parasites, 5) proper transplantation of young germlings to the field for cultivation, and 6) harvesting. In addition, he emphasized that a knowledge of the plant's biology and reproduction is fundamental to successful cultivation.

A further overview of seaweed mariculture was given by Mathieson (1975), including a discussion of some of the major biological, technological, and sociological problems. Some of his conclusions are summarized below. Foremost, protection of crops from biological (i.e., grazing) and physical effects is a major consideration in seaweed cultivation (Shacklock and Croft 1981). Extensive fish and urchin grazing (Randall 1965; Leighton et al. 1966) are known to occur in many areas and they can easily destroy a large-scale farm. Various predators and pests (Kohlmeyer 1973, 1979; Andrews 1976, 1977, 1979a, b; Bowie 1976; Dodds 1979; Kazama 1979; Yoshida and Akiyama 1979; Goff and Glasgow 1980) may cause an epidemic destruction of unialgal seaweed farms. Abiotic factors (North 1979a; Vadas 1979) may also reduce seaweed productivity. Adequate harvesting techniques must be devised for each of the different types of seaweeds, whether it be to maintain a farm with sufficient "seed" material or to maintain natural stock for commercial harvesting (Pringle and Semple 1976, 1978; Pringle et al. 1979). The effects of differential levels and times of harvesting should also be determined in order to maintain maximum productivity of seaweeds (Mumford 1977b; Waaland 1977).

A thorough understanding of the biology and environmental optima of seaweeds is fundamental to successful seaweed mariculture (Woessner 1979). In addition, breeding and selection studies will be required for successful seaweed mariculture programs. Specific examples would be genetic studies to enhance disease resistance or to select specific properties (Suto 1963). Several of the free-living seaweeds (Austin 1960) should be screened in order to enhance "seed stock" selection of vegetative fragments; i.e., many free-living seaweeds, such as *Furcellaria, Gracilaria, Gelidium, Pterocladia, Eucheuma,* and *Hypnea,* can survive and grow without orientation to light and gravity, are capable of rolling, can survive burial in mud and/or sand, and can carry out constant vegetative multiplication without the loss of clonal vigor.

Two major laboratory methods can be used to reduce the time required for selecting high-yielding, rapidly growing seaweeds (Dawes In press): The measurement of basic chemical constituents (ash, lipid, protein, and carbohydrate) and physiological measurements of tolerances for various physical factors (light, temperature, salinity, and nutrients). Chemical analyses will allow comparison of yields and chemistry of populations, chemical changes due to season or stage of the plant, utilization of such chemical changes to predict the stage of the plant, and the management of acclimation during culturing. The use of physiological measurements permits determination of tolerances to the mariculture site and conditions, selection of hardy species, and the determination of acclimation ability of species in culture. All of the procedures will aid in the monitoring of culture populations. Waaland (In press) also suggested that short-term photosynthetic measurements were useful in providing a rapid method for estimating the optimal density (i.e., viability) for semiclosed cultures of free-floating seaweeds.

A major precaution is to avoid careless handling of "foreign" seaweed strains, to prevent possible introduction of exotic species of algae and/or animals (Hanic 1973). The cases of *Sargassum muticum* (Scagel 1956; Farnham et al. 1973; Jones and Farnham 1973) and *Codium fragile* spp. *tomentosoides* (Coffin and Stickney 1966) can be cited as recent introductions. Hanic (1973) emphasized that adequate precautions will be expensive and time consuming, because foreign strains must be quarantined until they are decontaminated. Unialgal cultures might be employed in order to insure that only one species is introduced at a time.

A summary of the systems approach to food production from the sea and seaweed mariculture systems was given by Calhoun (1968) and McIntire (1977), respectively. Basically, both of the studies indicated that one should understand and take advantage of natural opportunities to adjust to nature and increase productivity. Calhoun cited nutrients as a means of increasing yields. The enhancement of seaweed growth by supplying nutrient-rich deep water is another example of a possible application in seaweed mariculture (Roels et al. 1971).

In the continental United States, legal and sociological considerations would appear to be the major hindrances of active mariculture (Anonymous 1978a), including seaweeds. The concept of multiple use and public ownership must be thoroughly integrated into any successful program of seaweed mariculture. Kane (1970) summarized a detailed review of ocean law and its applicability to aquaculture. Claims and decisions involving riparian landowners, navigation, fishing, recreation, and water quality were discussed.

Two recent articles on seaweed mariculture in the northwest Pacific (Suto 1974; Saito 1976) should be noted as they contain a variety of pertinent information. Saito (1976) noted that enhanced mariculture of seaweeds would require increased harvests per unit area, improved quality of harvests, reduced production costs, better propagation methods, and the prevention of grazers. According to Suto (1974), attempts to increase natural crops (in Japan) by setting stones or concrete blocks on sandy bottoms have been very successful. In Japan the expenditures for setting stones are recovered within 3-4 yr for *Porphyra* (nori), 4-5 yr for *Gelidium,* and 5-8 yr with *Laminaria,* but the recovery cost for *Iridaea* or *Chondrus* in the United States would be 20 yr. Suto further suggested that several U.S. seaweeds could be cultivated on surface nets, ropes, or rafts, whenever the water conditions were appropriate. Unfortunately, the net cultivation of *Gelidium, Gracilaria, Iridaea,* and *Chondrus* has not yet developed in the United States, because it is uneconomical, i.e., their cultivation requires too much labor. An epochal improvement in techniques will be required to make their cultivation practical. The net cultivation studies of *Iridaea cordata* by Mumford (1977a, b) should be noted, as he is attempting to obtain the data necessary for an economic analysis.

A variety of factors are important in determining the enhanced utilization and development of marine plant resources (Scagel 1961): 1) Accurate estimates of quantities of economically important species; 2) determinations of the distribution of underutilized species; 3) investigations of appropriate methods for harvesting; 4) growth studies of commercially important seaweeds; 5) observations of seasonal variations in stocks and the recovery of beds after harvesting by different methods; 6) evaluations of chemical composition of seaweeds at different seasons, habitats, depths, ages, and environmental conditions; 7) correlating management measures with life history details; and 8) introducing an educational program to acquaint the public with these resources and their wide range of uses.

The status and potentials of marine agronomy have been reviewed by Doty (1979a, b, c, In press a, b); much of this information is relevant to the present account on seaweed mariculture. He emphasized that marine agronomy programs should be seriously considered by any nation bordering the sea in view of man's needs and the fact that the territorial waters are as productive or more so than the adjacent land. Accordingly, a resource utilization plan must be initiated in order that the long-range gains will offset the losses. He recommended a broad range of understanding of seaweeds, including an identification of habitats available for their growth and information on their natural products. Such a broad base of information will provide a vehicle for resource optimization based upon scientific algal agronomics.

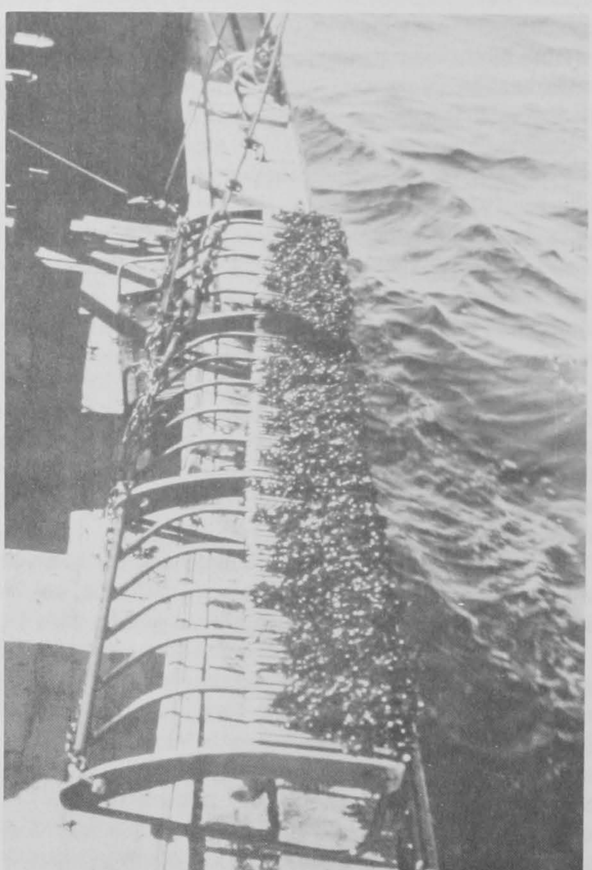
The need for a national mariculture research and development program in the United States has been outlined by Hanson (1974a, b), including four major areas of research and development: 1) Environmental conservation and predictive modeling; 2) biological research on the selection of organisms, hatchery requirements, primary productivity, nutrition, husbandry and disease, competition, and predation; 3) technological research and development dealing with containment and attraction, concentration and harvesting, feeding technology, and artifical upwelling; and 4) socioeconomic research dealing with legal and political questions. Suggestions concerning the appropriate roles of government, industry, and the academic community with respect to this proposed national program (United States) were also discussed (Hanson 1974a, b; Anonymous 1978a).

MARICULTURE AND ECOLOGY OF SEVERAL SEAWEEDS

This section summarizes current mariculture activities with 12 economically important seaweeds, including 10 red algae (*Chondrus crispus, Eucheuma, Gracilaria, Hypnea, Iridaea, Gigartina, Gelidium, Pterocladia, Palmaria palmata,* and *Porphyra*) and 2 brown algae (*Laminaria* and *Macrocystis*). A detailed compilation of information on their cultivation, as well as biology, ecology, and resource management, is given for these economically important seaweeds in North America, the United States' possessions, the Trust Territories of the Pacific Islands, and the Philippines.

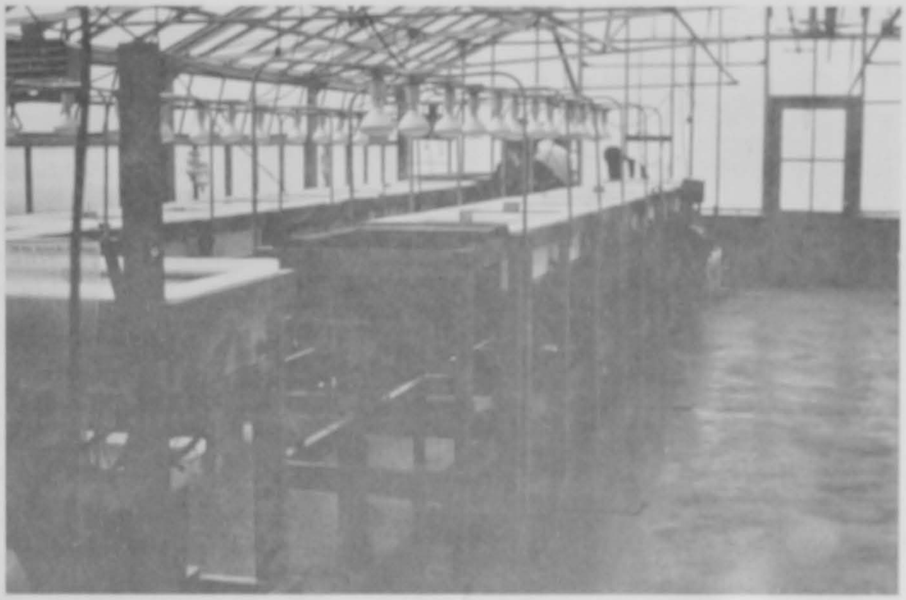
Chondrus crispus (Irish Moss)

Both the biology and ecology of Irish moss must be understood if it is to be maintained as a natural resource (Taylor 1972a). Such information is equally fundamental for the successful mariculture of *C. crispus.* A synthesis of information regarding Irish moss was recently summarized in a symposium dealing with *C. crispus* (Harvey and McLachlan 1973). Subsequently a variety of investigators in the United States and Canada have further expanded our knowledge of the growth (Taylor 1972a, b; Prince and Kingsbury 1973a, b, c; Taylor et al. 1974, 1975; Mathieson and Burns 1975; Hanic 1977; Chen and Taylor 1980a, b), reproduction (Prince and Kingsbury 1973a, b; Cheney and Mathieson 1978b; Craigie and Pringle 1978; Mathieson In press; Tveter-Gallagher et al. 1980), harvesting effects (Patell 1972; Taylor 1972a, b; Scaratt 1973; Taylor et al. 1974, 1975; Mathieson and Burns 1975; Pringle and Semple 1976, 1978; Cheney and Mathieson 1978b; Pringle 1979; Pringle et al. 1979; Pringle and Jones 1980), ecology (Burns and Mathieson 1972a; Kent and Buggeln 1972; Prince and Kingsbury 1973a, b, c; Mathieson and Burns 1975; Taylor 1975b, c; Craigie and Pringle 1978; Lubchenco and Menge 1978; Pringle and Jones 1980), life history-sporeling development (Burns and Mathieson 1972a; Chen and McLachlan 1972; Ring and Vadas 1972; Tveter and Mathieson 1974, 1976a, b; Chen and Taylor 1976; Tveter-Gallagher and Mathieson 1980), outplanting techniques (Hanic and Pringle 1978a, b), resource management (McDougall 1972, 1974; Pringle 1976, 1979; Pringle and Sharp 1980), carrageenan

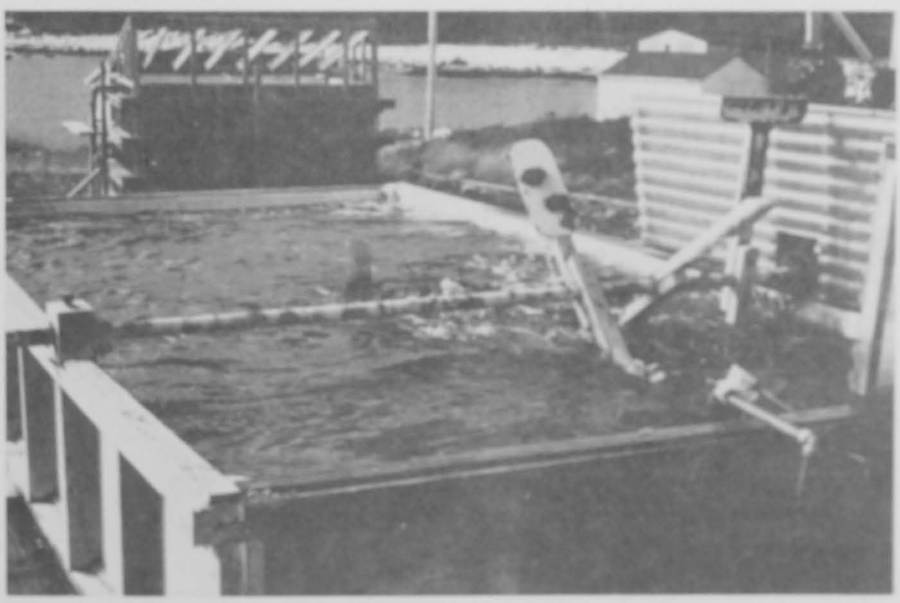


A drag rack used for dredging Irish moss in the Canadian Maritimes. Photograph by J. Pringle.

ecology (Fuller and Mathieson 1972; Lutwick 1973; Mathieson and Tveter 1974, 1975; McCandless and Craigie 1974; Craigie and Pringle 1978; Cheney and Mathieson 1979), physiology (Prince and Kingsbury 1973a; Brinkhuis and Jones 1974; Mathieson and Norall 1975; Rhee and Briggs 1977; Asare 1979b; Bird et al. 1979; Jackson and McCandless 1979; Simpson and Shacklock 1979), biochemistry (McCandless et al. 1973; Gordon-Mills and McCandless 1974, 1975, 1977; McCandless 1974; Hosford and McCandless 1975; Laycock and Craigie 1977; McCandless et al. 1977; Craigie and Pringle 1978; Gordon-Mills et al. 1978), population genetics (Cheney and Mathieson 1977, 1978a; Guiry In press), and economic importance (Ffrench 1971) of Irish moss. Much of the above information is fundamental for the future management, conservation, and husbandry of *C. crispus*, as well as a stimulus for future work.

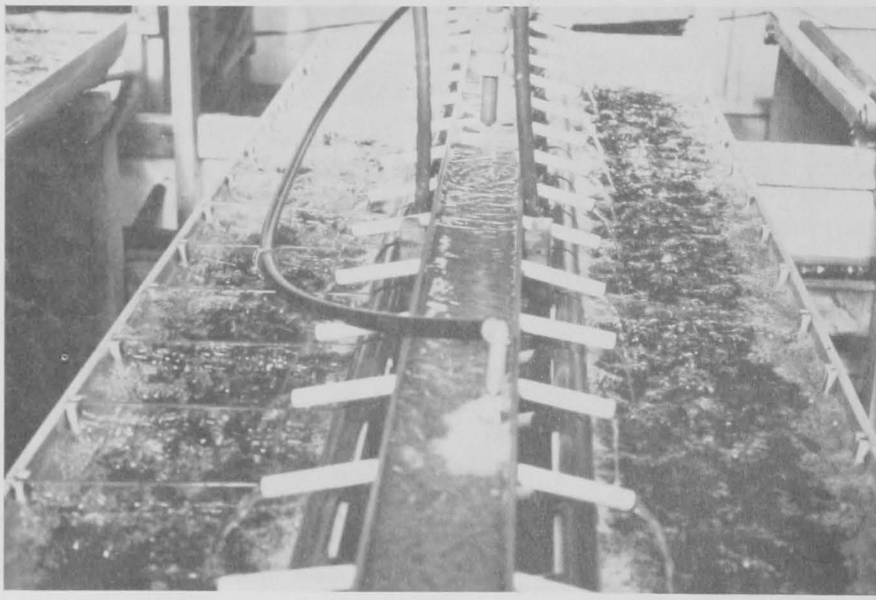


Interior of greenhouse at the National Research Council of Canada's culture facility at Fink Cove, Nova Scotia, Canada, showing tanks and lights. Photograph by A. Mathieson.



Exterior culture tank at the National Research Council of Canada's Fink Cove, Nova Scotia, research facility, showing the exterior ponds and paddlewheels for aeration. Photograph by D. Cheney.

Recent studies by A. Neish and associates at the National Research Council of Canada in Halifax demonstrated the potentials of Irish moss cultivation in greenhouse tanks flushed with seawater (Neish 1968; Neish and Fox 1971; Neish and Shacklock 1971; Anonymous 1977b; Brochu 1977; Neish et al. 1977; Simpson et al. 1978; Simpson and Shacklock 1979; Simpson et al. 1979). For example, Neish and Fox (1971) showed that detached macroscopic *C. crispus* plants grew in a greenhouse with flowing seawater and a temperature range of 5°-15 °C, with growth being most rapid at the warmest temperatures. The effects of aeration, addition of nutrients, and variation o photoperiod and light intensity were also evaluated. I evaluating the application of their work to commercial cultiva tion of Irish moss, Neish and Fox stated that it would not b profitable as a greenhouse crop, nor in a system employing sup plemental artificial illumination. However, cultures in outsid impoundments might be profitable from May to September a their latitudes. Adequate nutrients (particularly nitroge sources), controlled access to seawater, temperature >10 °C, an the availability of superior strains would be essential.



Individual tanks employed for "seed-stock" selection of fast-growing strains of Irish moss at the greenhouse cultivation facility of the Marine Colloid, Inc., Metagan, Nova Scotia, Canada. Photograph by D. Cheney.

Several plants of the T4 cultured strain of *Chondrus crispus* (Irish moss) growing in tanks at the Jackson Estuarine Laboratory, New Hampshire. Photograph by D. Cheney.

