## The Physiology of Zonation of Coastal Algae

## C. B. Trevarthen

Attention is confined to the longer and more complex benthic algae. Littoral zonation is defined as the regular horizontal arrangement of algae on coastal substrata.

Environmental Factors are divided into aerial and submarine. Complexity of the situation is emphasized. Aerial factors include water loss (connected with air humidity, temperature and movement), light and precipitation. Important among marine influences are spectral and intensity variations in light (in turn dependent upon water transparency and turbulence), hydrostatic pressure, temperature, salinity, pH, oxygen and carbon dioxide. Both these factor complexes are affected by tidal movement, which results in a vertical gradient of submersion and emersion conditions.

light energy and photosynthesis is expressed by the action spectrum, which gives the intensity of photosynthesis over a uniform energy content spectrum. Levring has shown that different natural conditions of light lead to photosynthetic rates which approach the result calculated in this way, although high lights reduce or inhibit activity. Fucoxanthin, physocyanin and phycoerythrin are proven photosynthetic sensitisers and can thus contribute to the action spectrum. Plants with a greater amount of pigment are more sensitive to light changes, and generally prefer shade.

Size and form affect photosynthesis, as when slender *Ectocarpus* and *Enteromorpha* quickly become less active upon emergence. These often grow in brightly lit, shallow pools.

Many higher algae exhibit adaptations to improve photosynthetic activity and to reduce loss of water. With no conducting system metabolic substances simply diffuse over the plant surface. Mucilage and hard cuticles (e.g., Hormosira) are common. Water is necessary for reproduction. Algae are not fundamentally different from other plants biochemicially speaking, but are essentially aquatic, with a high degree of "protoplasmic resistance."

Some experimental work has tested rates of water loss at different shore levels; and in addition Stocker and Holdheide have investigated effects of light and temperature. Massive fucoids cannot prevent fairly rapid desiccation upon exposure to air. Thin, membranous algae like *Porphyra* and *Enter*omorpha however can withstand relatively long exposure and high temperatures, since after rapid rehydration physiological activity is quickly resumed. Still, the assimilation/respiration balance is highest when both temperature and light are low. Infralittoral plants like Laminaria are slower to function normally after exposure.

Authorities disagree as to the significance of intensity and spectral quality of light in determining zonation. The relation between

## AN EXAMPLE—A STUDY OF Hormosira banksii

*Hormosira* is a primitive member of the Fucales. Repreductive bodies are protected in conceptacles, their discharge mechanism synchronised with the tides and influenced by other factors. Hormosira is restricted to cool — and warm — temperate coasts of Australasia in the lower mid-littoral or infra-littoral fringe of moderately sheltered waters, where there is suitable attachment.

The plant collapses in air, at first desiccating to a weight of only about 30% of that at full hydration, in 5 to 6 hours. Form, size and water content of bladders affect the rate of water loss, and assimilation is apparently enhanced by emergence. Gas in submerged bladders is mainly air, plus oxygen from photosynthesis—a respiratory reservoir. Lowering into the sea rapidly inactivates the pigment system. The compensation point is about 4 metres at 20°C. and 6 metres at 15°C., i.e., nearer the surface in summer. The depth profile of assimilation is thus typical for shallow water algae.

In the north, the lower limit of the Hormosira zone is due to reduced light; in the south it extends lower down. Desiccation



largely governs the upper limit. A typical pool inhabitant in the north, *Hormosira* may also be free-living at E.H.W.S. in pans of mangrove (*Avicennia*) swamps. In general, plants from higher latitudes have darker pigmentation (lower light) and have larger organs (a temperature effect?). Possibly lower temperatures result in more efficient photosynthesis in poor light. This would explain the depressed lower limit of the zone towards the south.

## CONCLUSION

Marine algae are plants with a restricted environment, owing to their limited ability to control water loss and to their precise light requirements.

The most important variables are the desiccation gradient. Another possibility is their possession of a photoperiodism akin to that of land plants, in response to tidal and solar cycles.