

during winter, markedly increased the temperature differential and stress on intertidal algae in Maine (Vadas et al.¹³). Biological interactions are also altered directly or indirectly. Grazing and encrustation of the fronds of *Macrocystis* increased more rapidly than growth at higher temperatures (North et al.²⁹). Black rot disease symptoms of *Macrocystis* invariably followed elevated temperatures (Scotten⁸). Thus, assessments of impacts from thermal effluents tend to be equivocal and, unfortunately, cannot be overly generalized.

Finally, the possibility that continued stress will lead to additional pathological problems must be considered. Andrews¹ suggested that thermal discharges probably have pronounced indirect effects on seaweed disease. Increased heating of aquatic systems will continue for the foreseeable future, and the added stress will weaken thalli and likely predispose seaweeds to biotic and perhaps other abiotic causal agents. Furthermore, the trend toward diffuse-type thermal plumes enhances the importance of sublethal effects (Vadas et al.²³). Such low level persistent heat may act insidiously by gradually altering growth, reproductive capacities, and defensive mechanisms in plants, and by encouraging the development of pathogenic organisms.

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Marine fungal pathogens among Ascomycetes and Deuteromycetes

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Knowledge of algae-inhabiting fungi and their activities is scanty, although 59, i.e. more than a quarter of all described 209 filamentous marine fungi live in, on, or with algae (Kohlmeyer and Kohlmeyer¹). Higher fungi considered here belong to the class Ascomycetes and the form class Deuteromycetes, whereas filamentous Basidiomycetes appear to be without algiculous (=algae-inhabiting) marine representatives. Marine fungi occurring on algae can be divided into 3 groups, viz., saprobes on dead hosts, symbionts living in lichen-like associations with algae, and parasites ob-

taining their nutrients from living hosts. True marine lichens form obligate morphological-physiological units in which the fungal partner determines the habit of the association¹. Borderline cases of lichenoid symbionts often defy classification and may possibly be included in the group of parasites when details of the life histories will become known.

It is difficult to separate marine fungal pathogens from parasites. Andrews² defines disease as '... a continuing disturbance to the plant's normal structure or function such that it is altered in growth rate,

appearance, or economic importance.' Since life histories and physiologies of many marine algae are unexplored, the pathogenicity of a parasitic fungus can usually not be determined.

1. Diseases caused by Deuteromycetes

The Deuteromycetes or Fungi Imperfecti are a group of higher fungi without sexual reproduction. Although about one-third of all described terrestrial fungi belong to the Deuteromycetes, only 1 algalicolous species has become known. This is *Sphaceloma cecidii* Kohnmeyer, forming its fruiting bodies (acervuli) in galls caused by Ascomycetes of the genus *Haloguignardia* in species of *Cystoseira*, *Halidrys* and *Sargassum* (Kohnmeyer³). Because of its restriction to tissues diseased by a primary parasite, *S. cecidii* is termed a 'hyperparasite'. The normally brown galls turn black under the influence of the Deuteromycete which also closes the openings of fruiting bodies of the *Haloguignardia* species and ruptures the outer cell layers of the gall.

Many of the algalicolous marine Ascomycetes produce pycnidia-like fruiting bodies in addition to ascocarps. Such fructifications occur in *Didymella fucicola* (Sutherland) Kohnmeyer, *D. gloiopeltidis* (Miyabe et Tokida) Kohnmeyer et Kohnmeyer, *Didymosphaeria danica* (Berlese) Wilson et Knoyle, in all *Haloguignardia* species, in *Massarina cystophorae* (Cribb et Cribb) Kohnmeyer et Kohnmeyer, *Phycomelaina laminariae* (Rostrup) Kohnmeyer and *Thalassoascus tregoubovii* Ollivier. The role of the hyaline, one-celled 'spores' produced in these fruiting bodies is unknown. Because of their small size it is most probable that they represent male gametes (spermatia) and not conidia for vegetative propagation.