The growth of a rapid-growing clone (T4) of *Chondrus* was studied at the National Research Council (Neish and Shacklock 1971). Irish moss is capable of unlimited growth if kept under favorable conditions, and clone T4 showed a 25,000-fold increase in weight during the investigation. Regeneration of a holdfast was never observed. Increases in weight as high as sixfold per month were obtained at low population densities, the greatest production per unit area (0.9 lb/ft^2 per mo or 1.7-fold/mo) was obtained with a population density of 1.2 lb/ft^2. In these dense populations, the plants grew well, fragmented spontaneously, and remained relatively free of epiphytes. Growth resulted in an increase in the number of plants, rather than the production of large plants. If phosphates were deleted from the cultures, excessive fragmentation and epiphytization occurred. Phosphate appeared to be the main nutrient deficiency for the growth of *Chondrus*. The exact level of fixed nitrogen required for maximum growth was not established.

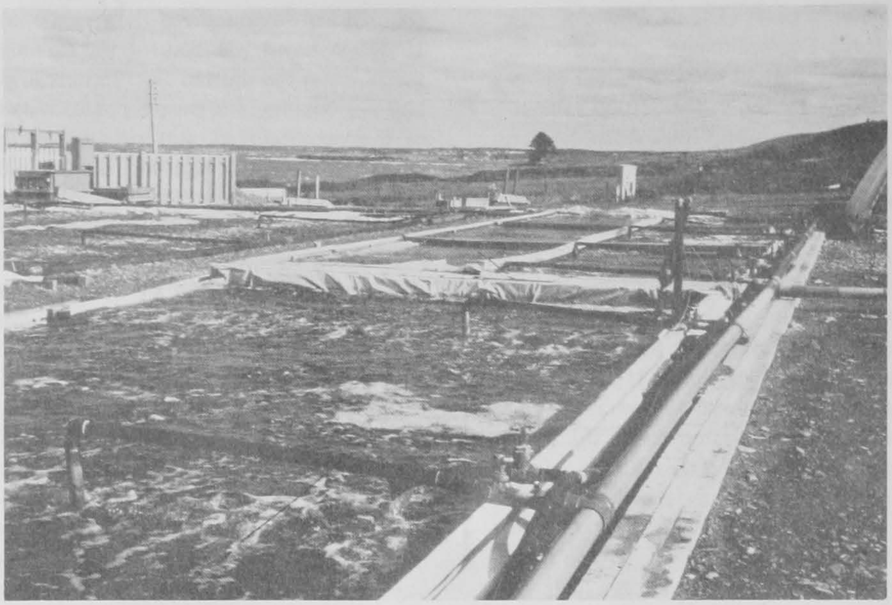
Further experiments on vegetative propagation of Irish moss strain T4 have been conducted (Shacklock, Robson, Forsyth, and Neish 1973; Shacklock, Robson, and Simpson 1973; Neish et al. 1977). Of particular interest was the finding that the chemical composition of cultured plants could be altered by changes in culture conditions. Thus, plants growing rapidly in nitrogen-enriched seawater have a low content of total solids and carrageenan, and a high content of nitrogenous materials. When nitrogen-enriched plants are transferred to unenriched seawater, there is a rapid increase in percent carrageenan and total solids and a decrease in nitrogen compounds, an effect which has recently been termed the "Neish Effect" (Neish et al. 1977). A "ripening" or "fattening" period with no nutrients should be incorporated in any aquaculture program with *C. crispus*. Wild plants growing in situ also appear to go through these same changes during the summer when nitrogen is low (Fuller and Mathieson 1972; Mathieson and Tveter 1975).

The effects of pH on growth and production of carrageenan from cultivated Irish moss populations (i.e., the T4 clone of *C. crispus*) were summarized (Simpson et al. 1978; Simpson et al. 1979). Without pH control (in flowing seawater tanks in a greenhouse) the diurnal fluctuations in pH ranged between 7.9 and 9.6. Maintaining the pH constant by the controlled addition of hydrochloric acid, sulfuric acid, or carbon dioxide resulted in improved yields. Carbon dioxide was superior to the inorganic acids or daily additions of sodium bicarbonate. Maximal yields were obtained at pH 7.0-8.0, depending upon the controlling agent. The effects of temperature on growth and carrageenan production of the T4 clone of *C. crispus* were similarly evaluated (Simpson and Shacklock 1979). High temperatures (15°-20°C) favored the accumulation of kappa carrageenan, whereas plants grown at 3° and 6°C had a higher nitrogen content.

As noted previously (Neish and Shacklock 1971) epiphytes may be a major problem during the mass cultivation of *C. crispus*. The biological control of one common epiphyte, *Ulva lactuca*, of *Chondrus* strain T4 was attempted with a series of factorially designed light intensity and temperature combinations (Enright and Chapman 1977; Enright 1979). Under some aquaculture conditions there was a lack of competitive interactions between the two species. Thus, the growth of *U. lactuca* was significantly reduced without a substantial decrease in *Chondrus* yield, i.e., by the control of parameters such as light. Harlin (1978) has further suggested that the varying nutrient efficiencies of ulvoid algae (e.g., *Enteromorpha* spp.) and *C. crispus* should be considered when designing feeding strategies for Irish moss aquaculture systems (see Polyculture section for further information on differential uptake strategies).

Marine Colloids, Inc. initiated a pilot cultivation program with Irish moss, in an ecologically balanced seawater installation in Nova Scotia (Anonymous 1977b). They hope to eventually have as many as 100 acres under cultivation within the next few years. The algal production is being done under a patent to the National Research Council of Canada, Atlantic Regional Laboratory (Chen et al. 1975). The cultivation program is being conducted in large ponds, which are lined with heavy gage

Greenhouse cultivation facility for the Irish moss cultivation program of the Marine Colloid, Inc., Metagan, Nova Scotia, Canada, showing tanks and plastic greenhouse. Photograph by A. Mathieson.



Seaweed culture ponds for the Irish moss cultivation program of the Marine Colloid, Inc., Metagan, Nova Scotia, Canada. Photograph by D. Cheney.

plastic. The seawater is fed at controlled rates with agitation provided by blowing air through the tanks. In the future, warm water from a nearby fossil fuel electric plant may be used in the tanks to grow seaweeds at optimum temperatures year-round.

Other pilot cultivation projects with Irish moss were recently underway in New York and Nova Scotia (Genu Products Canada, Ltd.) A preliminary account of an experimental farming program at Montauk, N.Y., which involved a landbased network of 15 reinforced-concrete tanks placed at descending heights, was given by Moeller et al. (1973). This employed a greenhouse to heat the networks by solar energy and boost year-round production. Detached populations of Irish moss were grown in the tanks to assay their yields of carrageenan, growth rates, viability, and cleanliness. The cultivation facility of Genu Products Canada, Ltd., in Nova Scotia used many of the biological and physical parameters developed by the National Research Council at Sandy Cove (Neish and Fox 1971; Neish and Shacklock 1971; Neish et al. 1977), but little specific information was available.

Several Canadian scientists recently showed that kappa carrageenan was restricted to the gametophytic plants of Irish moss, while lambda carrageenan was present in the sporophytic plants (Chen et al. 1973; McCandless et al. 1973; McCandless 1974). Similar results were reported from natural populations by comparing the differential gelling potentials and the presence or absence of 3,6-anhydrogalactose, respectively in the gametophytes and sporophytes of *C. crispus* (Mathieson and Tveter 1975; Craigie and Pringle 1978). As suggested by Shacklock and associates (Shacklock, Robson, Forsyth, and Neish 1973; Shacklock, Robson, and Simpson 1973) seed stock selection of differential phases would provide a uniform and consistent supply of the different carrageenan fractions.

A Sea Grant project by D. Cheney and A. Mathieson at the University of New Hampshire has attempted to apply genetic studies to enhance cultivation of *C. crispus* through seed stock selection and improvements in the plant. Specifically, the project has attempted to produce strains of *Chondrus* with high carrageenan yields and/or growth rates, as well as to select features potentially advantageous to cultivation, such as the ability to reproduce vegetatively by cloning. *Chondrus* populations from a variety of habitats (intertidal, subtidal, open coastal, and estuarine) and geographical locations have been compared for genetic variability and differentiation, using starch-gel electrophoretic techniques (Cheney and Babbel 1975, 1978; Cheney and Mathieson 1977, 1978a). Such information is being used to select diverse parental stocks for hybridization and the production of progeny which hopefully may show hybrid vigor. Electrophoretic screening (Adams and Allard 1977) is also being used to recognize polyploid plants that may exist in nature.

Attempts to induce polyploidy in *C. crispus* are also being carried out by Cheney and Mathieson using colchicine, which inhibits the production of the spindle apparatus during cell division, causing a doubling of chromosome numbers. It is hoped that a 2n gametophyte can be produced, which in turn will be crossed with a normal (1n) gametophyte, producing a 3n plant. The primary benefits of triploid plants are that they tend to grow larger and faster than 1n or 2n plants and that they are sterile. The ability to induce sterility in a plant will be a great benefit to seaweed mariculture, since the plant would reproduce vegetatively and could be cloned indefinitely. In addition to the value of the improved strains for cultivation, the basic knowledge and other developments in this study should be applicable to other economic seaweeds; e.g., the use of polyploidy to produce sterile clones of annual seaweeds, where maintaining viable seed stock throughout the year is a major problem.

One final development of *Chondrus* cultivation is the recently perfected isolation and axenic culture techniques by Chen and Taylor (1978) for medullary tissue explants from female gametophytic plants of Irish moss; Chen and Taylor were able to culture the colorless medullary filaments of *C. crispus*, producing fronds with the normal morphology of the parent plant. This is the first published report of successful preparation of axenic tissue culture of a multicellular alga. Such cultures could provide a dependable source of standardized material for a variety of biochemical, physiological, and genetic studies, which may have major relevance to the enhanced cultivation of *C. crispus*.

Eucheuma

The tropical red alga *Eucheuma* is a major source of carrageenan that has been harvested for years in the Indo-Pacific, the "cottonii" types producing iota carrageenan and the "spinosum" types kappa carrageenan (Doty 1970, 1973a, b). Because of overharvesting and variability of wild-crop procurement during the late 1960's, extensive *Eucheuma* programs were developed in the Philippines and Micronesia (Trono 1974) and research studies on the husbandry of Caribbean *Eucheuma* were initiated (Deveau and Castle 1976). It was mainly through the initial efforts of the Marine Colloids, Inc., the biggest importer of these seaweeds, and its general manager Vincente Alvarez, and M. S. Doty of the University of Hawaii that extensive seaweed (*Eucheuma*) farming was initiated. Trono (1974) summarized an interesting and detailed history of seaweed farming in the Philippines including the evolution of family farming methods and training courses, the estimation of operating costs of a 1-ha farm, the ecological characteristics of a good seaweed farming site, and many other details on the mechanics of farming.

Several other accounts of *Eucheuma* farming in the Philippines and Micronesia have also appeared (Doty 1973a, b, 1977, 1979c; Doty and Alvarez 1973, 1974, 1975; Braud et al. 1974; Parker 1974, 1976, 1977; Deveau and Castle 1976; Braud and Perez 1979; Ricohermoso and Deveau 1979, footnote 4). A case history of *E. cottonii* farming in the Philippines was given by Deveau and Castle (1976). They emphasized that the plant's ability to be cloned and grown vegetatively has made its large-scale farming possible in the southern Philippines, where it is currently produced in large quantities, particularly by family farms. For example, 0.5-ha family farms can produce approximately 22,500 kg wet weight in 90 d, from which a dry saleable weight of 2,250 kg is recovered. The annual farm production for the Philippines is approximately 287,000 kg dry weight, with an annual growth of 10%. Two systems of farming have been developed: 1) Net farming with 2.5 × 5.0 m nets, having 127 intersections, each with a 100 g piece of *Eucheuma*; and 2) monoline farming, in which the density of plants per square meter is lower than in net farming. A farm site for *E. cottonii* must be a protected coral reef, having good water flow and an annual temperature range between 26° and 32°C. White sandy bottoms and areas with herbivores should be avoided. Early technological, political, and economic difficulties in establishing seaweed farms have largely been overcome. However, Deveau and Castle emphasized that more research was required on faster growing strains with higher carrageenan yields and disease resistance.

The development of *E. spinosum* and *E. cottonii* cultivation in the Indo-Pacific was reviewed by Ricohermoso and Deveau (1979, see footnote 4), who pointed out that the system used today, although relatively simple, took over 5 yr to develop. Currently, 99% of the farmers employ a monoline system, which has been modified from the common Japanese *Porphyra* culture techniques ("hibi"). Monoline farming consists of monofilament lines (150-180 lb test) with 50 propagules attached to each line. At present, approximately 400 spinosum and 600 cottonii farms are operational in the Philippines, producing more than 24,600 kg dry wt/mo. Among developing company farms (e.g., Marine Colloids, Inc.), research is being conducted on the selection of high-yielding and fast-growing strains, as well as in the application of fertilizers to offset seasonality problems, the improvement of production techniques, the control of pests and diseases, and the reduction of labor requirements.

The development of net farming techniques in the Philippines and Micronesia was summarized by Doty (1973a, b) and Parker

[4]Ricohermoso, M. A., and L. E. Deveau. 1977. Commercial propagation of *Eucheuma* spp. clones in the south China sea. A discussion of trends in cultivation technology and commercial production pattern, 4 p. Privately mimeographed by the authors for IX Int. Seaweed Symp., Univ. California, Santa Barbara, 20-27 Aug. 1977.

A habit illustration of *Eucheuma isiforme* from the Florida Keys. Photograph by D. Cheney.

(1974). Successful farming techniques evolved after a variety of different propagation methods, growth studies, and biochemical and environmental investigations (Kraft 1970; Doty and Santos 1978). For example, constant-level planting techniques were developed because of extensive grazing by fish and sea urchins (Doty 1973a, b; Parker 1974). Basically, about 10 kg of *Eucheuma* are planted on a single net, with the nets being arranged in four modules with 800 nets each. The cost of installing and operating a 1-ha farm in the northern Sulu Sea area of the Philippines is about US$3,126.00/yr, based on a 3-yr amortization. It is estimated that about 10 tons of dry weed per hectare are produced, leaving 50-100 g of live weight of each thallus for seed. Large-scale *Eucheuma* farms seem to have the potential of competing advantageously with other crops, including sugar and coconuts (Doty 1973a, b).

There are four major problems associated with the increased production (agronomy) of *Eucheuma* (Doty 1977): 1) The danger of production monopolies in a developing country, which may change its politics, policies, and regulations; 2) the traditional advantage of merchants over individual farmers; 3) the need to improve farming methods; and 4) governmental bureaucracy and the management of introduced species. With respect to the first problem, Doty suggested that the best solution was to encourage farm development in several countries, including the U.S. Trust Territories of the Pacific Islands. In an economic sense such competition would stabilize the price of raw seaweed materials and improve the reliability of the supply. The unreliability of the price of *Eucheuma* has discouraged many farmers who cannot entrust their family's livelihood to a wildly fluctuating market.

A major theme of the University of Hawaii's marine agronomy program has been to enhance cooperation between farmers, as well as to initiate better management, which would increase and stabilize seaweed prices (Doty 1977). Different methods of planting (lawn, hollow, and pen), as well as the selection of fast-growing plants such as the very successful Tambalang strain, were conducted (Doty and Alvarez 1975). The introduction of strains may also be advantageous to a mariculture program. For example, Doty (1977) suggested that such introductions could aid in the stabilizing of supplies, the shortening of transport distances between farm and factory, and the possible purification of wastewater discharges into the sea. Even so, efforts to introduce new seaweeds in Hawaii currently have involved 11 Federal, State, and local agencies, and similar efforts in Guam required clearance from at least 7 Federal agencies. Doty emphasized that new crop species should only be introduced after careful consideration of possible damaging effects, but that they should not be strangled by bureaucratic complexities. he cited examples of the recent proposal for *Macrocystis* introduction to Hawaii, as well as experiments with the introduction of the Tambalang strain of *Eucheuma*.

A considerable amount of information is available on *Eucheuma* spp. found in Florida, including investigations of their biology (Cheney and Dawes 1973, 1974a, b; Cheney 1975; Cheney and Mathieson 1978b), ecology (Dawes, Mathieson, and Cheney 1974), physiology (Mathieson and Dawes 1972, 1974; Shipman 1974; Dawes 1976, 1979; Dawes et al. 1976; Moon and Dawes 1976a, b; Dawes et al. 1978), and biochemistry (Dawes 1974b, 1977; Dawes, Lawrence, Cheney, and Mathieson 1974; Shipman 1974; Cheney and Babbel 1975, 1978; LaClaire and Dawes 1976). Much of this information is relevant to the plant's mariculture and resource management. For example, the recent electrophoretic studies of *Eucheuma* spp. (Cheney and Dawes 1973, 1974a, b; Cheney and Babbel 1975, 1978; Cheney 1976) have obvious potential applications to both seed stock selection and genetic improvement programs, as noted in the section on *Chondrus crispus*.

A compilation of relevant data regarding the potential mariculture of *E. isiforme* was summarized by Dawes (1974a), who suggested that fragments could be dispersed and grown in either natural embayments, which are common in Florida, or in culture tanks. In a natural habitat a number of factors should be considered to optimize the growth of *E. isiforme* (Dawes, Mathieson, and Cheney 1974), including adequate water movement, water depth (0.5-3.0 m below MLW), firm substrata without sand, and adequate illumination. Plants grown on lines

A concrete block used for outplanting studies of Florida *Eucheuma* by C. J. Dawes and associates in the Florida Keys. Photograph by A. Mathieson.

showed growth rates of 4-6% wet weight increase per day during the spring and summer (Dawes, Mathieson, and Cheney 1974). Since more plants could be handled per unit area in aerated culture tanks, Dawes (1974a) calculated that a total of 24.3 kg dried, washed plants/m^2 per yr could be produced at an approximate value of \$9.72/m^2 per tank. He concluded that tank culture would yield a higher crop per unit area (\$9.72/m^2 per yr) than a 1-ha field culture plot (\$0.16/m^2 per yr). However, the more than sixtyfold increase in gross profit in tank culture must be considered in light of such expenses as tank construction, water movement costs, and temperature. Other information on the possible farming of *E. isiforme* has also been summarized (Anonymous 1974c).

Marine Colloids, Inc., in association with C. J. Dawes of the University of South Florida, attempted to develop domestic *Eucheuma* farming in Florida, based upon *E. isiforme* (Anonymous 1977a; Deveau and Castle 1976). The project was initiated in the Florida Keys during the summer of 1974, using a capital-intensive tank system, similar to that for *C. crispus* in Nova Scotia. The tanks were agitated by air to keep the alga in suspension and to provide adequate sunlight and nutrients. Temperature, light, and fertilization were controlled, with comparisons of growth being made between tank and field-grown plants. Two research programs were emphasized: 1) The location of perennial seed stock that could be maintained during the winter, and 2) the regeneration of seed stock each spring from

Seaweed culture tanks at an experimental site in the Florida Keys, where Marine Colloids, Inc. was cultivating *Eucheuma* and other economic red algae. Photograph by A. Mathieson.

Large earthen ponds used to grow detached populations of economic red algae such as *Eucheuma* at the experimental site of Marine Colloids, Inc. in the Florida Keys. Photograph by A. Mathieson.

winter-germinated spores. Unfortunately the project was discontinued in 1977 because of problems of maintaining seed stock throughout the year.

Gracilaria

Several Canadian scientists from the northeastern Atlantic have recently initiated a variety of biological (Goldstein 1974a; Bird, Edelstein, and McLachlan 1977a; Busby and Goldstein 1977; McLachlan and Edelstein 1977), taxonomic (Chapman et al. 1977; McLachlan 1979), ecological (Bird 1974-76, 1975; Edelstein et al. 1974; Goldstein 1974a, 1977; Taylor 1975a; Bird, Edelstein, and McLachlan 1977b; Busby and Goldstein 1977), genetical (Meer 1977; Meer and Bird 1977; Meer and Todd 1977; McLachlan et al. 1977), chemical (Hong et al. 1968; Duckworth et al. 1971; Young 1973, 1974), and cultural Edelstein et al. 1974; Goldstein 1974b, 1977; Bird 1975; Bird, McLachlan, and Grund 1977; Edelstein 1977; McLachlan and Edelstein 1977; Bird et al. 1979) studies of *G. tikvahiae* from the Canadian Maritime provinces.[5] Overall, their efforts are directed to an increased utilization of Canadian agarophytes, because of the growing commercial needs for agar (Mathieson 1975; Moss 1977). Preliminary summaries of many of these efforts have been presented at the Canadian "Agar and Agarophyte Workshops" (Anonymous 1973b, 1974b, 1975).

