EXPERIENTIA

Vol. 35 - Fasc. 4 Pag. 429-570 15.4.1979

GENERALIA

Pathology of seaweeds: Current status and future prospects

Introduction*

by John H. Andrews

Department of Plant Pathology, University of Wisconsin-Madison (Wisconsin 53706, USA)

The importance of seaweeds as an integral component of coastal ecosystems has long been acknowledged by biologists. Their economic significance, however, other than in areas of the world where they provide food, has only been emphasized relatively recently. This realization is largely due to rapidly expanding pharmaceutical, cosmetic, and processed food industries, wherein algal products have figured prominently, together with the prospective use of seaweeds in tertiary sewage treatment or as a supplementary energy source. Within the past decade, seaweed mariculture, both directly in the ocean and in raceways on land, has been established as a realistic venture. Overshadowing these trends are the exploitation of continental shelves for natural resources or waste disposal purposes, and accelerated tanker traffic with attendant risks of pollution damage to plants and animals.

These developments pose two critical questions: The first concerns the nature, severity and prospective control of pest problems generally, and diseases in particular, which can be anticipated in seaweed mariculture. The second question, more fundamental, difficult, and beyond the scope of this discussion, is how best to develop the coastal ecosystem so that it can be utilized without undue damage.

The following contributions represent the proceedings of a symposium held on August 17, 1978, at the 3rd International Congress of Plant Pathology in Munich. This marks the first time that plant pathologists and marine biologists have jointly addressed the issue of seaweed pathology. We present an overview of the ecological and economic importance of seaweeds (contributions by Vadas and Wheeler et al.), followed by a consideration of abiotic causal agents as exemplified by thermal effluents (Vadas), of representative pathogens (fungi, Kohlmeyer; viruses, Dodds), and of host-parasite interactions (red rot of *Porphyra* discussed by Kazama). These aspects are then integrated by a discussion (North) of biotic and abiotic problems from the perspective of a particular host, *Macrocystis*. The text is concluded with a comparison (Andrews) of terrestrial and marine pathology and recommendations for disease control. Throughout this article, disease is considered to be the abnormal, injurious and continuous interference with physiological activities of the host. Apart from the obvious esthetic and ecological implications, disease usually, but not invariably, results in loss of economic value.

---

* Contribution from the College of Agricultural and Life Sciences.

Seaweeds: An overview; ecological and economic importance

by Robert L. Vadas

Department of Botany and Plant Pathology and Departments of Oceanography and Zoology, University of Maine, Orono (Maine 04469, USA)

Seaweeds are heterogeneous groups of attached (benthic) photosynthetic plants characterized more by the lack of structures identifying them with higher green plants than by their commonality of character. Marine higher plants such as seagrasses and salt marsh grasses often are included with seaweeds because of similarities in habitat and function in nearshore marine ecosystems. Although the algae number only about 30,000 species (ca. 10% of the plant kingdom, Dawson[1]), they may well be the most diverse group of organisms alive today. Diversity exists not only in morphological and reproductive features (typical of higher green plants), but also in complex life history phenomena and in exotic physiological and biochemical properties. Thus, it is perhaps not surprising that in most classifications algae constitute one-third of the divisions within the plant kingdom (Bold[2]).

This paper provides an overview of seaweed ecology and relates algal diversity to ecologic and economic considerations. An attempt is made to provide some common ground by which algal diseases and mortality can be evaluated. Despite the apparent simplicity of the algal thallus, complex biochemical and life-history patterns and the nature of the marine environment will necessitate an imaginative approach to pathological research. Pathologists need to become familiar with the ecological problems encountered by seaweeds and with the evolutionary forces that have shaped the algal thallus to properly understand growth and mortality processes.

The medium surrounding algae was probably the major force involved in the early evolution of seaweeds. The 4 major benthic marine phyla (Cyanophyta, Chlorophyta, Phaeophyta and Rhodophyta) were all present by the Cambrian period (Schopf[3]) suggesting that basic biochemical differences such as pigments had evolved as primary features. These pigments, especially the bileproteins, carotenoids and xanthophylls, are adaptive to the differing light intensities and spectra of the sea. Photosynthetic action spectra show these pigments to be most active in the blue and green wavelengths, characteristic of the light spectra of subsurface waters (Haxo and Blinks[4]).

