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Abiotic disease in seaweeds: thermal effluents as causal agents

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

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

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

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

There is little published information on the direct effects of thermal effluents on algal thalli. Symptoms of thermal stress apparently include frond hardening, bleaching or darkening, plasmolysis and cellular disruption. Irreversible plasmolysis was used in laboratory studies to assess thermal death in siphonous tropical green algae (Bader et al.[6]). Foerster et al.[7] observed that heat-killed benthic diatoms lacked chloroplasts and cytoplasm. The economically important giant kelp, *Macrocystis pyrifera*, developed a black discoloration of fronds during periods of elevated temperature (Scotten[8]). The demise of extensive populations of this kelp from 1957-1959 was associated with abnormally high water temperatures in Southern California (North[9]).

Blades of the tropical seagrass, *Thalassia testudinum*, form large necrotic and discolored areas when stressed by high temperature (Wood and Zieman[10]). Persistent thermal stress in *Thalassia* beds resulted in the death and loss of leaves and eventually raised sediment temperatures by heat conduction. Higher sediment temperatures increased the respiration of rhizomes and caused the complete collapse of stressed populations. Similarly, the collapse of a boreal population of the intertidal salt marsh grass, *Spartina alterniflora*, occurred when elevated sediment temperatures and increased energy metabolism reduced stored food reserves in rhizomes (Vadas et al.[11]). Stressed plants (22-27 °C, summer temperatures) produced narrower, shorter and denser leaves. In contrast, plants of *S. alterniflora* exposed to higher temperatures (35 °C) in the Patuxent River, Maryland, were more robust than control plants at lower ambient temperatures (Anderson[12]).

A prolonged but intermittent thermal stress affected the growing (apical) parts of *Ascophyllum nodosum*, a dominant North Atlantic intertidal alga. Apical tips were not initiated the second spring (1.5 years) after the onset of the thermal discharge (Vadas et al.[13]). The basal portions of these plants survived but were weakly attached to substrates.

Elevated temperatures directly influence the metabolism of seaweeds. Photosynthetic rates increase linearly with increase in temperature at lower temperatures, but generally[5] continue upward well beyond ranges normally encountered in nature. Algae grow at summer temperatures of 27-30 °C in tropical or subtropical estuaries. Similarly, in *Thalassia*, net photosynthesis was optimal at 28-30 °C and dropped sharply on either side of this range (Zieman[15]). Laboratory studies showed that most algal species have high photosynthetic rates at 24-36 °C and low respiratory rates at 18-30 °C (Dawes et al.[14]).

Short-term studies in vitro do not appear to be suitable for predicting thermal impact. In most cases thermal optima derived from such studies greatly exceed tolerance limits. However, these studies provided valuable information on seasonal metabolic adaptation and on the growth dynamics of species over normal temperature ranges (e.g., Yokohama[16]). Thermal effluents influence the growth and productivity of seaweeds in several ways. Growth may be increased during spring or during the initial phases of discharge. Increases in the standing crop of *Spartina alterniflora* in Florida were 3 times greater during late winter-early spring in a thermally affected marsh than in a control area (Young[17]). A 2 °C-rise in water temperatures in Biscayne Bay, Florida, markedly increased the productivity of *Thalassia* (Thorhaug[18]). Growth rates in *Thalassia* decreased rapidly, however, when water temperature exceeded ambient summer temperatures (Zieman and Wood[19]). Mangroves, unlike most algae and seagrasses, do not appear to be living at their upper thermal limit, but if stressed, may produce significantly smaller seedlings which have a lower probability of survival (Banus and Kolehmainen[20]).

The growth of seaweeds appears to be one of the more useful indicators of thermal stress. Growth rates in *Macrocystis* were found to be strongly modified by temperature (North[21]). Tagged plants and apical tips of *Ascophyllum* indicated that growth was initiated earlier in thermally affected areas and that differences between these and control populations were significant by June (Vadas[22]). Similarly, growth of *Spartina* began earlier in the spring in areas with elevated temperatures. However, with time both species were severely stressed. Subsequent relocation of the effluent through a diffuser allowed *Ascophyllum* to regenerate from nearly moribund plants (Vadas et al.[23]). *Spartina,* however, has not recovered due to the collapse of the rhizome system (Keser et al.[24]).

The general effects of thermal effluents on benthic community structure are widely recognized and will be mentioned briefly. Typically in freshwaters there is a shift from diatoms in colder waters (< 22 °C) to green algae at intermediate temperatures (~ 23-32 °C) to blue-green algae at higher temperatures (> 33 °C) (e.g., Foerster et al.[7]). Marine blue-green algae in Florida replaced seagrasses and green and red algae in thermally elevated areas (Roessler and Zieman[25]). Reduced diversity usually accompanies thermally stressed marine systems (e.g., Zieman and Wood[19]). Abbott and North[26], however, indicated that in California warm tolerant algae likely would replace stressed species whereas, elsewhere, no significant changes in composition or diversity have been noted (e.g., Vadas et al.[13]).

There are numerous problems confounding nearly all field studies. Often thermal plumes produce or induce indirect effects, most commonly increased turbidity and sedimentation in discharge areas (Reeves[27]). Toxicity from chlorination to reduce fouling or from heavy metals eroded from cooling pipes may occur (Chesher[28]). Intermittent power output, especially 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 (Scotten[8]). 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. Andrews[1] 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 Kohlmeyer[1]). Higher fungi considered here belong to the class Ascomycetes and the form class Deuteromycetes, whereas filamentous Basidiomycetes appear to be without algicolous (= 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 obtaining their nutrients from living hosts. True marine lichens form obligate morphological-physiological units in which the fungal partner determines the habit of the association[1]. 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. Andrews[2] defines disease as '... a continuing disturbance to the plant's normal structure or function such that it is altered in growth rate,