The ecology of attached populations of *G. tikvahiae* at Barrachois Harbour, Nova Scotia, was described by Bird (1974-76). The growing season of the plant, which is characterized by water temperatures of about 20 °C, is < 3 m. Accordingly, the plant is restricted to shallow, warm-water embayments (Edelstein et al. 1967; Bird, Edelstein, and McLachlan 1977b). When sporelings of *Gracilaria* were transplanted to the field, they became reproductively mature within 6-10 wk (Bird 1974-76). Tetraspores were released in June and carpospores between July and September. The mode of reproduction of attached and detached populations was different. Attached populations reproduced via spores and exhibited an alternation of generations (Bird 1974-76). In contrast, free-floating populations, which were usually dominated by tetrasporophytes, primarily perennated by regeneration of adventitious branches (Bird, Edelstein, and McLachlan 1977a).

The in vitro life history of *G. tikvahiae* from the Canadian Maritime provinces was recently described (Bird, McLachlan, and Grund 1977). A typical *Polysiphonia*-type life history was observed in culture. The male to female ratio for plants originating from tetraspores was 1:1. In addition to a normal sex ratio, the requirement of males for carposporophyte formation in culture provided presumptive evidence for the necessity of fertilization to complete the life history. In contrast to earlier studies of free-floating populations of *Gracilaria* where a scarcity of reproductive material was noted (Causey et al. 1946; Stokke 1957; Kim 1970; Simonetti et al. 1970), detached plants of *G. tikvahiae* showed an enhanced potential for reproduction if aeration was applied. That is, the reproductive maturation of these detached and aerated plants occurred in 8-10 wk versus 8 mo for nonaerated cultures. The rapid induction of fertility in detached plants was attributed to favorable growth conditions (greater availability of nutrients and dissolved gases) and the detachment process itself. As noted previously, when young sporelings were transplanted to the field, they became reproductively mature within 6-10 wk, which was similar to that of aerated, detached macroscopic plants.

Temperature, rather than light, was the critical factor determining spore germination with *G. tikvahiae,* since it occurred in darkness but not at low temperatures (Bird, McLachlan, and Grund 1977). Carpospores showed a lower percentage of germination than tetraspores, presumably because carpospores were released simultaneously at various stages of maturity. Tetraspores showed a continual release with an apparent high germination percentage, which suggests they provide maximum opportunity for spore germination. The process of fertilization is not required for the production of tetraspores, which may be of considerable ecological importance.

A variety of field and laboratory studies on *G. tikvahiae* from Prince Edward Island, Canada, have been summarized (Goldstein 1974a). Three actively growing forms were observed in estuaries and embayments on the Island: 1) Plants securely attached by a true holdfast to benthic bivalve molluscs; 2) detached, free-floating fronds; 3) large, bushy plants anchored in benthic areas by byssus fibers produced by *Mytilus* (see also Goldsten 1974b). The latter form was very abundant in the late summer and was found producing tetraspores and, to a lesser degree, carpospores. Both spore types were readily isolated in culture and sporeling development was studied. Goldstein (1977) also described the artificial recruitment and cultivation of *G. tikvahiae* in Prince Edward Island. The tetraspores of the plants were seeded on scallop shells in the laboratory, and after 1-2 wk of incubation, 50,000 sporelings were outplanted at two sites in Cascumper Bay. The outplants were monitored for 13 mo. The greatest decline in sporelings, especially those incubated for only 1 wk, occurred during the first month after outplanting, due to burial by sedimentation, grazing by herbivorous snails, epiphytism, and competition for substrata with other animals and algae. Active growth ceased when the water temperature fell below 15 °C and the plants entered a quiescent phase which was characterized by dark pigmentation, brittle texture, and frond erosion. The plants remained quiescent from late September to mid-June, after which time active growth resumed. Most of the plants were sexually reproductive in August.

The recruitment of *G. tikvahiae* sporelings on ceramic tiles (11 × 11 cm), which were submerged weekly during the summers of 1975 and 1976, was evaluated by Busby and Goldstein (1977). After 1 wk in the field, as well as 2 wk under laboratory conditions, *G. tikvahiae* sporelings were counted on the tiles. High sporeling density was observed in late July, concomitant with an abundance of in situ tetrasporic plants. A significantly lower number of sporelings was noted during 1976 than 1975, coincident with lower light intensities and water temperatures. A well-defined "edge effect" was observed on the tiles. Overall the tiles appeared to have a substantial potential for augmenting recruitment of *G. tikvahiae.*

The growth of *G. tikvahiae* under greenhouse conditions (Neish and Fox 1971) has been determined (Edelstein et al. 1976). As would be expected from its natural distribution (Bird, Edelstein, and McLachlan 1977a, b), the plant's growth in tanks was dependent upon warm-water temperatures (i.e., 15 °-28 °C). Equally important was a proper combination of light and temperature. The highest yield was an increase of 423%/mo or 14.1%/d at 20 °C and 12-12 LD (light-dark) period. Gametophytes showed optimal growth with 18 h of artificial il-

[5]The species designated as *Gracilaria tikvahiae* from the northeastern coast of the north Atlantic has previously been designated as *Gracilaria* species or incorrectly referred to as *G. foliifera* (see McLachlan 1979).

lumination at 9,776 lux and with a temperature range of 20°-22°C. In contrast under natural light, maximum growth occurred at 25°-28°C, with decreasing productivity at higher temperatures. Continuous light was unfavorable for *G. tikvahiae*. The plant's maximum growth occurred in undiluted seawater, with a marked deterioration at salinities <10‰. The plants grew much better in tanks flushed with fresh than in recycled seawater, probably because of a greater availability of nutrients. Preliminary nutrient results suggested that *G. tikvahiae* was very sensitive to low concentrations of nitrogen and that it showed early signs of nitrogen deficiency. One of the most serious problems was the growth of epiphytes, particularly at high-nutrient and full-salinity conditions. The type of material used for the source of seed and inoculum was of major importance, because the quality of field material was both temporally and spatially variable (Bird, Edelstein, and McLachlan 1977b). Edelstein et al. (1976) concluded that it would be possible, by a combination of laboratory and greenhouse tank cultures, to obtain sufficient inoculum for commercial purposes within 6 mo. Most of the problems of large-scale *Gracilaria* mariculture would appear to be technical, although there may be economic constraints.

The importance of selecting fast-growing strains for inocula in commercial cultivation of *G. tikvahiae* has been described by Edelstein (1977). She isolated rapidly growing strains and evaluated their state of fertility and morphological variation under greenhouse conditions. She observed conspicuous differences in the rate of growth of field-collected plants from various sites. Tetrasporic fronds increased more rapidly in weight than gametophytic fronds. Male plants from laboratory cultures showed somewhat better growth than female plants. The size of the fronds used as inocula had little effect on the increments of growth; subapical portions quickly regenerated their tips after which growth was comparable to that of apical segments.

The morphological and anatomical variations of *G. tikvahiae* (as *Gracilaria* species) from six populations in the Lower Gulf of St. Lawrence and New England were reported by Chapman et al. (1977). Seven vegetative criteria of taxonomic importance to the genus were investigated, i.e., basal branch constriction, branch attenuation, degree of flattening, angle of branching, medullary cell diameter, subcortical cell diameter, and cortical cell diameter. There was significant interpopulation variation, but the samples overlapped. The absence of discontinuities in characters examined led Chapman et al. to conclude that in eastern North America there was only one highly variable species of *Gracilaria*.

Several recent genetic studies of *G. tikvahiae* have been conducted, which may have considerable relevance to its successful cultivation. For example, McLachlan et al. (1977) attempted hybridizations between *G. foliifera* from southern England and *G. tikvahiae* from the lower Gulf of St. Lawrence, Canada, but they were unsuccessful. The chromosome number of both plants is $n = 24$, with two chromosomes being noticeably larger in both forms. Although the hybridization attempts were unsuccessful, cystocarplike swellings occurred on female gametophytes in the presence of the opposite male entity. Syngamy probably occurred in both cases, since cystocarplike swellings did not form either in the presence of heat-killed spermatia or filtrates from suspensions of viable spermatia. Accordingly, they concluded that *G. tikvahiae* from the Canadian maritimes and *G. foliifera* were separate entities.

The inheritance of two spontaneous green variants of *G. tikvahiae* were summarized (Meer and Bird 1977). Both variants were transmitted as single recessive mutants. Complementation and recombination tests indicated that the mutants were defective in different unlinked loci. Crude pigment extracts revealed substantially less phycoerythrin in the green variants. Further studies of mitotic recombination, and their relationship to mixed phases in the life history of *G. tikvahiae*, were reported by Meer and Todd (1977). Diploid tetrasporophytes of the plant grown in culture produced functional male and female gametangia in addition to tetraspores. Sporelings resulting from fertilizations involving these gametangia were polyploid, their chromosome numbers indicating that gametes from the tetrasporophyte were diploid. The tetrasporophytes were heterozygous in twin spots of recombinant tissue at the same time that gametangia were formed. All the observations were consistent with the interpretation that both gametangia and recombinant twin spots arose as a consequence of mitotic recombination.

The genetic implications of cytokinetic failure during tetraspore formation in *G. tikvahiae* have been described (Meer 1977). Tetrasporangia can produce tetraspores of different sizes. The larger spores arise from a failure of cytokinesis in tetrasporangia after meiosis and consequently have two or more nuclei. By using nuclear marker genes, Meer was able to demonstrate that the largest spores usually contained all four meiotic products and hence could be used for tetrad analysis under appropriate conditions. Sexual mosaics with both male and female fronds developing from a single basal disc were commonly observed. He speculated that the formation of sexual mosaics increased the probability that at least a fraction of the females would be fertilized, even when the gametophyte population was very sparse. In addition, the larger spores may be better able to survive under some environmental conditions. However, it is possible that there may be no selective advantage at all, large spores existing simply because there is no selective pressure against them. To date there is no documentation as to how widespread the large spores are in nature. Perhaps the frequency of large spore production is dependent both on environmental conditions and on the genotypes of the plant.

Three additional genetic studies of *G. tikvahiae* should be noted. Foremost, the non-Mendelian gene transmission of three color mutations (pink, yellow, and green) was reported (Meer 1978). Tetrasporophytes obtained from reciprocal crosses between wild types and three color mutants had the phenotype of the maternal parent. Parental transmission of the wild or mutant phenotype was not observed among several thousand progeny. He concluded that *G. tikvahiae* had cytoplasmic as well as nuclear genes that affect the plastid phenotype, and that the former were transmitted maternally. Secondly, the isolation and characterization of mutant strains of *G. tikvahiae* have also been evaluated (Meer 1979a). Some mutants with morphological or pigmentation changes were obtained spontaneously, but hundreds more were isolated after mutagenesis with ethylmethanesulphonate. Many variants were crossed reciprocally with type and showed Mendelian single-gene transmission patterns. Most variants were recessive, but incomplete and complete dominance were also encountered. Lastly, the complementation and linkage analysis of pigmentation mutants in *G. tikvahiae* were determined and the beginning of a linkage map was outlined (Meer 1979b).

Various approaches to culturing *G. tikvahiae* in tanks are being evaluated (Brochu 1977), including using plants with three sets of chromosomes or triploids. Triploid plants seem to be larger and grow faster than the normal (1n or 2n) ones. Their use, along with other refinements in culture conditions, might make possible the commercial culture of *G. tikvahiae* in tanks or salt ponds.

Several other studies dealing with *G. tikvahiae* from the Atlantic coast of the United States have recently been conducted. Fralick (1974) summarized the growth of *G. tikvahiae* (as *G. foliifera* in Taylor 1957) as well as *Chondrus crispus* and *Neoagardhiella baileyi*, in a nutrient-enriched, multipurpose aquaculture system at the Woods Hole Oceanographic Institute's Environmental System Laboratory. Specific details regarding the Environmental System Laboratory are given in the section dealing with Polyculture systems. Growth rates as high as 40%/d were recorded, as well as the successful removal of nutrients from the system. Further descriptions of the growth of *G. tikvahiae* in the Environmental System Laboratory were given by Fralick et al. (1975), DeBoer (1979), and LaPointe and Ryther (1979). In addition, the net photosynthetic responses of the plant under a variety of different light, temperature, and salinity conditions were described by Fralick and DeBoer (1977). The optimal conditions for growth are 800-2,500 fc (footcandle), salinities of $<32‰$ and temperatures of 20°-30°C. The experimental results were interpreted in relation to seasonal variations in growth.

The seasonal changes in chemical constituents and reproductive generations for *G. tikvahiae* populations (designated as *G. foliifera*) from Great Bay, N.H., were enumerated by Penniman (1977). There were slight differences in agar yields between vegetative, cystocarpic, and tetrasporic samples. Agar yields were at a maximum from November to January, while protein and phosphate contents showed no consistent differences with season nor reproductive status. The maximum occurrence of cystocarpic and tetrasporic plants was in June and July, with cystocarpic plants showing their maximum somewhat earlier than tetrasporic plants. The innermost estuarine sites exhibited earlier reproductive maxima. Low percentages of cystocarpic plants were consistently found at all three sites. Tetrasporic plants were absent in the innermost estuarine sites during the winter.

An additional study of biochemical properties of *G. tikvahiae* was recently conducted in Rhode Island by Asare (1979a) in order to optimize its harvesting and agar yields; he found that tissue nitrogen was highest during the winter. In addition, he emphasized that factors apart from nitrogen status were involved in the increasing and decreasing of phycocolloid content in these plants.

The agar variations of *G. bursapastoris* and *G. coronopifolia* from Hawaii have been reported by Hoyle (1978a, b). Crude agar extracts from tetrasporic, male and female plants showed no significant differences in yield nor gel strengths (Hoyle 1978a), similar to that observed for *G. tikvahiae* (Penniman 1977). The thallus nitrogen content of both Hawaiian species of *Gracilaria* was correlated with NO_3-N in the seawater (Hoyle 1978b). In addition, the agar yields of both plants were inversely related to the total nitrogen of the thalli. The reproductive phenology and growth rates of *G. bursapastoris* and *G. coronopifolia* from Hawaii were also reported by Hoyle (1978c).

The summer growth potential of *G. foliifera* populations at Alligator Harbor on the Florida Gulf coast and at Beaufort, N.C., were determined by Kim and Humm (1965). Portions of plants weighing about 5 g each were fastened to vertical lines. The plants were attached at seven depths, which were constant at all stages of the tide. Initially the plants showed a lag in growth for 1-4 d, presumably because of a change in light intensity after having been transplanted. The growth rate of the experimental plants was correlated with light intensity, with the maximum growth occurring nearest the surface (0.3 ft), even though the plants were bleached. A comparison of the growth studies in Florida and North Carolina showed that plants which initially weighed 5 g increased 14-fold in 20 d at Alligator Harbor, Fla., versus 15-fold in Beaufort Harbor, N.C.

The growth rate of *G. foliifera* populations from North Carolina, which were under approximately optimal conditions, was only about one-half to two-thirds that of *G. verrucosa* under the same conditions (Causey et al. 1946; Kim and Humm 1965). Both species appear to be very tolerant of high light intensities, as their maximum growth occurs near the surface of the water; in addition the optimum growth for both is close to the maximum temperatures of inshore waters of the southeastern coast of the United States (28°-32°C). The temperature tolerances of the two species seem to vary, as *G. foliifera* is in good vegetative condition year-round throughout its geographical range, while *G. verrucosa* is absent or dormant during the winter north of Florida (Causey et al. 1946).

The physiological ecology of estuarine populations of *G. verrucosa* from Florida was recently studied (Dawes 1976; Dawes et al. 1978). The plant exhibited an increase in net photosynthesis from 50 fc (1,150 $\mu W/cm^2$) to 2,000 fc (13,800 $\mu W/cm^2$), as well as maximum net photosynthesis at 24°-36°C (30°C optimum) and 10-50‰ (30‰ optimum). Accordingly, *G. verrucosa* shows a broad tolerance to light, temperature, and salinity, characteristic of its estuarine-mangrove habitat. The effects of light quality on ammonium uptake with Floridian populations of *G. verrucosa* have also been described (Bird 1979). In nitrogen-enriched cultures there was an enhanced ammonium uptake under blue light, as compared to green or red light. In contrast, nitrogen-starved cultures of *G. verrucosa* showed no effect of light quality on ammonium uptake.

Additional investigations of *Gracilaria* from the Pacific coast of North America have recently been conducted. For example, Whyte and Englar (1976a) evaluated the growth and chemical composition of *Gracilaria* (= *G. verrucosa* ?) in culture, based upon British Columbia populations. The plants were propagated as free-floating entities in tanks which were flushed with fresh seawater and with effluent seawater originating from a fish rearing tank. After a 113-d culture period, the plants from the fresh seawater tank increased in mass by 21.3%. The plants from the effluent seawater tank showed a 1.37% growth/d and an increase in mass of 55% after 113 d. Cultured specimens had higher contents of dry matter and higher yields of agar than in situ populations. The phycocolloid yields and properties of other British Columbia populations of *Gracilaria* sp. have also been evaluated by Whyte and Englar (1979a, b, 1980).

The growth and productivity of *Gracilaria* (= *G. verrucosa* ?) from British Columbia, Canada, has also been studied (Saunders and Lindsay 1979). The reproductive strategy, biomass production, and agar quality and quantity of intertidal and subtidal populations were different. Regrowth in vegetatively propagating intertidal beds was more seriously affected than in subtidal beds, which rely on spore recruitment. Culture studies of free-floating populations were conducted, employing six different phenotypes. A series of floating net enclosures were designed and tested in order to determine growth as a function of depth, density, and phenotype, with the goal of selecting fast-growing strains. Further experimental cultivation of *Gracilaria,* plus several carrageenophytes, were conducted in air-agitated culture conditions in order to screen a large number of plants for fast-growing "strains" (Bunting et al. 1980).

The effects of light intensity and temperature on the growth rates of cultured *G. verrucosa* from Washington were reported by Carr and Waaland (1977). The highest growth rates were recorded at 28.2‰, 28 °C and 1,400 fc. In general, the growth rates increased with increasing light intensities at all temperatures. At varying light intensities, the growth rate either decreased or remained unchanged, especially as temperatures increased from 23° to 28 °C. Only at 1,400 fc was there a significant increase in growth rate above 23 °C.

In addition to the references discussed above, the reader should consult the extensive review of *Gracilaria* given by Hoyle (1975). He summarizes information regarding the taxonomy, morphology, ecology, phylogeny, and economic importance of *Gracilaria,* much of which is relevant to the future mariculture and resource management of this plant. Further descriptions of growth of *Gracilaria* in waste-recycling polyculture systems at Woods Hole, Mass., and in Florida (LaPointe et al. 1976; DeBoer and Ryther 1977; Hanisak et al. 1979), as well as in Rhode Island (Harlin et al. 1979; Asare 1980), are given in the Polyculture section.

Hypnea

The red alga *Hypnea* is a species of considerable economic value, as its cell wall contains the polysaccharide kappa carrageenan (Mollion 1973, 1979; Humm and Kreuzer 1975). At present wild stocks are insufficient to meet the requirements of the carrageenan producers; thus its mariculture may become profitable when large-scale cultivation procedures are perfected. Several recent studies summarize the seasonal growth (Humm and Kreuzer 1975; Mshigeni 1977; Mshigeni and Mziray 1979; Humm 1981), reproduction (Mshigeni 1976e), sporeling development (Mshigeni 1976a, b, c), biochemistry (Mshigeni 1979; Durako and Dawes 1980a), and physiology (Dawes 1976; Dawes et al. 1976; Durako and Dawes, 1980b) of *Hypnea*, much of which is relevant to the future mariculture of this species. An extended review of the literature on *Hypnea* is also available (Mshigeni 1974).