Subsequent adaptations to the marine environment should be considered secondary or tertiary. Morphological and physiological adaptations involving the uptake of nutrients by complex thalli, the attachment of spores to substrates in rigorous environments and the osmotic regulation of intertidal or estuarine species are examples of secondary adaptations. Tertiary adaptations probably evolved primarily as a result of biological interactions and involve mechanisms that reduce or avoid competition, provide defense against pathogens, epiphytes or herbivores and promote symbiotic associations. Obviously, these 3 adaptive levels are not mutually exclusive. It is likely that secondary and tertiary adaptations reciprocally coevolved. A case in point is illustrated by unicellular marine algae, in the excellent theoretical paper by Munk and Riley[5] in which phytoplankton size relationships were related to nutrient uptake, floatation and zooplankton grazing. They theorized that nutrient uptake and buoyancy in the water column would be maximized in a 20-nm spherical phytoplankton cell. However, they noted that the average cell size in several phytoplankton floras was considerably larger than 20 nm suggesting that the larger cell size reduced the effectiveness of grazers thereby conferring selective value on larger species.

The problem of extracting nutrients from seawater can be acute for seaweeds, especially in nutrient-deficient waters. Seawater is essentially a nutrient broth with varying mineral, organic and salt concentrations. Frequently, growth is limited by reduced nutrient levels, especially nitrogen (Ryther and Dunstan[6]). Accumulation of various ions, e.g. iodide, by seaweeds is well known. Similarly, the capacity for nutrient storage exists and potentially minimizes seasonal nutrient deficiencies (Chapman et al.[7]). Nutrient uptake in seaweeds is controlled primarily by the shape and thickness of thalli, boundary layer phenomena and flow rates (Munk and Riley[5]). Photosynthetic capacities apparently are also related directly to transfer processes across thalli (Wheeler[8]) and may be analogous to problems of gas exchange across leaves. According to the predictions of Munk and Riley[5], the large kelps could develop only in areas of extreme water movement and high nutrient levels such as upwelling regions, high energy coastlines (e.g. western continental shores), and rapids or constricted channels. Geographic and local distribution patterns of large kelps support these views (Chapman[9]).

The size and perhaps shape of thalli reflect problems of growth and mortality. Seaweeds on high energy shores experience high breakage and mortality. For example, on exposed coasts in Maine yearly survivorship of apical tips and whole plants for the economically important brown alga, *Ascophyllum nodosum* is respectively only 49% and 10% (Vadas[10]). Additional problems for seaweeds like *A. nodosum* which have thalli exposed on ebb tides are the rapid and extreme changes in light intensity, temperature, desiccation and osmotic concentration (Biebl[11]). These stresses imposed on intertidal seaweeds over a few vertical meters are analogous to stresses imposed on higher plants over vertical elevations of thousands of meters. The compounding of these variables and the reduced time in which they occur preempts the existence of normal homeostatic regulation in intertidal species. These algae concentrate salt and lose, leak or shed considerable quantities of water and mucilage when emersed (Kroes[12]). Intertidal species have wide tolerances to stresses and generally are widely distributed. Conversely, subtidal algae exist in relatively benign physical environments and have greatly reduced tolerance and distributional limits.

The loss or secretion of considerable quantities of organic matter as extracellular metabolites or ectocrines (Lucas[13]) are common and thought to function as antibiotics or allelopathic chemicals (Müller[14]) to reduce or eliminate pathogens and competitors. As much as 40% of the photosynthate of seaweeds is excreted as dissolved organic matter directly into seawater (Khailov and Burlakova[15]). Sieburth and Jensen[16] showed that the common intertidal rockweed, *Fucus vesiculosus*, produced ca. 1 g of phenol and 2 g of carbohydrate per m^2 per day. These phenolic materials precipitated protein and were toxic to fish larvae. These exudates affect the chemistry and ecology of nearshore waters. There are no comparable photosynthetic losses in higher plants with the exception of volatile compounds and nectar production, both of which have ecological or evolutionary significance.

Intercalary growth in many seaweeds, especially alginate-producing kelps, creates another major source of organic matter in coastal waters. Kelps, like grasses, grow as 'conveyor belts' but, unlike their terrestrial counterparts, break and erode at the older quiescent tips.

Seaweeds also produce exotic internal chemicals, many of which have biological activity similar to that described for higher plants. Antibiotic activity against various bacteria is well known (Pratt et al.[17]). Considerable variability, however, exists seasonally and between closely related species. Sieburth[18] provided an ecological perspective for the role of algal antibiotics in marine algal-algal and algal-animal interactions. His thesis supports the arguments used by Fraenkel[19] a decade earlier in discussing the function of secondary plant substances in higher plants.

Space frequently is a major factor limiting the growth and distribution of seaweeds. As a result, epiphytism and epizoism by both algae and invertebrates are common in marine communities. Antifouling or antibiotic phenols and tannins are produced by many of the larger and more long-lived algae, (e.g. Conover and Sieburth[20]). Generally, antibiotic activity (concentrated near the growing tips) and epiphytism are inversely related. Several halogens, important biochemically to red algae, also appear to have biological activity (Fenical[21]). Halogenated ketones in *Aspargopsis* are especially toxic to bacteria. *Caulerpa*, a tropical green alga, contains caulerpicin which produces a toxic effect on humans similar to ciguatera poisoning (Doty and Santos[22]).