2. Diseases caused by Ascomycetes

16 of 31 parasitic algalicolous Ascomycetes occur on brown algae, 13 on red algae, and only 2 on green algae. The small number of parasitized Chlorophyta may be explained by the fragile nature of most representatives in this group which decompose before the relatively slow growing Ascomycetes can reproduce.

The most interesting parasites on Rhodophyta belong to the genus *Spathulospora*, occurring on *Ballia* spp. in the southern hemisphere. Sections through the algal filaments under and near the fungal thalli show that the parasite penetrates only 1 cell and forms an intracellular stroma composed of assimilating cells (Kohnmeyer and Kohnmeyer⁴). Adjoining host cells do not contain any fungal material but their chloroplasts are damaged. Obviously, nutrients are transported from neighboring cells into the parasitized cell and then into the stroma surrounding the algal filament. Infection by *S. calva* Kohnmeyer regularly causes wild growth of hairs in the host, *B. callitricha* (C. Agardh)

Kützing. These proliferations of hairs which are sometimes induced also by *S. adelpha* Kohnmeyer and *S. phycophila* Cavaliere et Johnson are comparable to 'witches' brooms', a symptom caused by insects or fungi in vascular terrestrial plants.

Other parasites in red algae cause discolorations, e.g. *Chadefaudia marina* Feldmann (Feldmann⁵), *Didymella gloiopeltidis* and *Lulworthia kniepii* Kohnmeyer (Bauch⁶) which induce pale spots in their hosts, *Rhodymenia palmata* (L.) J. Agardh, *Gloiopeltis furcata* Post. et Rupr., and calcified Rhodophyta, respectively. Black ascocarps develop eventually in these affected areas, and are responsible for the name 'black-dots disease' of *G. furcata* (Miyabe and Tokida⁷).

Another Rhodophyte, *Chondrus crispus* (L.) Stackhouse is often attacked by *Didymosphaeria danica*, an Ascomycete blackening the cystocarps of its host (Wilson and Knoyle⁸). The fungal stroma containing ascocarps and spermogonia prevents reproduction in the infected alga. However, the disease is not serious since the fungus remains restricted to the cystocarps.

Fungal diseases in Phaeophyta may be manifested as black discolorations or gall formations. The most common fungus on brown algae is *Phycomelaina laminariae* (Sutherland⁹, Kohnmeyer¹⁰) causing 'stipe blotch of kelps' (Andrews²) in species of *Laminaria*. The parasite forms black circular or oblong patches on the stalks of the hosts. These stromata which are mostly restricted to the cortex may eventually surround entire portions of the stipes and contain ascocarps and spermogonia. Although *P. laminariae* appears not to kill its host, the infected areas are severely damaged and permit penetration of secondary perithyphitic or saprobic fungi. An Oomycete is frequently found parasitizing ascocarps of *P. laminariae* (Kohnmeyer¹⁰). This hyperparasite impedes formation of asci, but no information on its life history and the process of infection is available.

A frequent parasite forming black crusts on stipes of species of *Aglaozonia*, *Cystoseira* and *Zanardinia* in European waters is *Thalassoascus tregoubovii* (Ollivier¹¹, Kohnmeyer¹²). Also this fungus does not injure its hosts severely.

The most obvious fungal infections are caused by species of *Haloguignardia* and *Massarina* which induce the formation of galls in their phaeophycean hosts. These subglobose, ellipsoidal or elongate outgrowths have more or less prominent protuberances containing asci and spermogonia. Algal genera attacked by *Haloguignardia* spp. are *Cystoseira*, *Halidrys* and *Sargassum*, and *Massarina cystophorae* forms galls in *Cystophora retroflexa* (Labill.) J. Agardh (see literature review in Kohnmeyer and Kohnmeyer¹).