The field cultivation of *H. cervicornis* spores in Hawaii has been described by Mshigeni (1976d). Carpospores and tetraspores developed into reproductively mature plants (67-100 mm in length) in 3 mo, and it was possible to raise four harvestable crops from spores per year. In contrast, only a single crop of *Chondrus crispus* plants can be obtained (from holdfasts) per year (Chen and McLachlan 1972), which makes *H. cervicornis* a good prospect to culture for its kappa carrageenan (Mshigeni 1976d). Mshigeni (1978) also evaluated the effects of nitrate fertilization on the growth of three Hawaiian *Hypnea* species in culture, i.e., *H. cervicornis, H. chordacea,* and *H. nidifica.* At reduced light intensity (200 fc) the growth rate of all three species was slow, even when nitrate fertilization was applied. Under high light intensities (1,000 fc), nitrate application significantly enhanced the growth rates. Accordingly, Mshigeni emphasized that the use of nitrate fertilization would be beneficial in *Hypnea* farming. Unfortunately, no evaluation was given of the levels of nitrate necessary to balance the synthesis of protein and carbohydrates (Dawes, Lawrence, Cheney, and Mathieson 1974), nor how to produce the "ripening" of carrageenan, as outlined earlier (Neish et al. 1977) for *C. crispus.*

The growth of *H. musciformis* in an artificial upwelling system at St. Croix, U.S. Virgin Islands, was evaluated by Haines (1975). In contrast to Mshigeni's (1976d) studies with *H. cervicornis, H. chordacea,* and *H. nidifica,* Haines found that the growth of *H. musciformis* was positively correlated with ammonia concentration, but not with nitrate or phosphate concentration. In addition, growth was stimulated by effluent from the mariculture system if the deep water (870 m) was enriched with ammonia alone or with a chelated iron-trace metals-vitamin mix. Increasing the ammonia supply, while keeping the chelated iron-trace metals-vitamins mix enrichment constant, produced an increased growth rate. Enrichment of deep water with 4% primary-treated sewage increased growth of *H. musciformis* relative to its growth in deep water alone. The carbon and nitrogen contents of the seaweed were inversely related to their growth rates measured during the period of most active growth. The carrageenan yields for *Hypnea* grown in the artificial upwelling system were 16-29% of the dry weight, as compared to 20-26% for *Hypnea* collected from nature.

Additional information on the growth of *H. musciformis* in the outdoor continuous-flow cultures at St. Croix has also been summarized (Haines and Monahan 1976; Roels et al. 1976a, b; Haines and Wheeler 1977; Langton et al. 1977). The studies of Roels et al. (1970, 1976a, b) are discussed in the section dealing with Artificial Upwelling Systems. Haines and Monahan (1976) recorded the rapid growth (up to 0.2 doubling/d) of *H. musciformis,* the development of an optimal medium for physiological and environmental tolerance studies, and the evaluation of nutrients and aeration effects. The ammonia and nitrate uptake rates of *H. musciformis* were further described by Haines and Wheeler (1977).

Recent growth studies of *H. musciformis* by Humm and Kreuzer (1975) are also relevant to its future mariculture; they showed that *Hypnea* grew very rapidly when tied to monofilament lines, similar to those employed in monoline farming of *Eucheuma* in the Pacific. The plants were capable of doubling their weight in 2 d at depths of 150-190 mm. Humm and Kreuzer proposed that *H. musciformis* could be grown economically in vats along the shore, through which water was pumped, with one-half the crop being harvested every few days.

A comparative study of the biochemistry of *H. musciformis* from the east and west coasts of Florida has been documented (Durako and Dawes 1980a). Protein and carbohydrate percentages were inversely related in both populations, with carbohydrate levels being highest in the summer and protein levels highest in winter. The Gulf (i.e., western) populations contained a significantly greater amount of protein than the Atlantic (i.e., eastern) coast plants. Carrageenan levels were highest in spring and lowest in fall, and the Atlantic coast population generally had higher levels than the Gulf coast population. Durako and Dawes concluded that there were significant differences between these two populations with respect to seasonal plant chemistry.

An evaluation of the photosynthetic rates of *H. musciformis* has been suggested as a useful and predictive model for its mariculture (Dawes et al. 1976). A summary of the photosynthetic responses of estuarine and open-coastal populations of *H. musciformis* to 48 combinations of light intensity, temperature, and salinity showed a broad tolerance to all three factors. Significant differences in the tolerances to light intensity and salinity between estuarine and coastal populations were noted, which might be relevant to potential seed stock selection of fast-growing strains. Such methods can be employed to assay the physiological state as well as strain tolerances to environmental parameters. Further descriptions of the physiological ecology of *H. musciformis* are given by Dawes (1976) and Durako and Dawes (1980b).

A model for the growth of detached *H. musciformis,* based upon the extensive outdoor cultivation program of the Marine Colloids, Inc., at Summerland Key, Fla., from January 1975 to March 1976, was also summarized by Guist et al (1977). The culture system consisted of large tanks with running seawater, and was basically similar to that used by Marine Colloids, Inc., for *C. crispus* and *Eucheuma isiforme* (Deveau and Castle 1976). The model related growth under a wide range of ambient temperatures and light intensities to concurrent laboratory measurements of the photosynthetic and respiratory activity of *H. musciformis.* The model allowed a more quantitative determination (assay) of the effects of water temperature and illumination on the growth rate of this species in culture.

Iridaea-Gigartina

The marine red alga *Iridaea cordata* has a very high carrageenan content (52-66%) and is of considerable economic potential (Mumford 1977b; Waaland 1977). Several investigators have studied *Iridaea* evaluating the plant's growth (Fralick 1971; Waaland 1972, 1973a, b, 1974b, 1976, 1977, 1979, In press; Hansen 1974, 1975, 1976, 1977a; Hansen and Doyle 1976; Adams and Austin 1977; Packard 1977), development (Norris and Kim 1972), reproduction (Norris and Kim 1972; Waaland 1972, 1973a, b, 1974b, 1977, 1979; Hansen 1974, 1975, 1976; Hansen and Doyle 1976), cytology (Fralick and Cole 1973), physiology-biochemistry (Waaland 1973a, b, 1974a, 1975; McCandless et al. 1975; Hansen 1977b), ecology (Fralick 1971; Waaland 1972, 1973a, b, 1974b; Austin et al. 1973; Austin and Adams 1974; Hansen 1974, 1975, 1976, 1977a; Hruby 1974, 1975, 1976; Foster 1975b; Hansen and Doyle 1976; Adams and Austin 1977; Packard 1977), biogeography (Kim and Norris 1974; Kim 1976), and taxonomy (Abbott 1971, 1972; Kim 1976). Much of this information should be helpful in furthering the mariculture and conservation of *Iridaea.*

Detailed accounts of the successful seeding of nets with carpospores and tetraspores of *I. cordata,* as well as their subsequent yields and growth rates in various locations in Puget Sound and the San Juan Islands, Wash., have been given (Kemp and Mumford 1976; Mumford 1977b). Three types of nettings were evaluated: A white type-66 nylon seine netting made of no. 60 cord, black plastic Vexar[6] (Dupont, Inc.), and orange polypropylene. The plant's growth on the expanded nylon and polypropylene netting was excellent, while the plastic Vexar was unsuitable. The density of the plants on the best netting was approximately 10 times that in natural populations in Washington (Fralick 1971; Waaland 1976) and British Columbia (Austin and Adams 1974) and approximately 1.5 times that in central California (Hansen 1976). The location and season of net emplacement were found to be very important. For example, in 1975 only about one-half of the nets placed were seeded with enough *I. cordata* to produce 100% cover the following year. There was no appreciable increase in cover from additional seedings during the second and third years, due to colonization by ulvoids and kelps. Thus, artificial seeding of nets in tanks may be required. As the tetrasporic plants of *I. cordata* contain only lambda carrageenan and the gametophytic plants only kappa carrageenan (Waaland 1974a, 1977; McCandless et al. 1975), it is possible to seed for one phase of the life history and get a particular carrageenan. Two harvests are possible per year with the first occurring in spring and the second during August or September when the maximum standing crop occurs.

Fertilization techniques (e.g., ammonia) for rope-cultured populations of *I. cordata* are being perfected in order to determine their effects on growth, phenology, and carrageenan content (Mumford 1977b). No major diseases were recorded on rope outplants of *I. cordata,* although several herbivores caused extensive damage. Thus, Mumford (1977b) concluded that the major obstacles to any aquaculture program, including *I. cordata,* may be social and legal, rather than biological, technological, or economical. However, if the use of artificial substrata for the culture of seaweeds continues in Puget Sound, he suggested that the current techniques could open up wide areas of the ocean for production of hydrocarbons, energy, food, chemicals, and pharmaceutical products. Further descriptions of *I. cordata* farming in the Pacific Northwest have been given (Jamison and Beswick 1972; Kemp and Mumford 1976; Mumford 1977a, 1979; Anonymous 1977[7]; Mumford et al. 1979), including a historical account of research sponsored by the Washington State Department of Natural Resources and the Washington Sea Grant Program.

Growth experiments with free-floating populations of *I. cordata,* as well as *Gigartina exasperata,* have been conducted in semiclosed culture systems, consisting of large tanks supplied with running seawater (Waaland 1976, 1977, 1979, In press; Cooper 1981). He used several tank designs, which were basically similar to those employed by Marine Colloids, Inc., for *Chondrus crispus* and *Eucheuma isiforme* (Deveau and Castle 1976.) The major factors regulating the growth and optimal production of *I. cordata* were plant size, rate of seawater flow, ratio of biomass to surface area, and light intensity. The yield of *I. cordata* in such a culture system was estimated as 5,700 kcal/m^2 per yr or 1,950 g ash-free dry matter/m^2 per yr, which was sixfold that of natural populations (Waaland 1976). A comparison of the annual production of *I. cordata* with some major terrestial plants indicated that it compared favorably with the biomass produced from the highest yielding corn, wheat, and rice farming techniques (Waaland In press). A comparative summary of the summer growth rates (as percent dry weight per day) of 13 Pacific Northwest marine algae showed that *I. cordata* and *G. exasperata* were ranked first (9.5%) and fourth (8.3%), with *Porphyra perforata* (8.8%), *I. cornucopiae* (8.7%), and *I. heterocarpa* (8.1%) showing comparable growth rates (Waaland 1977).

A major requirement for a sustained seaweed aquaculture operation, such as with *I. cordata* and *G. exasperata,* is the availability of sufficient inocula each spring, prior to the major growing season (Waaland 1977). In the case of *G. exasperata* this is not a problem, as its large perennial blades are present throughout the year, and they produce new blades from surface and marginal proliferations. In contrast, *I. cordata* is a pseudoperennial species, which has a perennial holdfast and

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[7]Anonymous. 1977. Seaweed farming in the Pacific northwest. Aquaculture Newsletter #34, p. 1-3. Jerden Industries, Inc., Bellevue, Wash.

blades that die off each year following reproduction. Even so, if net cultures of *I. cordata* were established, they could produce new blades each year from the perennial holdfasts (Mumford et al. 1979). According to Waaland (1977), the blades of *I. cordata* frequently produce spores 1-2 mo earlier in culture than in situ; no such observations have been made with *G. exasperata*. One particularly fast-growing strain (m-11) of *G. exasperata* was maintained by Waaland through three winters in outdoor cultivation tanks. Two major factors made this possible: The plant can be propagated vegetatively by means of cuttings or outgrowths from the blades; and the plant can be sustained through the winter, when the solar radiation is at a minimum, by adjusting the plant density per tank. Unfortunately, the same procedures cannot be followed with *I. cordata,* and in tank cultures the spring seed material must be initiated either by juvenile sporelings (i.e., new plants), by the perennial holdfast system, or by artificial substrata inoculated in the field. Thus, Waaland (1977) suggested that *G. exasperata* was a better candidate for tank mariculture than *I. cordata,* especially if strains with faster growth rates and yields were developed. In this vein, Waaland (1977, 1979) has conducted some strain selection studies by growing a variety of plants under uniform conditions for 4-6 wk periods. He found that fast-growing strains can be isolated, propagated by vegetative means, maintained in semiclosed culture for at least 2 yr, and grown in large quantities. For example, the m-11 strain increased its fresh weight at a rate of 4.25%/d versus 3.11%/d for wild material.

A variety of productivity studies of *I. cordata* have been described (Hansen 1977b). The time periods required for a doubling in dry weight, as well as carbon and nitrogen contents, were used to evaluate the gap between laboratory-determined and in situ estimates of productivity as well as to identify limiting parameters. During the winter, spring, and summer, in situ weight and thallus carbon doubling times were similar, indicating that laboratory-determined photosynthetic rates, for these seasons, were indicative of field production rates. During the fall, when natural populations senesced, laboratory-determined photosynthetic rates gave inaccurate estimates of field production. Doubling time comparisons of in situ populations suggested that production was light-limited during winter and spring but limited by other factors during summer and autumn. Laboratory-determined doubling times for thallus nitrogen were longer than in situ times during all seasons except winter. This suggested that in situ thalli utilized additional nitrogen sources not considered in this study or that the thalli carried out luxury consumption and stored nitrogen for utilization when seawater sources were depleted.

The photosynthetic rates for a fast-growing strain (m-11) of *G. exasperata* were evaluated by Merrill and Waaland (1978, 1979). The photosynthesis and respiration rates of the plants (i.e., blades) were measured and compared with values similarly obtained from wild material of the same species. Measurements were made with an oxygen electrode over a wide range of light intensities (5-750 $\mu E/m^2$ per s) and temperatures (6°-22°C), in order to predict the effects of manipulation of light intensities and temperatures in aquaculture operations.

Genetic improvement studies of seaweeds may be critical in expanding the production of certain limited and/or underutilized economic red algae, such as the carrageenophyte *Gigartina* (J. West[8], In press). Thus, West and his associates have initiated a genetic program for the improvement of carrageenan production in *Gigartina* subgenus *Mastocarpus,* a kappa carrageenan producing species of high quality. Most of their efforts have centered on *G. papillata* and *G. agardhii,* which may exhibit two life histories, a heteromorphic alternation of generations between a gametophytic *Gigartina* phase and a crustose tetrasporophyte (*Petrocelis*) or an apomictic recycling of *Gigartina* (West 1972, In press; West and Polanshek 1972, 1975, 1977; Polanshek 1974, 1975; Polanshek and West 1975, 1976, 1977; West et al. 1978). A major premise in West's efforts is that there is a genetic control of carrageenan synthesis in several Gigartinalean red algae (Chen et al. 1973; Pickmere et al. 1973, 1975; McCandless et al. 1975; Waaland 1975), with the primary types of carrageenans being linked to the nuclear and morphological phases of the life history, i.e., gametophytes primarily produce kappa carrageenan and tetrasporophytes produce mainly lambda carrageenan. Accordingly, a knowledge of the plant's life history, whether it be apomictic or a heteromorphic alternation of generations, may enable a selection of specific carrageenans via different reproductive generations or strains of *Gigartina*. At present West is attempting to produce high-yielding strains of *G. papillata* and *G. agardhii.* In addition, promising strains have been grown and crossed in the laboratory and their progeny transplanted into the field. Analyses are being conducted in order to determine the types and quantity of carrageenans in both the parents and progeny.

The influence of substrata and spore concentration on spore survival and germination in *G. agardhii* and *Petrocelis franciscana* has been evaluated (West and Crump 1974). The carpospores of *G. agardhii* and the tetraspores of *P. franciscana* were germinated on three different substrata: Microscope slides, polystyrene petri dishes, and Plexiglas (acrylic) plates. Spores liberated 24 h or more showed greater developmental abnormalities than freshly liberated ones (0-6 h old). A greater number of spores developed as discs on smooth polystyrene and glass than on Plexiglas. In addition, growth was more rapid on polystyrene and glass than on Plexiglas. At the lowest concentration tested (1,080 spores/cm^2) *P. franciscana* spores did not survive; however, at higher concentrations many spores germinated and developed as normal discs. With *G. agardhii* on polystyrene, carpospore concentration had little apparent influence on the percentage germination. However, it did have a dramatic effect on germling development. More carpospores of *G. argardhii* developed as discs in low concentrations (63%) than in high concentrations (9%). Only spherical germlings developed on Plexiglas and about 10% were discoid on glass. Of the substrata tested, Plexiglas was least suitable for outplanting, whereas polystyrene appeared best because it permitted rapid spore germination and attachment of discs.

Additional information on *Gigartina* carpospore discharge periodicity was summarized by West and Crump (1975). Each papilla discharged carpospores at 14(10-16)-d intervals with discharge occurring on 2-3 successive days during each cycle. In addition, each papilla discharged 5,000-100,000 spores/d. Thus, the total spore production per papilla averaged 3,600,000.

A variety of studies have been conducted on *G. stellata,* a plant which is often harvested in mixed lots with *C. crispus* as a source of carrageenan (Burns and Mathieson 1972a). For example, the seasonal growth, reproduction, and ecology of natural and harvested populations have been evaluated (Burns and Mathieson 1972b). In addition, culture and morphological

[8]John West, Botany Department, University of California, Berkeley, pers. commun. January 1975.

studies were made to determine the plant's life history (Chen et al. 1974; Edelstein et al. 1974; Tveter and Mathieson 1976a), and growth and ecology (Burns and Mathieson 1972a). The physiological ecology (Mathieson and Burns 1971) and carrageenan ecology of *G. stellata* (Mathieson and Tveter 1974, 1976) have also been investigated. Abbott (1980) has recorded similar evaluations of colloid variations in several red algae in central California, including the kappa-carrageenan producing species *Gigartina leptorhyncos*.

Gelidium-Pterocladia

Extensive reviews of the gelidioid algae, including their taxonomy, morphology, ecology, phylogeny, and economic importance, have been summarized (Santelices 1974, 1976a, 1977, 1978a, b). Most of the agronomy-related studies of this group have been oriented towards improving harvests and protecting the species as a natural resource (Santelices 1974). Barilotti and Silverthorne (1972) gave an excellent evaluation of resource management of subtidal populations of *G. robustum* in southern California, based upon a variety of ecological information including biomass and agar variations, growth, reproduction, regeneration capacity, and seasonal and habitat differences (Cooper and Johnstone 1944; Johnstone and Feeney 1944; Barilotti 1974). Silverthorne (1973, 1977) also developed a harvesting model for *G. robustum* based upon the above information. According to this model, a natural population has a standing crop of about 500 g/m^2 (fresh weight). After harvesting and regrowth for 14 quarters, the standing crop would be 900 g/m^2 and it could be reharvested with minimal effects. The harvesting model permits a prediction of yields under various management schemes.

The ecology, distribution, and abundance of *G. robustum* in southern California was described by Barilotti (1974). He suggested that light, water motion, and their interactions influenced vegetative growth rates. Transplant studies indicated that water motion, through its effect of limiting grazing pressure, was responsible for determining frond density. Barilotti also suggested that the disappearance of *G. robustum* from large areas of the California coastline was due to pollution.

The growth, reproduction, and harvesting of the commerically important agarophyte *G. robustum* (as *G. cartilagineum* var. *robustum*) in Baja California has also been described (Guzmán-del Proó and de la Campa-de Guzmán 1969). The growth of harvested and nonharvested (control) plants was assessed, in order to evaluate their regrowth potentials. Tetrasporic plants were predominant throughout the year, while carposporic plants were observed in smaller numbers and for more limited periods. The spore dispersal of the plants was found to be predominantly southeast from the parent populations. Spore shedding and germination of *G. robustum* was also studied by Guzmán-del Proó et al. (1972). The plants showed a maximum reproductive activity during August and September, and minimal activity in January and February. Both tetrasporic and carposporic plants showed diurnal discharge periodicities; in each case, carposporic plants released the greatest number of spores. Guzmán-del Proó and de la Campa-de Guzman (1979) further summarized a variety of synoptic, ecological, and biological information for *G. robustum* populations in Baja California.