In addition to secretions, seaweeds produce numerous gums and mucilaginous compounds within their cell walls including several of major economic value. Sulfated galactans such as agar and carrageenan (used as gelling agents) are produced as amorphous matrices in the cell walls of red algae. Agar is extracted from *Gelidium* and several other genera with fleshy-cartilaginous and moderately long-lived thalli. Carrageenan is produced by *Chondrus crispus*, *Gigartina* spp., and *Eucheuma* spp. Thalli of these and most hydrocolloid-producing red algae are similar to the agar producers. Also, most have remarkable regenerative powers, many are perennial and several reproduce only vegetatively (Boney[23]).
The cell walls of brown algae have a slimy alginic acid layer of economic significance. Most notable for their commercial value are the forests of giant kelp, *Macrocystis pyrifera* (North's contribution), in the upwelling areas of the Pacific coasts of North and South America. Several of the larger and perennial intertidal brown algae, e.g., *Ascophyllum* and *Fucus*, are also harvested for their alginates which are used as emulsifers or stabilizers. The interesting parallel in both the red and brown algae is the association of hydrocolloid production with fleshy-cartilaginous and long-lived thalli.

Secondary plant substances in seaweeds are also thought to have evolved in response to herbivores (e.g. Sieburth[18], Ogden[24]). Although there is little direct evidence of defensive activity by specific algal products against herbivores, there are several lines of evidence supporting such an interpretation: a) distinct food preferences exist in several grazers including sea urchins (Vadas[25]), mollusks (Lubchenco[26]), and fish (Ogden and Lobel[27]) which suggest that herbivores react to chemical signals; b) avoidance of particular algae by herbivores has been demonstrated in several preference studies (e.g. John and Pople[28]); c) many algal chemicals have antibacterial activity as noted above; d) many of the purported defensive compounds in algae are similar to defensive compounds in higher plants; e) chemical defenses are not limited to algae but appear to be general adaptations in many sessile marine organisms, especially in warmer seas. Soft corals, for example, appear to be protected by toxins produced by their symbiotic Zooxanthellae (Faulkner[29]).

Defense need not be limited to chemical activity. Certain structural and life history features may have evolved in response to grazing pressure as well as the aquatic medium. Neushul[30] suggested that the form and orientation of fronds and stipes of kelps in surge zones minimized boundary layer problems and breakage, and increased nutrient uptake. However, it is possible that some of the structural modifications may also reduce or eliminate browsing. In general, stipes of most kelps are preferred less than fronds suggesting that stipe morphology represents both biotic and hydrodynamic selective pressures. It is interesting in this context that Parker[31] found significant quantities of silica in the cell walls of several related kelps. Silica in higher plants has an abrasive effect on the mouth parts of mammals and reduces browsing (Whittaker[32]). Similarly, the incorporation of calcium carbonate into the thalli of red and green algae may be regarded as structural defense (Paine and Vadas[33]).

Diversity in algal life forms and life histories provides yet another means of evaluating the ecological environment and adaptations of seaweeds. There are 3 basic longevity patterns: ephemerals, annuals and perennials. Most algae occur in the first 2 categories, but most economically important species are perennials. Ephemeral species occur in all phyla, most environments, and employ an escape strategy in time and space (patchiness) (Vadas[25]). These algae have high growth rates, high reproductive capacities, relatively simple thalli and moderately high caloric values, suggesting that energy is shunted primarily into reproduction and dispersal (r-selection strategy, Pianka[34]) rather than into thallus development. Most are associated with stressed and unstable environments, early successional stages and are analogous to terrestrial 'weeds'.

Perennials represent the other extreme or K-selection. This strategy is best typified by most seaweeds of economic value. Growth rates and turnover times are slower than for 'weedy' species (Kanwisher[35]). Energy in these forms seems to be directed more into thallus structure (massive and differentiated) than reproduction (Vadas[25]). Calcification, silicification, production of antibiotics, etc. represent investments of energy in non-reproductive material and reinforce and solidify the K-selection mode. Vegetative reproduction often accompanies the perennial habit and permits growth (often in the absence of sexuality) in stressed environments (Dixon[36]).

Seaweeds with heteromorphic life histories may be under bimodal selection pressures with the 2 phases responding to different environmental constraints and evolving simultaneously toward opposing ends of the r and K selection continuum. Neushul[30] aptly described the hydrodynamic and life history problems facing kelps with heteromorphic life stages. Several red algae also have heteromorphic life stages, and may contain large upright thalli and small crust-like stages, e.g., *Petrocelis franciscana*, a crust, produces a *Gigartina* thallus (West[37]).