Certain lichenoid associations between marine Ascomycetes and algae are borderline cases between symbiosis and parasitism. Among these are some myco-

phycobioses, namely obligately symbiotic associations between a systemic fungus and a marine macroalga (Kohlmeyer and Kohlmeyer¹³), e.g., *Turgidosculum* spp. in the chlorophytes *Blidingia* and *Prasiola*. Hyphae of *T. ulvae* (Reed) Kohlmeyer et Kohlmeyer form a network between the upper and lower cell layer of *B. minima* var. *vexata* Norris, whereas the mycelium of *T. complicatulum* (Nylander) Kohlmeyer et Kohlmeyer separates the thalli of *P. borealis* Reed and *P. tessellata* (Hook et Harvey) Kützinger into tetrads of irregular groups of cells. Ascocarps and spermogonia of both fungi develop in the infected algal tissue. Supposedly, fungus-free plants of the algal hosts, *Blidingia* and *Prasiola*, occur together in the same habitat with the infected plants (Reed¹⁴), but it has to be clarified whether the lichenized and non-lichenized plants are identical. If both belong to the same species, the fungi may be parasites rather than symbionts.

3. Key areas for research on fungal pathogens in algae

The field of algae-inhabiting marine fungi is largely unexplored and only a few mycologists and phycologists have been involved in such research. In the past, most marine mycologists have concentrated on wood-inhabiting fungi, probably because of the easier accessibility of the substrates and the possibility to culture these saprobes. The most common algicolous fungi have probably been described, but our knowledge of this group is still scanty and the following topics are in urgent need of investigation.

A. *Host physiology, life history and culture.* To understand infection processes we have to know what constitutes a healthy alga and what physiological changes lead to a disease, for instance to the production of galls. The basic topics of algal physiology and life history need to be tackled by phycologists.

B. *Mode of host infection.* The settlement and germination of spores, and the penetration of the germ tube or other hyphae into the host cell or tissue are unknown for almost all algicolous fungi.

C. *Fungal growth in the host.* The fungal-algal relationships must be examined microscopically, with the light as well as with the electron microscope to observe the growth of hyphae in the host tissues and possible morphological changes in the cells.

D. *Infection experiments.* The experimental transfer of higher fungi from diseased to healthy algae has not been performed so far. In nature, *Laminaria* spp. parasitized by *Phycomelaina laminariae* often occur close to uninfected plants. Although the fungal stroma rubs against neighbouring algae, the parasite is not transmitted. Also cases of mycophycobioses need clarification by infection experiments, e.g. how *Ascophyllum nodosum* (L.) Le Jol. is invaded by its mycobiont *Mycosphaerella ascophylli* Cotton.

E. *Predisposition of host.* The susceptibility of an alga

to attack by fungi may depend on extraneous factors, for instance weakening by thermal or chemical pollution. The influence of pollutants in combination with reaction to fungal attack should be explored.

F. *Life cycles.* The ontogeny of most algae-inhabiting fungi is unknown. Cultures of hosts will be needed in most cases to observe all stages of development of the parasite.

G. *Geographical distribution.* Since algicolous fungi have been treated with a lack of interest by most mycologists, only few collections of each species have been made, and information on their geographical range is scarce. Most fungal pathogens are host-specific; therefore, their distributions will probably coincide with those of their hosts. An exception are *Spathulospora* species which appear to be more limited in their distribution by temperatures than are their hosts, *Ballia* spp. (Kohlmeyer and Kohlmeyer⁴). Especially the Indian Ocean has not been explored for marine fungi in general, and for algae-inhabitants in particular.

H. *Fossil records.* The search for fossil algae-inhabiting fungi is, in my opinion, the most important topic needed to be undertaken. Such research may uncover missing links of fungi, significant to support phylogenetic hypotheses on the origin of fungi. As fungal parasites occur in extant calcified algae, it is conceivable that related fossilized fungi have been overlooked so far, but will be found on fossil calcareous red algae. According to one theory, Ascomycetes and red algae evolved from a common ancestor (Kohlmeyer and Kohlmeyer¹). Fossil records would help in clarifying the origin of fungi.

A common question is: How important are higher fungi as pathogens of marine algae? No epidemics caused by these fungi have become known, and parasitic higher fungi on algae are small in number and occurrence. Without doubt, they are biologically fascinating, but they also may present a potential danger when algae become predisposed to fungal attack by environmental factors, such as chemical or thermal pollution, for instance after a major oil spill.

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