The multiple interaction of several factors in defining the distribution and abundance of three Hawaiian Gelidiales (*Gelidiella acerosa, Pterocladia caerulescens,* and *P. capillacea*) were recently interpreted (Santelices 1978b). The plants' biological cycles were significantly correlated with seasonal changes in light intensity and water movement but not with seasonal changes of water temperature and salinity. Laboratory experiments tested the effects of five single factors and nine types of interactions on plant growth. Water movement and light intensity were the primary factors regulating growth. Water enrichment compensated for water movement, as all three species attained maximum growth at comparatively low water movement intensities when grown in fertilizer-enriched media.

A preliminary account of an artificial flotation technique for the cultivation of *Gelidium* sp. was summarized by Gibor (1976). He described a simple and inexpensive system for floating *Gelidium* plants near the surface of water with perlite particles, i.e., aerated volcanic rocks. Small fronds of *Gelidium* were glued to the particles, while other plants such as *Bryopsis* attached themselves. Gibor suggested that the potentials for mass cultivation of *Gelidium* using these methods were excellent.

One of the few papers dealing with mass culture of gelidioid algae (i.e., *P. caerulescens, P. capillacea,* and *Gelidiella acerosa*) is given by Santelices (1976b). Working with Hawaiian material, he evaluated the growth of unattached specimens as well as minimum water volume requirements per unit of algal mass. *Gelidiella acerosa* was unable to grow detached. However, *P. caerulescens* and *P. capillacea* grew continuously for 50 d, reaching maximum daily growth rates of 2.3 and 1.6% respectively. Both of the latter species adopted a globose or subglobose habit, showing modifications similar to other free-floating species of algae (Austin 1960). The optimum volume per unit of algal mass was 1 liter of enriched seawater per 3.3 g for *P. caerulescens* and 1.7 g for *P. capillacea*.

Little is known about the nutrient physiology of seaweeds, including that of the gelidioid algae. Bird (1976a, b) evaluated the physiological responses of the agarophyte *Gelidium nudifrons* to various combinations of ammonia and nitrate. He observed a simultaneous assimilation of both nitrogen sources in culture experiments, employing four different combinations of the two nutrients. His study suggested that there were pools of both nutrients which were simultaneously available for algal assimilation.

Palmaria palmata (Dulse)

An appraisal of the dulse industry in Canada, including a historical analysis of the industry, an evaluation of the resource, and its marketing and developmental opportunities, was recently given by Ffrench (1974). Dulse is usually harvested by hand (rake), air dried and packaged as a source of food (Morgan et al. 1980; Sirota and Uthe 1979). One company, Atlantic Mariculture Ltd. of Grand Manan Island, New Brunswick, Canada, has utilized impoundment and cultivation techniques (Anonymous 1974a; Neish 1976a), which consisted of ferrocement tanks and air agitation. The company held detached plants in tanks until they were processed; any growth that occurred offset the operating cost of impoundment. Neish (1976a) stated that dulse harvesting is only carried out during very low tides of spring and fall, so the flow of raw material through a processing facility is uneven. A capacity for holding live material greatly enhances processing efficiency. Dulse is cleansed of dirt, mussels, epiphytes, and other contaminants in the storage tanks.

Yields of over 60 g dry wt/m² per d were obtained with stocking densities of approximately 10 kg fresh wt/m². He suggests that *P. palmata*, which has an annual frond and a perennial basal system, must be propagated differently than perennial species like *Chondrus crispus*. Such techniques may require the development of new methods involving grow-out from hatchery seed. Some commercially significant marine plants have been successfully brought through their life-cycle in the laboratory, and the commerical production of hatchery seed is well established in the *Porphyra* industry in Japan (MacFarlane 1968; Okazaki 1971; Korringa 1976).

The effects of total carbon supply, irradiance, pH, temperature, and salinity on the short-term photosynthetic rates of *P. palmata* were enumerated by Robbins (1979), based upon oxygen and pH measurements. Photosynthetic, but not respiratory, rates showed some seasonal adaptation. Maximal photosynthesis occurred at 10°-15 °C, 32‰, and pH values of 6.5-7.5. Light saturation was at approximately 212 μE/m² per s and *P* max was temperature dependent. The compensation point in late winter was 6.6 μE/m² per s. Raising the total carbon dioxide concentration to 6.0-7.0 mM/l resulted in photosynthetic stimulation up to 2.7 times normal levels. A photosynthetic quotient of about 1.28 was determined for *Palmaria palmata* by measuring carbon dioxide flux with infrared gas analysis.

The life history and cytology of *P. palmata* from the Atlantic coast of Canada have recently been studied (Meer and Chen 1979). Tetraspores from diploid tetrasporophytes, the most obvious plants in situ, gave rise to two types of haploid sporelings, one of which grew more robustly and was less branched than the other. A 1:1 ratio of the two types was obtained from random spores. The more robust plants were males, while the smaller plants, which were believed to be females, grew more slowly and eventually formed sporangia. The sporangia on the female plants aborted without releasing viable spores, presumably because of nuclear abnormalities associated with haploid meiosis. On one occasion fertile (i.e., diploid) tetrasporic fronds of *P. palmata* were obtained from gametophytes in culture, and these gave rise to a second generation of segregating sporelings. As noted by Meer (1976) in an earlier cytological study of *P. palmata*, a complete elucidation of the plant's life history will only be achieved when it is determined how the diploid state is attained. Since diploid tetrasporic plants appear to give rise only to haploid plants, a compensating mechanism such as fertilization or somatic chromosome doubling must exist to generate diploid plants. Hopefully, this mechanism can be found by future studies. An ultrastructural study by Pueschel (1979) has also demonstrated that meiosis occurs during tetrasporogenesis in *P. palmata*.

Porphyra (Nori)

Porphyra, or nori as it is commonly called, is extensively cultivated in the Orient (Korringa 1976) and is one of the most important economic seaweeds in the world (Mathieson 1975). Imada et al. (1972) stated that the annual sales of nori in 1970 were about US$140 million, which was higher than any other marine product in Japan. As a result of increased pollution of Japanese coastal waters (culture areas), as well as increased demand for the product, the Japanese are seeking additional sources of foreign *Porphyra*. Accordingly there is considerable potential for the development of culture systems of nori in North America (Hunter and Nyegaard 1974; Hunter 1975). Increased interest in oriental cookery by Americans as well as the presence of large numbers of Japanese in the United States and Canada have also stimulated the markets for nori.

Porphyra is a potentially important food resource in the United States, as approximately US$700,000 worth of nori is imported through San Francisco alone (Neushul[9]). In addition, the rate of consumption of nori is increasing in the United States. As a result, Neushul and his associates (Woessner 1974, 1979; Woessner et al. 1977) at the University of California, Santa Barbara, have initiated several biological and economic studies on *Porphyra nereocystis*, in order to provide necessary information for intelligent management and cultivation of this underutilized, but potentially important, species. Neushul (footnote 9) estimated that the natural crop within a 55-mi distance of the California coastline could be worth in excess of US$500,000.

Extensive nori cultivation may be possible in Puget Sound because the area has moderate winter (6°-8 °C) and summer temperatures (seldom >15 °C), a lack of sea ice, high nutrients due to runoff from nearby mountains, adequate currents, and sufficient light for the growth of many *Porphyra* species (Hunter and Nyegaard 1974). Because the amount of stable substrata is limited in shallow water, artificial substrata would have to be employed in order to use the great body of water in Puget Sound for seaweed production. Commercial culture of nori would also require a mechanical harvesting system and local processing of nori sheets.

One of the few accounts of mass cultivation of *Porphyra* in North America (i.e., in Washington) is given by Waaland (1977). He compared the growth of free-floating populations of *P. perforata* in a semiclosed culture system with 12 other Pacific Northwest red algae, including the carrageenophytes *Iridaea cordata* and *Gigartina exasperata*. *Porphyra perforata* showed a summer growth rate of 8.8% dry weight increase per day, with *I. cordata* being the only species tested with a higher growth rate (9.5%).

Sea Grant studies by M. B. Allen and C. P. McRoy at the University of Alaska examined the feasibility of *Porphyra* cultivation in Alaska (W. Shaw[10]). The studies included an evaluation of favorable sites for cultivation, a determination of the time course of the alga's life history under Alaskan conditions, laboratory cultivation of germlings suitable for inoculation in favorable habitats, and the establishment of an experimental "farm."

Another Sea Grant project by D. Kapraun of the University of North Carolina (Wilmington) was initiated in 1977, in order to determine the feasibility of establishing a nori harvesting industry in North Carolina. He assessed the distribution and standing crop of *Porphyra* in North Carolina tidal marshes, determined harvesting and processing techniques, and initiated a pilot production plant and marketing procedures for the local product.

The nutritional composition (McLachlan et al. 1972), life history (Bird et al. 1972; Bird 1973), and ecology (Bird 1973) of *P. linearis* have recently been studied in Canada. McLachlan et al. (1972) determined that *P. linearis* was superior to many other

[9]Michael Neushul, Biology Department, University of California, Santa Barbara, pers. commun. January 1975.

[10]William Shaw, NOAA Office of Sea Grant, Washington, D.C., pers. commun. March 1971.

species of nori used in the Orient, with its desirable flavor resulting from a high concentration of isofloridoside and several free amino acids. The life history of *P. linearis* was completed in culture through five generations (Bird et al. 1972). Conchosporangia formed at 5°-20°C, but release of conchospores began only at 13°C and continued at a slower rate at 5°C. The conchocelis phase was long lived despite continuous sporulation and attrition. Variations in ability to shed conchospores indicated the existence of different strains of conchocelis. Additional details regarding the life history and ecology of in situ populations of *P. linearis* were summarized by Bird (1973).

A detailed account of sexual reproduction in *P. gardneri* was recently summarized by Hawkes (1978). He observed fertilization and diploid chromosome numbers in the carpospores and vegetative cells of the conchocelis phase, which was the first unequivocal evidence for sexual reproduction in *Porphyra*. Hawkes (1977a, b) further summarized a variety of field, culture, and cytological studies of *P. gardneri*.

The growth of detached *P. umbilicalis* in a flowing seawater system at the Marine Plant's Experimental Station near Miminegash, Prince Edward Island, Canada, was reported by McDougall (1974). In one experiment, detached specimens gained 107% weight (wet) during 42 d, showing that *P. umbilicalis* could be successfully cultured as unattached plants. Several small rocks bearing attached reproductive plants were also cultured in shallow tanks (18 in deep) with running seawater. The tanks were drained each day, leaving the plants exposed to air for about 4 h, approximating the conditions prevailing in nature. *Porphyra umbilicalis* grew well under these conditions, almost doubling in length in 42 d. Furthermore, small plants developed on the rocks, suggesting the potential use of various substrata for the growth and transfer of sporelings as is done with the Japanese nori industry (Mathieson 1975; Korringa 1976).

A variety of other studies dealing with the life histories (Hollenberg 1958; Krishnamurthy 1969a, b; Bourne et al. 1970; Chen et al. 1970; Conway and Cole 1973; Mumford 1973a, b, 1975; Kapraun and Luster 1980), taxonomy (Krishnamurthy 1969a, 1972; Mumford 1973a, b, 1975; Conway 1975; Conway et al. 1975), ecology (Edelstein and McLachlan 1966; Mumford 1973a), and cultural perspective-significance (Williams 1979) of *Porphyra* have been conducted in North America. As noted earlier, such studies may ultimately aid in the utilization and development of such marine plant resources.

Laminaria

In contrast to the substantial production of *Laminaria* in China (Cheng 1969) and Japan (Hasegawa 1976), this species is not cultivated commercially in North America, presumably because there is little market for its product (e.g., kombu). However, there is considerable interest in its ecology and productivity because of the plant's major role in nearshore ecosystems. Much of the recent work on *Laminaria* in North America and Europe (Boden 1979; Kain 1979; Lüning 1979) has direct applications to its potential mariculture and resource management, and will be reviewed herein.

The productivity and growth strategy of *L. digitata*, *L. longicruris*, and *Agarum cribrosum* were studied in St. Margaret's Bay, Nova Scotia (Mann 1972a, b, 1973; Mann and Chapman 1975). The growth of individual plants was measured periodically for 2 yr by recording the distance between holes that were initially spaced at 10 cm intervals along the blades. As the punctures approached the tips of the blades, new ones were made at the base. The blades behaved like moving belts of tissue, eroding at the tips while growing at the bases, so that a year's growth amounted to 1-5 times the initial length. Surprisingly, growth was most rapid from January to April, i.e., during periods of short day length, low light intensity, and low water temperatures. Conversely, it was slowest during July to October, when contrasting environmental conditions occurred. The authors suggest that during the winter the plants are using some of the dry matter stored in the summer as an energy and material source for part of their growth. Since winter is a time of high concentration of dissolved nitrogen and phosphorous in the sea, it seems possible that the plants are making some of their new tissue by using a stored carbon source and taking up nutrients from the seawater. This could obviously place them in an advantageous position for making maximum use of sunlight for photosynthesis in early spring.

The summer biomass of kelps in St. Margaret's Bay has a turnover of 4-10 times in the course of 1 yr (Mann 1972b). Mann estimated that the annual production of kelps in St. Margaret's Bay amounts to 603 g C/m^2 averaged over the whole bay, 1,750 g C/m^2 averaged over the seaweed zone, or 648,000 g C/m of shoreline. The approximate caloric equivalents were 6,030 kcal/m^2 over the whole bay or 648×10^3 kcal/m of shoreline. Overall, the growth strategy of kelps seems to center around their ability to carry out intensive photosynthesis in the summer, as well as to store and mobilize carbon reserves during periods of low light intensity (Mann 1973; Mann and Chapman 1975). Such a growth strategy would greatly extend their growing season and allow the plants to use the nutrients for growth during a time (winter) when the phytoplankton show slow growth due to the lack of an energy source.

The seasonal fluctuation in dissolved inorganic nutrients, internal reserves of nitrogen, and growth rates of *L. longicruris* in St. Margaret's Bay were summarized by Chapman and Craigie (1977). The onset of winter growth, as noted by Mann (1972b), correlated with improved nitrate conditions in the sea. During the winter, tissue reserves of nitrate reached 150 μM/g fresh weight in March, which was a concentration factor of approximately 28,000 over ambient (water) levels. Depletion of this nutrient pool followed the disappearance of the external nitrate with a lag period of up to 2 mo. Rapid kelp growth was measured at this time. Reserves of organic nitrogen also reached maximum values in March and declined slowly throughout the summer into autumn. Accordingly Chapman and Craigie (1977) suggested that the combined inorganic and organic nitrogen reserves sustained rapid growth rates into July and reduced rates through the late summer. Fertilization of an experimental kelp bed with $NaNO_3$ increased the internal plant reserves of nitrate and produced a much improved summer growth rate. The enriched plants developed very small reserves of carbohyrate during this period.

The role of carbohydrate reserves as a carbon source during the seasonal growth of *L. longicruris* has been determined (Chapman and Craigie 1978). Seasonal variations in the levels of laminarin and mannitol showed maximum values during late summer. Minimum values occurred in February at the time when growth rates were increasing rapidly. Erosion of the blades in winter carried away much of the tissue containing carbohydrate reserves accumulated during the previous summer. Experimental reduction of carbohydrate reserves by fertilization with sodium nitrate during the summer did not affect subsequent winter growth rates. Truncation of the plants in

November significantly reduced growth rates. The lower rate of growth was attributed to a reduction in photosynthetic area rather than a loss of storage products. An additional description of the annual carbon budget for *L. longicruris* in St. Margaret's Bay was given by Hatcher et al. (1977).

The seasonal patterns of nitrate uptake in *L. longicruris* were determined by Harlin and Craigie (1976), based upon populations from St. Margaret's Bay. Their experiments suggested that *L. longicruris* was capable of using nitrate under winter conditions, and that it did not depend upon stored compounds for a nitrogen source during periods of rapid growth, i.e., late winter and spring. Discs were punched from the thin edges of *L. longicruris* plants and they were subjected to external nitrate in a series of concentrations under different light and temperature regimes. The optimal rate of uptake, with summer material (June and July) was 7-9 μM/g dry wt/h at 15 °C and approximately 700 fc. At 5 °C, uptake was 60%, and at 0 °C it was 40% of that at 15 °C. The uptake in the dark was 60-80% of that in the light. Algae pretreated for 12 h with antibiotics removed nitrate from the medium at a rate of 84% of the untreated material. Nitrate uptake was inhibited in proportion to the concentration of nitrate in the medium. Further studies of nitrate uptake by *L. longicruris* have been reported by the same investigators (Harlin and Craigie 1978).

The growth and production of *L. longicruris* are interrelated with nutrients, water motion, and other parameters (Gerard and Mann 1979). That is, measurements of internal inorganic nitrogen (i.e., nitrite and nitrate) reserves and dry organic weight indicated that low concentrations of dissolved nutrients in summer and low levels of illumination in fall and winter were more limiting to growth at exposed than sheltered sites.

The morphological differentiation of nondigitate *Laminaria* populations from the North Atlantic was evaluated by Chapman (1973a, b), who found that the occurrence of long, hollow stipes (the *L. longicruris* types) decreased with increasing exposure. The differentiation of populations in relation to exposure was clinal with overlap in the variation patterns. The major taxonomic finding of the analyses was the lack of nonoverlapping criteria by which *L. agardhii* and *L. longicruris* may be delimited. Subsequently, Chapman (1973b, 1974a) has conducted heritability tests between the two morphological types within the Simplices section of *Laminaria.* The production of fertile hybrids established interfertility between populations from the extremes of the morphological range. Reciprocal transplantation experiments between exposed and sheltered sites produced no significant changes in stipe morphology. Quantitative genetic analysis of the degree of resemblance between relatives indicated a high genetic component in the interpopulation differentiation. Estimates of within-population heritability at the exposed site were low, perhaps because of intensive local stabilizing selection which reduces genetic variability.

The inheritance of mucilage canals in *Laminaria,* section Simplices, from eastern Canada has also been described by Chapman (1974b, 1975). A matrix of heritability tests showed complete interfertility between all mucilage canal types, fertile F_1 hybrids being produced in all cases. Quantitative genetic analysis revealed a large environmental component in the phenotypic variance of degree of mucilage canal development. Only plants from Nova Scotia bred true with respect to mucilage canals. This characteristic was considered unsuitable for taxonomic and biological species determinations, though there was evidence for intraspecific genotypic differentiation in some Nova Scotian populations. Lüning et al. (1978) conducted crossing experiments in the nondigitate complex of *Laminaria* from both sides of the Atlantic. *Laminaria longicruris* from Nova Scotia and two forms of European *L. saccharina* were successfully crossed. Parental and hybrid sporophytes were cultivated in the sea near Helgoland, where they reached maximum frond lengths of 40-120 cm. After 7 mo all experimental plants were nonsporogenous and were removed from the sea. The authors discussed a variety of observations on genetically fixed traits and problems of the relationships between nondigitate *Laminaria* forms from the eastern and western sides of the North Atlantic Ocean.

A quantitative genetic analysis of alginate content in *L. longicruris* was conducted by Chapman and Doyle (1979), in order to partition the plant's phenotypic variance into genetic and nongenetic components. Regression analysis of mean offspring on midparent values and artificial selection were used to estimate heritability and realized heritability, respectively. Both estimates showed that there was a low additive genetic component in the phenotypic variance and that a simple mass selection program would produce a very small genetic response.

A summary of the experimental and numerical taxonomy of the Laminariales was given by Chapman (1978). He described crossability tests, transplant experiments, standard laboratory cultivation, and quantitative genetics of the Laminariales, much of which is relevant to the genetic improvement of kelps and their ultimate mariculture. In most cases the crossability tests showed relatively easy hybridization between taxa having close orthodox taxonomic affinities. Conversely, distantly related taxa, in a classical taxonomic sense, showed little or no hybridization. In the same way, transplant experiments have demonstrated that some closely related taxa were the phenotypic manifestations of plastic responses to diverse habitats.