Although it is questionable whether or not biotic succession occurs in marine ecosystems (Connell and Slatyer[38]), the small, simple, and relatively fast-growing species precede the larger slower-growing forms. Despite this and the extremely high productivities and biomasses of nearshore marine ecosystems (Mann[39]), there is little permanence in seaweeds, with the exception of stipes, calcified or encrusted thalli, and basal perennating structures. Unlike terrestrial plants, fronds are continually being replaced and turnover times can be as short as 28 days for seagrasses (Zieman[40]) and 4-5 months for kelps (Mann[39]). Perhaps less energy is consumed with shorter turnover times since it appears that the longer a frond survives the more likely it is to contain structures and chemicals that have defensive functions and presumably cost more to produce. Similar developments occur in the leaves of higher plants (McKey[14]) and in terrestrial plant succession (Cates and Orians[42]). Lignin and wood seem to typify one extreme of structure and defense in higher plants. The absence of both in seaweeds is probably related to the fact that buoyancy, structure and nutrient uptake are provided by the water itself. However, the parallel development of tough, rubbery stipes (almost woody in *Pterygophora*) suggests that these seaweeds represent, in part, a compromise between nutrient uptake (expressed as frond thickness and rarely over a few mm), hydrodynamic stability (expressed as elasticity of stipes and fronds) and herbivore defense (expressed as unedible qualities).

Seaweeds have been discussed herein from a non-classical approach to encourage reflection, thought and research. For too long phycologists have avoided evolutionary speculation, despite the fact that algae have been evolving longer than any other group of plants. Seaweeds clearly have considerable economic potential (Wheeler's following contribution). As that potential is realized, problems affecting growth and mortality will be amplified. Discovering the accommodations that marine algae have made to their environment, therefore, will continue to be both a challenge and a requisite for understanding seaweed pathology. For despite its apparent simplicity, the algal thallus represents the product and constraints of a complex and continually evolving environment.

1 E.Y. Dawson, in: Marine Botany, p.371. Holt, Rinehart and Winston, New York 1966.
2 H.C. Bold, in: Morphology of Plants, 2nd edn, p.541. Harper and Row, New York 1967.
3 J.W. Schopf, Biol. Rev. *45*, 319 (1970).
4 F. Haxo and L. Blinks, J. gen. Physiol. *33*, 389 (1950).
5 W.H. Munk and G.A. Riley, J. mar. Res. *11*, 215 (1952).
6 J.H. Ryther and W.M. Dunstan, Science *171*, 1008 (1971).
7 A.R.O. Chapman, J.W. Markham and K. Luning, J. Phycol. *14*, 195 (1978).
8 N. Wheeler, J. Phycol. *13*, suppl., 72 (1977).
9 V.J. Chapman, in: Seaweeds and Their Uses, 2nd edn. p.304. Methuen and Co., London 1970.
10 R.L. Vadas, Maine Yankee Atomic Power Co., Environmental Studies, vol. 1, p.250, 3rd annual Report, 1971.
11 R. Biebl, in: Physiology and Biochemistry of Algae, p.799. Ed. R.A. Lewin. Academic Press, New York 1962.
12 H.W. Kroes, Botanica mar. *13*, 107 (1970).
13 C.E. Lucas, Biol. Rev. *22*, 270 (1947).
14 C.H. Müller, Vegetatio *18*, 348 (1968).
15 K.M. Khailov and Z.P. Burlakova, Limnol. Oceanogr. *14*, 521 (1969).
16 J.M. Sieburth and A. Jensen, J. exp. mar. Biol. Ecol. *3*, 290 (1969).
17 R. Pratt, H. Mautner, G.M. Gardner, Y. Sha and J. Dufrenoy, J. Am. pharm. Ass. *40*, 575 (1951).
18 J.M. Sieburth, in: Advances in Microbiology of the Sea, vol. 1, p.63. Ed. M.R. Droop and E.J.F. Wood. Academic Press; New York 1968.
19 G.S. Fraenkel, Science *129*, 1464 (1959).
20 J.T. Conover and J.M. Sieburth, Botanica mar. *6*, 147 (1964).
21 W. Fenical, J. Phycol. *11*, 245 (1975).
22 M.S. Doty and G. Aguilar-Santos, Nature *211*, 990 (1966).
23 A.D. Boney, Adv. mar. Biol. *3*, 105 (1965).
24 J.C. Ogden, Aquatic Bot. *2*, 103 (1976).
25 R.L. Vadas, Ecol. Monogr. *47*, 337 (1977).
26 J. Lubchenco, Am. Nat. *112*, 23 (1978).
27 J.C. Ogden and P.S. Lobel, Env. Biol. Fish. *3*, 49 (1978).

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

Marine agriculture: Progress and problems

by W.N. Wheeler*, M. Neushul and J.W. Woessner

Marine Sciences Institute, University of California, Santa Barbara (California 93106, USA)

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

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

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

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

Concomitant with increase in size of marine farms in both Japan and China came problems in providing inorganic nutrition and in combating diseases. Devel-