The destructive grazing of kelp beds by common green urchins, *Strongylocentrotus droebachiensis,* and its relationships to lobster, *Homarus americanus,* abundance have been reported in Nova Scotia (Mann and Breen 1972; Breen and Mann 1976a, b; Mann 1977). As in other geographical areas (North 1971) sea urchins have a major effect on the abundance of kelps, as well as on preventing the return of kelps with continued sea urchin settlement. Lobster harvesting was shown to have interrelated effects on the abundance of kelps. For example, in one site in St. Margaret's Bay, the abundance of lobsters decreased by nearly 50% in 14 yr. The lobster is a major predator of sea urchins, and during the past 6 yr (1970-76) the sea urchins have destroyed 70% of the beds of *Laminaria* spp. in the area. As the kelp beds are destroyed, their high primary productivity is lost (Mann 1972b), which will cause substantial changes at higher tropic levels. The authors suggest that a management program may be required to increase the abundance of lobsters in order to protect the remaining kelp-bed communities.

The *Laminaria* spp. from the Pacific coast of North America have also been extensively studied. For example, the role of sea otters in structuring nearshore kelp communities, including *Laminaria* spp., has been extensively studied (Dayton 1974; Estes and Palmisano 1974). In addition, a summary of the kelp species and their distribution in the northeast Pacific was outlined, in relation to oceanographic conditions (Druehl 1965, 1968, 1969, 1970, 1972). A detailed autecological study of several nondigitate *Laminaria* species from western Canada was completed (Druehl 1965, 1967; Druehl and Hsiao 1977), including culture tolerance studies of gametophytes and juvenile sporophytes, as well as studies of the physiological tolerances, seasonal growth, and transplant ecology of macroscopic plants. Basically, the species of nori used in the Orient, with its desirable flavor resulting from a high concentration of isofloridoside and several free amino acids. The life history of *P. linearis* was completed in culture through five generations (Bird et al. 1972). Conchosporangia formed at 5 °-20 °C, but release of conchospores began only at 13 °C and continued at a slower rate at 5 °C. The conchocelis phase was long lived despite continuous sporulation and attrition. Variations in ability to shed conchospores indicated the existence of different strains of conchocelis. Additional details regarding the life history and ecology of in situ populations of *P. linearis* were summarized by Bird (1973).

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A variety of other studies dealing with the life histories (Hollenberg 1958; Krishnamurthy 1969a, b; Bourne et al. 1970; Chen et al. 1970; Conway and Cole 1973; Mumford 1973a, b, 1975; Kapraun and Luster 1980), taxonomy (Krishnamurthy 1969a, 1972; Mumford 1973a, b, 1975; Conway 1975; Conway et al. 1975), ecology (Edelstein and McLachlan 1966; Mumford 1973a), and cultural perspective-significance (Williams 1979) of *Porphyra* have been conducted in North America. As noted earlier, such studies may ultimately aid in the utilization and development of such marine plant resources.

Laminaria

In contrast to the substantial production of *Laminaria* in China (Cheng 1969) and Japan (Hasegawa 1976), this species is not cultivated commercially in North America, presumably because there is little market for its product (e.g., kombu). However, there is considerable interest in its ecology and productivity because of the plant's major role in nearshore ecosystems. Much of the recent work on *Laminaria* in North America and Europe (Boden 1979; Kain 1979; Lüning 1979) has direct applications to its potential mariculture and resource management, and will be reviewed herein.

The productivity and growth strategy of *L. digitata, L. longicruris,* and *Agarum cribrosum* were studied in St. Margaret's Bay, Nova Scotia (Mann 1972a, b, 1973; Mann and Chapman 1975). The growth of individual plants was measured periodically for 2 yr by recording the distance between holes that were initially spaced at 10 cm intervals along the blades. As the punctures approached the tips of the blades, new ones were made at the base. The blades behaved like moving belts of tissue, eroding at the tips while growing at the bases, so that a year's growth amounted to 1-5 times the initial length. Surprisingly, growth was most rapid from January to April, i.e., during periods of short day length, low light intensity, and low water temperatures. Conversely, it was slowest during July to October, when contrasting environmental conditions occurred. The authors suggest that during the winter the plants are using some of the dry matter stored in the summer as an energy and material source for part of their growth. Since winter is a time of high concentration of dissolved nitrogen and phosphorous in the sea, it seems possible that the plants are making some of their new tissue by using a stored carbon source and taking up nutrients from the seawater. This could obviously place them in an advantageous position for making maximum use of sunlight for photosynthesis in early spring.

The summer biomass of kelps in St. Margaret's Bay has a turnover of 4-10 times in the course of 1 yr (Mann 1972b). Mann estimated that the annual production of kelps in St. Margaret's Bay amounts to 603 g C/m^2 averaged over the whole bay, 1,750 g C/m^2 averaged over the seaweed zone, or 648,000 g C/m of shoreline. The approximate caloric equivalents were 6,030 $kcal/m^2$ over the whole bay or 648×10^3 kcal/m of shoreline. Overall, the growth strategy of kelps seems to center around their ability to carry out intensive photosynthesis in the summer, as well as to store and mobilize carbon reserves during periods of low light intensity (Mann 1973; Mann and Chapman 1975). Such a growth strategy would greatly extend their growing season and allow the plants to use the nutrients for growth during a time (winter) when the phytoplankton show slow growth due to the lack of an energy source.

The seasonal fluctuation in dissolved inorganic nutrients, internal reserves of nitrogen, and growth rates of *L. longicruris* in St. Margaret's Bay were summarized by Chapman and Craigie (1977). The onset of winter growth, as noted by Mann (1972b), correlated with improved nitrate conditions in the sea. During the winter, tissue reserves of nitrate reached 150 $\mu M/g$ fresh weight in March, which was a concentration factor of approximately 28,000 over ambient (water) levels. Depletion of this nutrient pool followed the disappearance of the external nitrate with a lag period of up to 2 mo. Rapid kelp growth was measured at this time. Reserves of organic nitrogen also reached maximum values in March and declined slowly throughout the summer into autumn. Accordingly Chapman and Craigie (1977) suggested that the combined inorganic and organic nitrogen reserves sustained rapid growth rates into July and reduced rates through the late summer. Fertilization of an experimental kelp bed with $NaNO_3$ increased the internal plant reserves of nitrate and produced a much improved summer growth rate. The enriched plants developed very small reserves of carbohyrate during this period.

The role of carbohydrate reserves as a carbon source during the seasonal growth of *L. longicruris* has been determined (Chapman and Craigie 1978). Seasonal variations in the levels of laminarin and mannitol showed maximum values during late summer. Minimum values occurred in February at the time when growth rates were increasing rapidly. Erosion of the blades in winter carried away much of the tissue containing carbohydrate reserves accumulated during the previous summer. Experimental reduction of carbohydrate reserves by fertilization with sodium nitrate during the summer did not affect subsequent winter growth rates. Truncation of the plants in

November significantly reduced growth rates. The lower rate of growth was attributed to a reduction in photosynthetic area rather than a loss of storage products. An additional description of the annual carbon budget for *L. longicruris* in St. Margaret's Bay was given by Hatcher et al. (1977).

The seasonal patterns of nitrate uptake in *L. longicruris* were determined by Harlin and Craigie (1976), based upon populations from St. Margaret's Bay. Their experiments suggested that *L. longicruris* was capable of using nitrate under winter conditions, and that it did not depend upon stored compounds for a nitrogen source during periods of rapid growth, i.e., late winter and spring. Discs were punched from the thin edges of *L. longicruris* plants and they were subjected to external nitrate in a series of concentrations under different light and temperature regimes. The optimal rate of uptake, with summer material (June and July) was 7-9 μM/g dry wt/h at 15 °C and approximately 700 fc. At 5 °C, uptake was 60%, and at 0 °C it was 40% of that at 15 °C. The uptake in the dark was 60-80% of that in the light. Algae pretreated for 12 h with antibiotics removed nitrate from the medium at a rate of 84% of the untreated material. Nitrate uptake was inhibited in proportion to the concentration of nitrate in the medium. Further studies of nitrate uptake by *L. longicruris* have been reported by the same investigators (Harlin and Craigie 1978).

The growth and production of *L. longicruris* are interrelated with nutrients, water motion, and other parameters (Gerard and Mann 1979). That is, measurements of internal inorganic nitrogen (i.e., nitrite and nitrate) reserves and dry organic weight indicated that low concentrations of dissolved nutrients in summer and low levels of illumination in fall and winter were more limiting to growth at exposed than sheltered sites.

The morphological differentiation of nondigitate *Laminaria* populations from the North Atlantic was evaluated by Chapman (1973a, b), who found that the occurrence of long, hollow stipes (the *L. longicruris* types) decreased with increasing exposure. The differentiation of populations in relation to exposure was clinal with overlap in the variation patterns. The major taxonomic finding of the analyses was the lack of nonoverlapping criteria by which *L. agardhii* and *L. longicruris* may be delimited. Subsequently, Chapman (1973b, 1974a) has conducted heritability tests between the two morphological types within the Simplices section of *Laminaria.* The production of fertile hybrids established interfertility between populations from the extremes of the morphological range. Reciprocal transplantation experiments between exposed and sheltered sites produced no significant changes in stipe morphology. Quantitative genetic analysis of the degree of resemblance between relatives indicated a high genetic component in the interpopulation differentiation. Estimates of within-population heritability at the exposed site were low, perhaps because of intensive local stabilizing selection which reduces genetic variability.

The inheritance of mucilage canals in *Laminaria,* section Simplices, from eastern Canada has also been described by Chapman (1974b, 1975). A matrix of heritability tests showed complete interfertility between all mucilage canal types, fertile F_1 hybrids being produced in all cases. Quantitative genetic analysis revealed a large environmental component in the phenotypic variance of degree of mucilage canal development. Only plants from Nova Scotia bred true with respect to mucilage canals. This characteristic was considered unsuitable for taxonomic and biological species determinations, though there was evidence for intraspecific genotypic differentiation in some Nova Scotian populations. Lüning et al. (1978) conducted crossing experiments in the nondigitate complex of *Laminaria* from both sides of the Atlantic. *Laminaria longicruris* from Nova Scotia and two forms of European *L. saccharina* were successfully crossed. Parental and hybrid sporophytes were cultivated in the sea near Helgoland, where they reached maximum frond lengths of 40-120 cm. After 7 mo all experimental plants were nonsporogenous and were removed from the sea. The authors discussed a variety of observations on genetically fixed traits and problems of the relationships between nondigitate *Laminaria* forms from the eastern and western sides of the North Atlantic Ocean.

A quantitative genetic analysis of alginate content in *L. longicruris* was conducted by Chapman and Doyle (1979), in order to partition the plant's phenotypic variance into genetic and nongenetic components. Regression analysis of mean offspring on midparent values and artificial selection were used to estimate heritability and realized heritability, respectively. Both estimates showed that there was a low additive genetic component in the phenotypic variance and that a simple mass selection program would produce a very small genetic response.

A summary of the experimental and numerical taxonomy of the Laminariales was given by Chapman (1978). He described crossability tests, transplant experiments, standard laboratory cultivation, and quantitative genetics of the Laminariales, much of which is relevant to the genetic improvement of kelps and their ultimate mariculture. In most cases the crossability tests showed relatively easy hybridization between taxa having close orthodox taxonomic affinities. Conversely, distantly related taxa, in a classical taxonomic sense, showed little or no hybridization. In the same way, transplant experiments have demonstrated that some closely related taxa were the phenotypic manifestations of plastic responses to diverse habitats.

The destructive grazing of kelp beds by common green urchins, *Strongylocentrotus droebachiensis,* and its relationships to lobster, *Homarus americanus,* abundance have been reported in Nova Scotia (Mann and Breen 1972; Breen and Mann 1976a, b; Mann 1977). As in other geographical areas (North 1971) sea urchins have a major effect on the abundance of kelps, as well as on preventing the return of kelps with continued sea urchin settlement. Lobster harvesting was shown to have interrelated effects on the abundance of kelps. For example, in one site in St. Margaret's Bay, the abundance of lobsters decreased by nearly 50% in 14 yr. The lobster is a major predator of sea urchins, and during the past 6 yr (1970-76) the sea urchins have destroyed 70% of the beds of *Laminaria* spp. in the area. As the kelp beds are destroyed, their high primary productivity is lost (Mann 1972b), which will cause substantial changes at higher tropic levels. The authors suggest that a management program may be required to increase the abundance of lobsters in order to protect the remaining kelp-bed communities.

The *Laminaria* spp. from the Pacific coast of North America have also been extensively studied. For example, the role of sea otters in structuring nearshore kelp communities, including *Laminaria* spp., has been extensively studied (Dayton 1974; Estes and Palmisano 1974). In addition, a summary of the kelp species and their distribution in the northeast Pacific was outlined, in relation to oceanographic conditions (Druehl 1965, 1968, 1969, 1970, 1972). A detailed autecological study of several nondigitate *Laminaria* species from western Canada was completed (Druehl 1965, 1967; Druehl and Hsiao 1977), including culture tolerance studies of gametophytes and juvenile sporophytes, as well as studies of the physiological tolerances, seasonal growth, and transplant ecology of macroscopic plants. Basically, the distribution, abundance, and phenology of the kelps are interrelated with their differential tolerances to temperature and salinity. Axenic culture techniques were perfected (Druehl and Hsiao 1969) to evaluate the control of gametogenesis (Hsiao and Druehl 1971, 1973a, b,; Hsiao 1972) by such factors as light, different culture media, nutrient content, and halogen concentration. Furthermore, the in situ development of gametophytes and young sporophytes of *L. saccharina* was described (Hsiao and Druehl 1973c). Zoospores were labeled with fluorescent stain (calcofluor white), cultivated, and recoved (examined) at frequent intervals. The gametophytes produced gametes throughout the year. However, the production of macroscopic sporophytes appeared to be limited by survival of microscopic sporophytes, particularly during the summer. Macroscopic sporophytes were evident during the late winter and autumn.

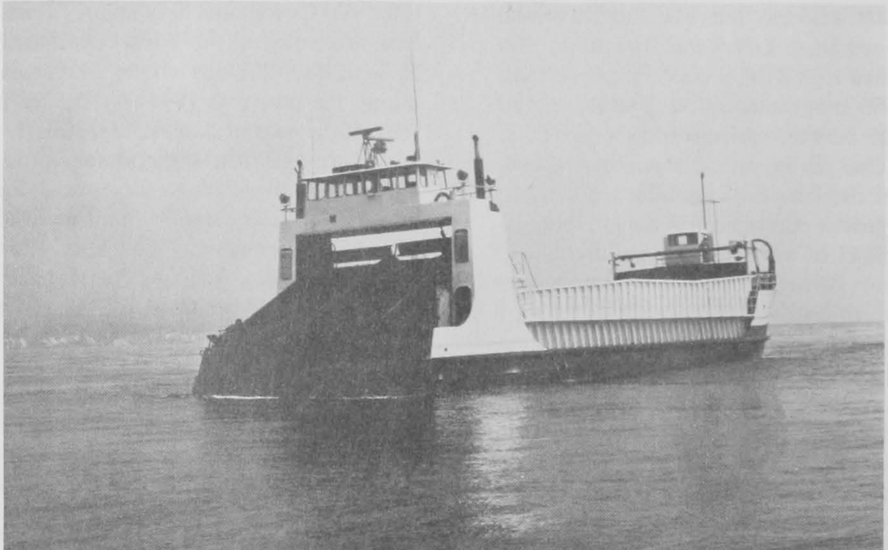
In addition to the references summarized above, the reader should consult the extensive review of *Laminaria* given by Kain (1979). She summarized information on the taxonomy and distribution, life history, structure, physiology, and ecology, much of which is relevant to the future mariculture and resource management of this plant.

Macrocystis

Macrocystis is one of the most important natural resources on the Pacific coast of North America, for it is both a major source of alginic acid and a significant component of the nearshore kelp bed community. In addition to North's (1971) extensive monograph on the plant, several recent papers dealing with the growth (Neushul et al. 1972; North 1972a; Coon 1974; Coon and Wheeler 1976; Neushul et al. 1976; Jackson 1977c; Neushul 1977 In press; Neushul et al. 1977; Lobban 1978a, c; Coon 1981), reproduction (Chi and Neushul 1972; Gherardini and North 1972; Neushul 1974, 1977; Sanbonsuga and Neushul 1978, 1979, In press), ecology (Charters 1974; Harger et al. 1974; North 1974; Pace 1974; Rosenthal et al. 1974; Foster 1975a, c; Harger 1976, 1977; Pearse and Hines 1977a, b; Rhoades 1977; Devinny and Volse 1978; Lüning and Neushul 1978), physiology (Wheeler 1974, 1976; Lobban 1975, 1977, 1978b; Schmitz and Lobban 1976; Whyte and Englar 1976b, 1978; Fankboner and de Burgh 1977; Schmitz and Srivastava 1979a, b; Wheeler 1980a, b), and nutrient uptake (W. Wheeler 1976, 1977; Jackson 1977a, b; North and Wheeler 1977; P. Wheeler 1977, 1979) should be consulted, as they also contribute substantially to our understanding of the plant's biology, management, and potential mariculture.

The southern California kelp beds, *Macrocystis pyrifera*, have undergone a rapid deterioration since 1940, the kelp crop being at an all-time low in the early 1960's (North 1971, 1976; Branning 1976). An extensive study was conducted by North and his associates from 1956 to 1962 to determine the cause of this decline (North 1971). Their studies indicated that many former kelp areas had become dominated by populations of small purple urchins, *Strongylocentrotus purpuratus,* which grazed seaweeds and exhibited a preference for *M. pyrifera.* In addition, a decline in an important predator of the sea urchin, the sea otter, was documented (Leighton 1962; Leighton et al. 1966). In 1962, the Kelp Habitat Improvement Project was initiated (North 1972c, 1973) in order to control urchin populations and to restore the vanishing kelp beds. The first large-scale urchin control experiments at Point Loma, Calif., were very successful. However, similar experiments at other sites met with varying success. A number of factors influenced the outcome of a given urchin-control operation. For example, juvenile *M. pyrifera* plants did not appear in abundance unless a stand of adult plants occurred near the area cleared of urchins. Kelp spores can only propagate the species within a few hundred feet of an established stand (Anderson and North 1966, 1967). Eventually only the urchins close to adult *M. pyrifera* plants were removed, allowing juvenile plants to proliferate. Thus, urchin control was primarily initiated around the periphery of the beds, gradually permitting the colony to expand.

A detailed description of the *Macrocystis* cultivation programs, developed during the Kelp Habitat Improvement Project studies, was given by North (1972b, c, 1973, 1974, 1976, 1979b). He emphasized that a natural evolution of mariculture techniques occurred during their programs. Initially, transplant



Kelco's kelp-harvesting boats in a southern California kelp forest. Photograph by A. Mathieson.

techniques were attempted with large *Macrocystis* plants (North 1964), particularly in areas where the giant kelp had vanished completely. Such transplants were very laborious and often frustrating, for many plants did not survive. In some cases, the transplants were too small to achieve ecological stability, due to heavy urchin and fish grazing. North (1976, 1979b) summarized his transplanting techniques for macroscopic plants, including descriptions of the anchoring systems used, transporting procedures, and optimum plant size for viable transplants. He indicated that in one joint effort with Kelco Corporation (a kelp-harvesting company in San Diego, Calif.), approximately 20,000 juvenile kelp plants were transplanted and installed to repopulate one kelp bed in La Jolla.

Ultimately, mass culture techniques were developed which incorporated the use of microscopic sporophytes as seed for natural reforestation (North 1972b, 1974, 1976). One very successful technique used in the program involved the attachment of spores on strips of polyethelene film 8.5 m long, folded in pleats so as to fit in a refrigerated aquarium with a dense inoculum of spores. After the spores had settled on the film for several days and developed as gametophytes, the film was transferred to a sloping tray with a swiftly flowing seawater source. Juvenile sporophytes were produced after only 1-2 wk because of enhanced growth due to the vigorous water motion. The external surfaces of the sporophytes are sticky. Accordingly, sporophytes can be scraped off the polyethelene strips and immediately dispersed in the sea, or if necessary, held in culture prior to dispersal if aerated and kept in suspension. North (1973, 1976) estimated an average survival rate of 1/100,000 with the present techniques. Consequently culturing techniques were developed to produce billions of sporophytes very inexpensively. He emphasized that the seeding techniques should be economically feasible for use in the United States, with its high labor costs.

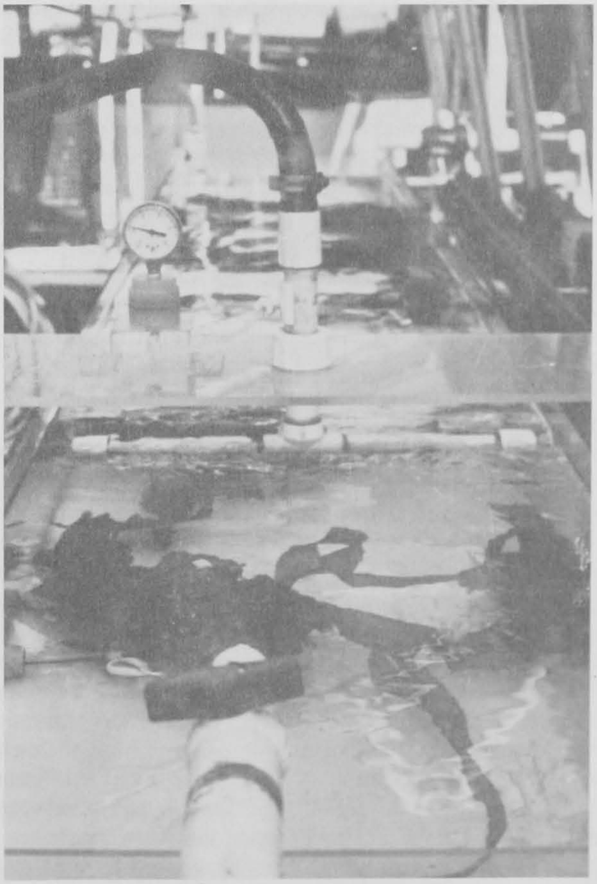
A number of factors were shown to influence the sporophyte dispersal operations, including seasonal variability of the seed, turbidity, sedimentation of rocky surfaces, and the age and amount of seed used (North 1976). The summer and fall were the poorest seasons for dispersing sporophytes. Unfortunately a considerable length of time (3-4 mo) was required before the success of a seeding experiment could be evaluated. An additional 6-9 mo must elapse before a juvenile kelp develops sufficient canopy to be visible.

A variety of other transplant techniques were attempted (North 1972b, 1973, 1976), including the growing of juvenile kelps on plastic (PVC) rings (¼-12 inches in diameter), which could be attached to a rocky bottom by epoxy resin. The method involved considerable labor so it was used only in special circumstances. For example, such techniques were employed to select for heat-tolerant strains. Such strains exist primarily in southerly regions. They showed good potential as transplants to areas where heated discharges were produced from coastal generating stations (North 1971), thus creating kelp beds with considerable immunity to thermal effects.

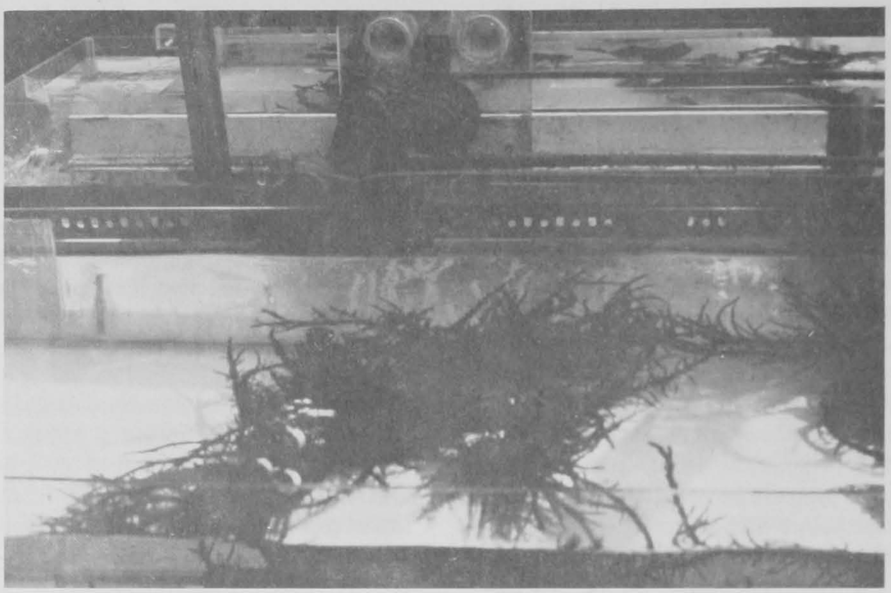
Devinny and Leventhal (1979) have also outlined several new methods for the mass culture and dispersal of juvenile *M. pyrifera* sporophytes. Basically, they have attempted to reduce costs for laboratory space, refrigeration, and water filtration, i.e., as compared to those previously developed by North (1976). In addition, diatom contamination was successfully controlled by washing cultures with turbulent seawater.

Other summaries of the kelp restoration program in southern California have been given (Wilson et al. 1977, 1979). The latter investigators suggested that although techniques have evolved to the point where it is possible to strongly influence competing vegetation and sea urchin populations, the ultimate success of a kelp restoration effort will be the identification, protection, and maintenance of a healthy environment.

As noted in the section dealing with Marine Biomass, there has been a rapid enhancement of techniques for the domestication of *M. pyrifera* (Neushul 1977, In press). Even so, there are several priority areas necessary for the mariculture of the giant kelp, including selective breeding of fast-growing strains, the storage of germ plasm of genetically identical progeny, and a detailed understanding of the recruitment and loss of juvenile stages. With respect to the first two priorities, a greenhouse and tank complex at the University of California at Santa Barbara have been perfected (Neushul 1977, In press; Neushul et al. 1977; Charters and Neushul 1979) where it is possible to raise kelp sporophytes to reproductive maturity and to make controlled crosses. With such a system various crosses can be initiated and their progeny raised to verify and evaluate the heritability of growth characteristics. Intergeneric hybrids have been established between *M. pyrifera* and *Nereocystis leutkeana* and between *M. pyrifera* and *Pelagophycus porra* (Sanbonsuga and Neushul 1978, 1979, In press). In each case the hybrids were very different from either parental types. Neushul (1977, In press) has further suggested that while the implications of intergeneric hybridization are not yet fully appreciated, the ability to produce these plants implies that *Macrocystis* itself, when known



Seaweed cultivation facility at University of California, Santa Barbara, showing a close-up of kelp cultivation in a long, rectangular tank with a "water-broom" aeration unit. Photograph by A. Mathieson.



Cultivation of *Eucheuma uncinatum* at University of California, Santa Barbara. Photograph by A. Mathieson.

varieties are crossed and the progeny grown, will be amenable to genetic manipulation. In addition, it has been possible, using appropriate culture conditions, to maintain *Macrocystis* gametophytes for prolonged periods in culture vials, thereby providing a means of stockpiling genetic strains as a gene bank.

Several fouling-plate studies have been conducted to evaluate the in situ growth, recruitment, and survival of seaweeds, including *M. pyrifera* (Harger et al. 1974; Neushul 1974, 1977; Harger 1976; Neushul et al. 1976). The fouling plates were horizontally positioned to concrete parking bumpers and attached on the ocean floor (−12 m); they were periodically taken from the sea, subjected to nondestructive microscopic survey in the laboratory, and then replaced in the ocean in order to quantify the growth and reproduction of seaweed populations. Neushul et al. (1972) made direct microscopic observations of algal spores under natural conditions by taking a microscope into the sea that was equipped for incident light and high magnification. The techniques of outplanting and microscopic examination in the laboratory and field should provide detailed understanding of the in situ biology of seaweeds such as *M. pyrifera*.

The interrelations of nutrients and productivity with *M. pyrifera* were determined by Jackson (1977a, b). The most limiting condition for *M. pyrifera* was the low concentration of dissolved nutrients, especially nitrogenous substances. Translocation of nitrogenous compounds by the kelps from depths where concentrations were higher compensated for this limitation.

Other accounts of nutrient uptake kinetics in *M. pyrifera* have also been summarized. Haines and Wheeler (1977) showed that *M. pyrifera* exhibited saturable kinetics for nitrate-N. Ammonia uptake showed saturable kinetics at concentrations below 22 μM; at higher concentrations the uptake increased linearly. Nitrate and ammonia were taken up simultaneously; the presence of one form had no effect on the other. According to W. Wheeler (1976, 1977), the photosynthetic rates of *Macrocystis* increased in situ as the rate of water flow increased from 0 to 6 cm/s. The development of a turbulent boundary layer adjacent to the blade at such low water velocities was enhanced by the corrugate morphology of the blade. The uptake of nitrate-N, as well as ammonia and phosphate, varied with light intensity and nutrient concentration. P. Wheeler (1977) summarized further information on ammonia-N uptake rates in *M. pyrifera*.

The growth of *M. pyrifera* is limited by the availability of certain micronutrients (North 1977c). Renewal of nutrients other than nitrogen and phosphorous probably depends on runoff and local regeneration from decomposition processes. According to North, *M. pyrifera* increased its nitrogen content when transferred to nitrogen-enriched media, which suggested a storage function. Thus, fertilizing strategies should consider these characteristics, and certain classes of limiting micronutrients might best be dispersed continuously while others applied only as needed. North further emphasized that caution must be used when delineating the nutritional quality of seawater by inorganic nitrogen, for micronutrients may be limiting. That is, experiments have shown that growth rates of juvenile *Macrocystis* sporophytes in seawater are greatly stimulated by proper nutrient enrichment (North 1977a, b). Fertilizing programs should foster the production of commercial kelp farms (North and Wheeler 1977).

Further descriptions of the growth of *M. pyrifera* have been given by Jackson and North (1973), Bryce (1977), Flowers and Bryce (1977), Jackson (1977c, 1980), Neushul (1977, In press), and Hart et al. (1979) in the section dealing with Marine Biomass. A variety of biological, technical, and cultivation information is summarized by the above investigators, in order to evaluate the production potentials of methane from kelp biomass.

A Sea Grant project by J. Pearse at the University of California, Santa Cruz, evaluated the population dynamics and interactions within the giant kelp forests off the central California coast. One of the major differences between the central and southern California kelp beds, other than hydrographic variations, is the presence of sea otters in some of the central California forests (e.g., the Hopkin Marine Life Refuge) and their imminent establishment in others (e.g., Santa Cruz). Basically, Pearse and associates studied the productivity of the giant kelp (Towle and Pearse 1973), as well as the population dynamics of important invertebrate grazers and their predators (Pearse and Hines 1977a, b). A detailed description of the densities, sizes, and distribution of abalones and sea urchins, as well as the spatial distribution of grazing snails, was summarized (Lowry and Pearse 1973; Lowry et al. 1974). Pearse's studies have provided a unique opportunity to document changes in kelp bed communities (e.g., Santa Cruz) after the reestablishment of an important carnivore—the sea otter (Pearse and Hines 1977a). Such studies will ultimately provide the information needed for predictive manipulation of the complex interactions within kelp forests. For example, the giant kelp provides the major trophic base, particularly in the form of debris (drift) and detritus, for many animals within the kelp forest, including economically important species such as abalone and crabs.

The potential use of NASA-LANDSAT data to make annual evaluations of the sea otter-urchin-kelp relationship was outlined by Rhoades (1977). He suggested that an annual census of the kelp canopy in California could be prepared to evaluate the stability and resilience of all kelp beds from Point Sur to Diablo Canyon.

A variety of studies were recently initiated in British Columbia, Canada, in order to enhance the management of *M. integrifolia* (Druehl 1977, 1978, 1979; Druehl et al. 1977). The species is restricted to regions having little seasonal variation of temperature and salinity or sites where the lower salinities occur during the winter (Druehl 1978). A provision of substrata adequate for the giant kelp but inadequate for herbivorous invertebrates, such as urchins and turbon snails, allows the establishment of new beds. The distribution of photosynthetically fixed carbon, respiratory requirements, exuded dissolved carbon, and detritus were determined (Druehl 1978). As a result, the standing crop of *M. integrifolia* was circumscribed in terms of total biomass, pigments, carbon, nitrogen, and alginic acid. Major invertebrate and vertebrate inhabitants of the kelp beds have also been defined, as well as the food chains originating from *M. integrifolia* (Druehl et al. 1977). Druehl (1979) emphasized that an understanding of the total ecology of giant kelp beds in British Columbia was necessary for continued management of this valuable natural resource.

SELECTED MARICULTURE PROGRAMS

This section describes the growth and potential benefits of seaweed populations in three mariculture programs. That is, the mariculture of several economically important seaweeds is described at the artificial upwelling system in St. Croix, U.S. Virgin Islands, as well as in association with the Marine Biomass Program and several polyculture waste-recycling projects.

Artificial Upwelling Systems

The improvement of seaweed growth by supplying nutrient-rich deep water from an artificial upwelling system should be cited as a good technological application in mariculture. A detailed description of an artificial upwelling site at St. Croix, U.S. Virgin Islands, and its application to mariculture was summarized (Roels et al. 1970; Roels et al. 1971; Roels 1975; Sunderline et al. 1975; Sunderline 1976). Basically, nutrient-rich deep water (870 m) was pumped into ponds (45,000 liters) where phytoplankton were grown as food for filter-feeding shellfish. The deep water employed in the mariculture system was free of pollutants, parasites, diseases, and predators. In addition to the primary unialgal culture system described above, seaweed cultures were included as a final phase in the system (Haines 1975; Haines and Monahan 1976; Roels et al. 1976a, b; Haines and Wheeler 1977). In order to recover some of the nitrogen losses from the system and to reduce a potential environmental hazard, the carrageenan-producing red alga *Hypnea musciformis* was grown very successfully in the effluent from shellfish tanks. *Hypnea* grew five times faster in the shellfish tank effluent than in unaltered deep seawater and about three times faster than in surface seawater (Roels et al. 1976a). The seaweed grown in the effluent doubled its weight every 60 h (Haines 1975). The average ammonia-N utilized by the seaweed was 51%, varying between 41% in one study (Roels et al. 1976a) and 61% efficiency in another study (Roels et al. 1976b). Higher efficiency of ammonia-N utilization would be possible if a slower turnover volume were employed, i.e., <95/d. A variety of other details regarding the growth of *H. musciformis* in the artificial upwelling system at St. Croix (Haines 1975) were given in the section dealing with *Hypnea*.

Economic seaweeds were employed in the deep-water upwelling mariculture system, in order to reduce its costs (Roels et al. 1976a). For example, the potential yield of *H. musciformis* alone would be 165 tons dry wt/ha per yr; at $650/ton this would represent a yield of $107,250/ha per yr.

Marine Biomass

The Office of Technology Assessment of the U.S. Federal Government conducted a feasibility study, "Energy From Marine Biological Processes," at the request of the Senate Committee on Commerce (Committee on Commerce, Science, and Transportation 1980). The study, which was also referred to as the "Energy From Marine Biomass," addressed a variety of topics as follows: 1) The potentials for specific seaweeds as biomass producers; 2) the status of the technology of ocean farming; 3) the status of marine plant culture research; and 4) regulatory, environmental, and social impacts. In addition to the above investigation, several other studies have also evaluated the potentials of seaweeds for marine biomass production and/or the conversion of marine biomass to methane (Jackson and North 1973; Leese 1976; Bryce 1977; Flowers and Bryce 1977; Goldman and Ryther 1977; Krauss 1977; Mitsui et al. 1977; Neushul 1977, In press; Anonymous 1978c; Hruby 1978; Michanek 1978; North 1978, 1979b; Hart et al. 1979; Committee on Commerce, Science, and Transportation 1980; Doty In press b; Jackson 1980; Rao et al. 1980; Hanisak 1981). Some of the major conclusions of these investigations are given in the subsequent paragraphs of this section.

An extensive review of the problems and potentials of marine biomass production through seaweed aquaculture was given by Jackson (1980) and Jackson and North (1973). They emphasized the need for more basic physiological and ecological information in designing seaweed aquaculture systems, particularly modeling evaluations. For example, little is known about the interactions of high temperatures and low nutrient concentrations, two factors that could be separately controlled in an aquaculture facility. A simple model was presented which suggested that yields of the giant kelp, *Macrocystis pyrifera*, could be increased 50% by increasing water temperatures 10°C. Observations about the size and type of culture facilities were also reviewed by Jackson and North (1973). They suggested that a closed system would require an exchange of water at least once per day, as slower exchange rates would lead to carbon depletion by seaweeds and unwanted phytoplankton accumulations.

Carbon concentrations can be regulated by bubbling carbon dioxide through the system, but it would be prohibitively expensive. Oceanic culture facilities would have to be 1 km or more in length, if the nutrients were to be efficiently used by the desired seaweed. However, if an oceanic system becomes too large, its flushing requirements would be similar to those of a closed system.

Additional information regarding the selection of the giant kelp, *M. pyrifera,* for possible cultivation on offshore marine farms has been summarized (Jackson and North 1973). The major advantages of *M. pyrifera,* as abstracted from Flowers and Bryce (1977), are as follows: 1) The giant kelp is easily cultured and has a relatively simple life cycle; 2) *M. pyrifera* is sufficiently tough to resist rough water conditions and harvesting stresses; 3) the size of the adult plant is substantial, approximately 60 m, and it requires a minimum of supporting structure for its cultivation; 4) *M. pyrifera* makes maximum utilization of sunlight at the surface and is therefore relatively efficient at capturing solar energy; 5) the morphology of the giant kelp allows a portion, at the surface, to be harvested, leaving the remainder to replace lost tissue, thus replanting after harvest is not required; 6) the flotation mechanism of *M. pryifera* facilitates mechanical harvesting. Three critical considerations involved in cultivation of *M. pyrifera* are growth substrata, nutrient supply, and harvesting.

The Energy From Marine Biomass program has as its overall goal the determination of the technical and economic feasibility of a commercial-sized system for the production of methane from kelp biomass (Anonymous 1977c; Flowers and Bryce 1977). *Macrocystis* could be cultivated on artificial substrata in the open ocean and harvested and converted by biological or physical/chemical processes into substitute natural gas. Residual by-products of commercial value would be separated, further processed, and used for feed and fertilizer.

A quarter-acre module (QAM) marine farm has been designed to demonstrate the feasibility of growing and harvesting giant kelp in the open sea (Flowers and Bryce 1977). The marine farm would be moored in a minimum of 500 ft of water, approximately 5 mi offshore from Corona Del Mar, Calif. A substratum structure, consisting of a tension grid system, was selected for the marine farm. This system is a netlike unit having discrete, flexible cable members which are capable of supporting loads by axial tension. Flowers and Bryce summarized two general approaches for the conversion of *Macrocystis* to methane: Anaerobic digestion and hydrogasification. Since anaerobic techniques are fairly well defined, while processes for hydrogasification of biomass are just now being investigated, the program emphasis is placed on biological conversion. Further details regarding methane generation and the different phases of the Energy From Marine Biomass program are summarized. Prelimianary approximations indicated that the costs of methane from *Macrocystis* biomass would be in the same range as gas produced by coal gasification.

The domestication of *M. pyrifera* as a marine plant biomass producer was discussed by Neushul (1977, In press). He emphasized that preliminary research in the use of seaweeds as collectors of energy is underway (Jackson and North 1973), and with improved techniques, progress in domestication will be rapid. Of particular importance will be the long-term storage of germ plasm or single-cell isolates (gametophytes) of genetically identical progeny, similar to that described by Saga et al. (1978) for clones of single isolated cells of *Laminaria.* A number of other problems exist, including the necessity to improve the methods for seeding *M. pyrifera* on natural substrata in the sea. North (1976) has already made considerable progress in this area. An evaluation of the recruitment and loss of juvenile stages is an important consideration in future management and cultivation. Thus, Neushul (1977, In press) suggested that the experimental manipulation of fouling-plate populations of *M. pyrifera,* as well as other plants, would allow identification and eventual control of the "environmental turnstiles" postulated by North to contribute to the high mortality of young sporophytes in the sea.

A description of the research and development program to assess the economic feasibility of methane production from *M. pyrifera* was summarized by Bryce (1977). Pilot plant evaluations were given in a variety of areas: 1) Controlled cultivation in the open ocean; 2) pretreatment processing of raw material to enhance anaerobic digestibility; 3) selection of specific anaerobic microorganisms for kelp degradation; 4) optimization of the anaerobic digestion process for production of commercial quantities of methane gas; and 5) development of a system model for economic and technical evaluation of the marine farm concept.

A fermentation process for preparing methane from *M. pyrifera* was described (Hart et al. 1979), which reduced the inhibitory or toxic levels of salts, reduced water content, and increased bulk density. Pretreatment, in the presence of $CaCl_2$, was followed by compression to remove 75% of the moisture and 70% of the ash initially present, while retaining 70% of the volatile solids for fermentation.

The potentials of algae for entrapping solar energy via photosynthesis were summarized by Doty (In press b). He suggested that the photosynthetic entrapment potential was only difficult because of the scale required to obtain the enormous amounts of energy needed. Oswald and Benemann (1977) have suggested that the utilization of all the sewage waste in the United States as fertilizer would provide <1% of the U.S. energy needs. To meet these needs (Hall 1977) some 3.89×166 km^2 of efficient algal farms would be required. Accordingly, Doty (In press b) suggested that considerable phycological manpower would be necessary to meet the worldwide energy needs of the future.

A variety of other information on marine biomass was summarized at a recent conference entitled "The Economics and Engineering of Large-Scale Algae Biomass Systems," held at the Massachusetts Institute of Technology during January 1978. The conference reviewed the state of the art on various marine biomass systems (Anonymous 1978b). A synopsis of the workshop on fuels from marine biomass pointed out that 1) there was potential error in extrapolating today's small systems to the projected 100 mi^2 farms because of the relatively primitive state of the art in mass culture of algae; 2) the designing, building, and operating of a large algal biomass system solely for the energy product would be prohibitively expensive based on current knowledge of mass algal culture and extrapolations from this knowledge; also, such a system would provoke considerable environmental concern, because of competing uses for land and water; 3) for very large systems, providing the required nutrients would be the major engineering and cost problem; 4) basic research in genetic engineering would be needed to obtain additional valuable end products, such as feedstocks and protein, in addition to energy, as economic justification of mass culture; 5) small, 1-mi^2 systems using sewage sludge as nutrients may merit further study; 6) the advantages of disposing of undesirable sewage sludge may, in site-specific cases, make energy production commercially viable. An opportunity brief summarizing many of the above described economic and engineering considerations associated with algal biomass energy systems was recently published (Anonymous 1978c).

Polyculture

Several recent experiments involving the growth of unattached economic seaweeds have been conducted in the outdoor mass culture facilities (tanks, raceways, and ponds) of the Environmental Systems Laboratory of Woods Hole, Mass., and of the Harbor Branch Laboratories in Fort Pierce, Fla. (Ryther et al. 1972; Anonymous 1973a; Fralick 1974; Goldman, Tenore, Ryther, and Corwin 1974; Goldman et al. 1974; Prince 1974; Ryther 1975, 1976, 1977; Ryther et al. 1975; DeBoer, D'Elia, and Lapointe 1976; DeBoer and Lapointe 1976; DeBoer, Lapointe, and D'Elia 1976; DeBoer, Ryther, and Lapointe 1976; D'Elia et al. 1976; Lapointe and DeBoer 1976; Lapointe et al. 1976; DeBoer et al. 1977; DeBoer and Ryther 1977; Nicotri 1977; Hanisak et al. 1979; Ryther et al. 1979; Stenberg 1979). Basically the studies incorporated seaweeds as well as phytoplankton in a waste-recycling marine polyculture system, which also included fish and shellfish (Ryther et al. 1972; Ryther 1975, 1976, 1977; DeBoer, Ryther, and Lapointe 1976; Fralick and Ryther 1976). Such a system has the potential of removing inorganic nutrients from treated sewage effluent, prior to its discharge into the environment, and recycling these nutrients into commercially valuable products. The basic concept of the system is to involve three or more cultured organisms. For example, unicellular marine algae can be grown in ponds with a continuous flow of mixtures of seawater and secondarily treated sewage effluent. The unicellular algae are then fed to shellfish in order to remove nutrients from the wastewater. Finally the effluent from the shellfish cultures passes through tanks containing seaweeds, which remove the dissolved nutrients regenerated by the animal cultures before the final effluent is discharged.

A preliminary account of the pilot plant waste-recycling marine aquaculture system at Woods Hole, Mass., was summarized by Ryther (1975, 1977). Successful cultures of unicellular algae and seaweeds were sustained for several months with only minor problems. Algal yields and nitrogen-removal capacity varied seasonally by threefold to fourfold and appeared to be primarily controlled by solar radiation. The combined unicellular algae-shellfish-seaweed system was capable of completely removing nitrogen from wastewater effluent within an area of 48 acres. Ryther estimated an annual production of 183 tons of oyster meat (38,000 bu of whole oysters), 3,350 tons (wet weight) of seaweeds, and undetermined quantities of flounder and/or lobsters per treated effluent of 10,000 people. The seaweed system alone was capable of complete nitrogen removal in an area of 60 acres with an annual production of 16,300 tons wet weight. The above figures were for year-round operations such as would be possible in tropical to semitropical climates. Operation of the system in temperate climates would be possible within the same areas but only on a seasonal basis (approximately 6 mo), with one-half the above yields.

The removal efficiencies (i.e., stripping potentials) and algal bioassay procedures employed for inorganic nitrogen removal in a combined tertiary treatment-marine aquaculture system at the Environmental Systems Laboratory have been described (Goldman, Tenore, Ryther, and Corwin 1974; Goldman, Tenore, and Stanley 1974). A prototype facility consisting of growth containers for marine algae, oysters, and seaweed, joined in a series, was fed secondarily treated wastewater diluted 1:4 with seawater for 11 wk. During this time, 95% of the influent inorganic nitrogen was removed by algal assimilation. The oysters in turn removed 85% of the algae, but regenerated 16-18% of the original nitrogen contents of the algal cells as soluble ammonia. All of the regenerated nitrogen was removed by the seaweed system so that the total inorganic nitrogen removal efficiency was 95%. Phosphorus removal, on the other hand, was less efficient, as only 45-60% was removed. The algal bioassay studies (Goldman, Tenore, and Stanley 1974) demonstrated that nitrogen removal was necessary to prevent increased algal growth of coastal marine waters receiving

Seaweed culture tanks at the Environmental Systems Laboratory, Woods Hole Oceanographic Institute, Woods Hole, Mass. Photograph by D. Cheney.

wastewater discharges. Assays of effluent from the seaweed system showed that the removal of regenerated nitrogen lowered the potential growth to that of natural seawater.

The outdoor mass culture of *Gracilaria* and *Hypnea musciformis* in the third stage of a nutrient removal-aquaculture system at Fort Pierce, Fla., was reported by Lapointe et al. (1976). Mixtures of secondary-treated wastewater and seawater constituted the initial nutrient source to the system, which included microscopic algae and oysters. The *Hypnea* cultures could not be maintained during the summer when tank temperatures reached 30 °C, but *Gracilaria* grew during the entire year. On the basis of periodic harvesting, yields were kept consistently between 12 and 17 g dry wt/m² per d for both species. Such yields were as high as those achieved for mass cultures of microscopic marine algae and fast-growing commercial crops such as sugar and rice.

The nutrient assimilation and growth of juvenile *Chondrus crispus* plants in mixtures of seawater and secondary sewage treatment effluents were summarized by Prince (1974). Overall, the growth of *C. crispus* was similar whether nitrogen was provided by ammonia-N or nitrate-N. Optimal growth of juvenile *C. crispus* plants occurred in a sewage-seawater mixture upon addition of trace elements. The plant's growth in a 10% sewage-seawater mixture was not inhibited, probably because the ammonium levels were approximately one-half those of typical sewage (compare Dunstan and Menzel 1971).

Three additional nutritional studies of red algae (DeBoer et al. 1978; D'Elia and DeBoer 1978; DeBoer 1979) have been summarized, based upon culture experiments at the Environmental Systems Laboratory of the Woods Hold Oceanographic Institution. DeBoer (1979) and DeBoer et al. (1978) evaluated the growth rates of *G. tikvahiae* (designated as *G. foliifera*) and *Neoagardhiella baileyi* as a function of nitrogen source and concentration. Growth rates appeared to follow saturation-type nutrient uptake kinetics for plants receiving ammonium, nitrate, urea, or sewage effluent enrichments. Ammonium enrichment produced higher growth rates than nitrate or sewage enrichment. The lowest growth rates occurred in unenriched seawater or urea. Half-saturation constants (K) for growth were approximately 0.2-0.4 μM N for all nitrogen enrichments examined. D'Elia and DeBoer (1978) evaluated the kinetics of ammonium and nitrate uptake with the same two red algae. Nitrate-N was taken up in a rate-saturating fashion described by the Michaelis-Menten equation. Ammonium-N uptake was multicomponent, with a saturable component being accompanied by a high K component showing no evidence of saturation. Nitrogen-starved plants showed higher transient rates of ammonium-N uptake at a given concentration than nonstarved plants. Ammonium-N was preferred over nitrate-N, even with plants preconditioned in nitrate-N as a sole nitrogen source. Nitrate-N uptake was suppressed at 5 μM (NH_4^+), but simultaneous uptake occurred at unsuppressed rates at lower concentrations. The potentials for nitrogen accumulation were greater via NH_4^+ than NO_3^- uptake.

The production yields of *G. tikvahiae* and *N. baileyi,* which were grown in a waste-recycling raceway system at Woods Hole, were summarized by DeBoer and Ryther (1977). As noted in an earlier section dealing with *Gracilaria,* the plant is an important agarophyte. *Neoagardhiella baileyi* contains iota carrageenan (DeBoer, D'Elia, and Lapointe 1976; DeBoer, Ryther, and Lapointe 1976), and although not yet harvested, it has potential commercial value. *Noeagardhiella baileyi* had very high rates of production during both spring (22-41 g dry wt/m² per d) summer (20-36 g dry wt/m² per d). The production rates o *tikvahiae* were variable, increasing from 4 g dry wt/m² per April to 43 g dry wt/m² per d in early June and then decre again during late summer to 7-18 g dry wt/m² per d. The duction rates of both species declined during fall and winter. By mid-December the production rate for *G. tikv* had fallen to zero, and the plants deteriorated; *N. baile* mained viable with a production rate of 6 g dry wt/m² p Overall the gross seasonal changes in production were corre with water temperature and incident solar radiation. How from 1 June to 1 October, when water temperatures and radiation were presumably optimal for seaweed gr (DeBoer, Lapointe, and D'Elia 1976), production showed correlation with these variable. Low production rates were probably due to the high seaweed densities in the raceway high as 12.3 and 10.2 kg fresh wt/m² for *N. baileyi* an *tikvahiae,* respectively).

The mean annual dry weight production for *N. baileyi* w g/m² per d (63 t/ha per yr) versus 9 g/m² per d (33 t/ha p for *G. tikvahiae* (DeBoer et al. 1977). These rates may be hi than those of a commercial enterprise because the raceways maintained at elevated temperatures for approximately 6 m the year. Annual production rates based on a 5.5-mo gro season when the raceways were not heated (8 May-20 Oct 1975) were 46 t/ha per yr and 28 t/ha per yr for *N. baileyi* *G. tikvahiae,* respectively. Overall, the yields obtained in study were similar to those reported for *Gracilaria* and *Hy* *musciformis* in Florida (Lapointe and DeBoer 1976). In small-scale, short-duration experiments (Haines 1975; De Lapointe, and D'Elia 1976; Neish 1976a, Waaland 1976, production rates of cultured seaweeds were recorded as two to threefold higher; however, these yields were not substant by large-scale, long-term production studies.

Several operational considerations for improved sea mariculture have been reviewed (DeBoer and Ryther 1977). consideration is the maintenance of seaweeds biomass at sities that provide maximum yield per unit area. For exam the density of *G. tikvahiae* and *N. baileyi* should be mainta at 1,800-2,800 g/m² during the winter, 2,800-4,500 g/m² d late spring and summer, and at intermediate densities durin remainder of the year. The optimum depth of the culture sy is another variable that is best determined empirically. perience with various types of culture enclosures and mod circulation showed that the optimum depth for the two spec 60-110 cm. Another critical operating parameter is the co tration of nutrients necessary to sustain a maximum gr rate. For example, ammonia-N was limiting below 0.8 μ another study, DeBoer, Lapointe, and D'Elia (1976) deter that the half-saturation constants for growth of *G. tikv* and *N. baileyi* were approximately 0.5 μm ammonia- nitrate-N. Since such constants were very low when compar phytoplankton, they indicated that seaweeds utilized ver concentrations of inorganic nitrogen. Further informatio the nutrient uptake kinetics of *N. baileyi* was summariz D'Elia, DeBoer, and Ryther (1976).

The impact of grazing by herbivorous crustaceans *phithoe* and *Idotea*) on mass cultures of *G. tikvahiae* ar *baileyi* raised in the Environmental System Laboratory (W Hole) was summarized by Nicotri (1977). Grazing rates estimated in the laboratory and approximate crustacean sities determined in the raceways. Grazing losses were gen very small in comparison to algal productivity, but they significant when crustacean populations were abundant and algal productivity was low.

The effects of sewage effluent on the growth of *Ulva lactuca* in a recirculating seawater system were reported by Guist and Humm (1976). Plants in 5, 10, and 15% effluent grew progressively faster than controls; all plants grown in effluent exhibited higher nitrogen content than controls. In all experiments, ammonia was rapidly reduced to a low level or zero, while phosphate was not taken up more rapidly than it was regenerated. Asare (1980) has also evaluated the possibilities of utilizing animal wastes as a nitrogen source for the red algae *Gracilaria tikvahiae* and *Neoagardhiella baileyi*. Both sheep and rabbit wastes were good nutrient sources for these economically important seaweeds.

The nitrate uptake of *Enteromorpha intestinalis* and *E. linza* was evaluated to determine their potential usefulness in closed polyculture and tertiary sewage treatment systems (Harlin 1978). Both species exhibited a rapid uptake of nitrate, particularly at high temperatures (15 °C) and illumination (ca. 1,800 $\mu W/cm^2$ per s). The optimal nitrate uptake for *Enteromorpha* spp. differs from that of *Chondrus crispus,* a red alga it frequently contaminates in culture (Enright 1979). Thus, Harlin (1978) suggested that varying nutrient uptake efficiencies should be considered when designing feeding strategies for aquaculture systems. For example, nitrate-rich seawater might be pulsed through tanks of *Enteromorpha* spp. during the day, while night feeding of *C. crispus* culture tanks would capitalize upon the differences in nitrate uptake strategies between the two algae, thereby minimizing uptake by the nuisance seaweed.

A recent Sea Grant study at the University of Rhode Island (Harlin 1976; Harlin et al. 1979) has evaluated the potential mariculture of macroalgae in silo-type fish culture facilities. The optimal growth of *G. tikvahiae* in large tanks containing salmonid fish was described.[11] The seaweeds were used to remove nitrogenous wastes from the culture systems and to produce a commercially valuable polysaccharide (agar) as a byproduct to an existing industry (Meade 1976). The plant appeared to preferentially remove ammonia-N, as nitrate-N was only removed after ammonia disappeared. In addition, ammonia-N was only removed when there was new growth on the thallus, i.e., when new internal pools of ammonia-N were established. The uptake rate (K_m) of ammonia-N was light dependent and influenced by pretreatment conditions. Further information on the ammonia uptake characteristics of *G. tikvahiae* with respect to light intensity, temperature, and ammonia-N pretreatment levels were summarized by Ventura and Harlin (1976) (also see footnote 11).

The articles by Jokela and Jokela (1977) and Woodwell (1977) on water reclamation and aquatic systems should also be noted, as they are relevant to the topic of polyculture. Jokela and Jokela suggested that aquatic ecological principles could provide economical methods for the development of wastewater reclamation programs suitable for wetland management and/or aquaculture. Woodwell stated that the ability of terrestrial and aquatic systems to absorb nutrients and toxins from sewage offered new promises for waste management and pollution control. He emphasized that the protection of man from his own wastes and the preservation of such essential resources as water and nutrient elements required the development of systems for recirculating these resources in usable forms.

[11]The plants studied by Harlin and associates were designated as *G. verrucosa,* but they should probably be designated as *G. tikvahiae* (Chapman et al. 1977; McLachlan 1979).

SUMMARY AND RECOMMENDATIONS

1. A variety of technical, biological, and sociological problems associated with seaweed cultivation are reviewed.
2. A synopsis of the cultivation as well as the biology, ecology, and resource management of the economically important seaweeds in North America, the United States' possessions, the Trust Territories of the Pacific Islands, and the Philippines is given. Included in this account are descriptions of *Chondrus crispus, Eucheuma, Gelidium, Gigartina, Gracilaria, Hypnea, Iridaea, Palmaria palmata, Porphyra, Pterocladia, Laminaria,* and *Macrocystis.*
3. The *Eucheuma* cultivation programs in the Indo-Pacific are currently producing large quantities of iota carrageenan, and they are very successful commercially. Most of the other cultivation programs are in a "pilot" stage and have not reached full commercial production. The net cultivation programs of *Iridaea* being developed in Puget Sound, Wash., show excellent potential for generating a large-scale domestic source of iota carrageenan. The mariculture of the giant kelp, *Macrocystis pyrifera,* has reached a very sophisticated level with many applications.
4. The needs for efficient energy production (i.e., methane) have been a major stimulus for seaweed cultivation programs dealing with "Energy From Marine Biomass." The kelps, including *Laminaria* and *Macrocystis,* have excellent potentials as biomass sources. A variety of other seaweeds should also be assessed, including plants such as *Sargassum muticum.*
5. The polyculture and artificial upwelling systems have considerable merits for seaweed cultivation, as they have many economic benefits which can reduce the total costs of their cultivation programs.
6. In contrast to most Asiatic seaweed mariculture activities, the majority of the North American programs have been directed towards intensive raceway-tank cultivation programs. The latter systems have a relatively high capital cost. Thus, their ultimate success will depend upon further technological-biological improvements and/or the enhancement of several economic benefits (e.g., nutrient removal) which can reduce their total costs.
7. A coordinated knowledge of plant growth, reproduction, physiology, biochemistry, phycocolloid ecology, and population genetics (compare Wilkins 1981) is fundamental for the future husbandry, management, and conservation of economic seaweeds. Simultaneously, a detailed consideration of engineering and economic principles is critically important for the enhanced and sustained utilization-mariculture of economic seaweeds.
8. Several recommendations are made for the advancement of seaweed mariculture programs in North America:
   a) An enhancement of industrial research support for academic marine phycologists-mariculturists should be initiated.
   b) A continuity, as well as an enchancement of research support by the United States and the Canadian Governments is fundamental for the successful completion of several cottage cultivation programs of economic seaweeds.

c) There is a continuing need for the support and training of talented phycological manpower (students) who will be the seaweed farmers of the future.

d) An enchancement of scientific information (i.e., exchanges) with Asiatic phycologists-aquaculturists is similarly important in the development of current and future seaweed mariculture programs.

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