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100 INFLUENTIAL PAPERS – LONGER COMMENTARY

32 Stephenson, T. A. & Stephenson, A. (1949)

The universal features of zonation between tide-marks on rocky coasts. *Journal of Ecology*, **37**, 289-305.

The sea shore was always a magnet for naturalists. The receding tide gave a brief glimpse of marine animals and plants, albeit when they were out of action. By the early nineteenth century European biologists had commented on the discrete bands of vegetation and sedentary invertebrates on rocky shores and Edward Forbes gave names to different zones. His pioneering dredging expeditions revealed that there were also hidden zones below out of sight.

Subsequent marine biologists around the world described their local shores and emphasised the unique inhabitants. Alan Stephenson, a zoologist, took a contrary view. While at the University of Cape Town for ten years he compared temperate shores to the west of the Cape with tropical ones to the east. He concluded that despite their differences there were underlying similarities and these were of widespread occurrence. He was able to make such a sweeping statement because he had studied more shores around the world than anyone before him. With his wife Anne he had visited innumerable sites in Britain, the Indian Ocean, both seaboards of North America, the Red Sea and the Great Barrier Reef in Australia (Stephenson & Stephenson 1972).

He wrote: “So much has already been discovered about life between the tide-marks that it has become difficult to see the wood for the trees.” It was seaweeds rather than trees that were the trouble. On sheltered shores in temperate Europe the five species of fucoid algae occupied well-defined zones, but they overlaid and obscured what was beneath. On wave beaten sites where seaweeds cannot survive all is revealed - a white band of barnacles is topped by a band of black lichens and both are boldly painted on the rock.

In the 1949 paper he outlined his findings and his aim, which was "to introduce a system . . . which we believe may be of universal application." He defined four recurring zones that were characterised by types of organisms.

The **supralittoral fringe** was the area wetted largely by spray and inhabited by lichens and littorinid snails; the **midlittoral zone** of barnacles and limpets was covered and uncovered daily by the tide; the **infralittoral fringe** of encrusting calcareous algae that were uncovered only by low spring tides and the **infralittoral zone** that was permanently submerged and often dominated by seaweeds. As few marine species are ubiquitous the zone-defining organisms are not necessarily the same species or even the same genus, but they are usually close relatives.

The scheme did not address *why* different organisms inhabited various levels on the shore, it provided a standard nomenclature to enable researchers worldwide to specify exactly where they were working in a steep environmental gradient. This was particularly useful when from the 1960s onwards the seashore became a test bed for exploring the interactions between stress tolerance, predation and interspecific competition.

There are stories, perhaps apocryphal, that Stephenson was so good at surveying that he could do it at a distance. Sometimes for an inaccessible coastline he would scan the shore with binoculars from the cliffs above and dictate to his wife: 'barnacles abundant, periwinkles sparse, top shells seemingly absent.'

For his descriptive papers of particular shores he managed to persuade editors to include expensive fold-out coloured diagrams (Stephenson & Stephenson 1950, 1952). He was a talented artist and produced striking semi-diagrammatic illustrations to give a vivid picture of zonation patterns (Stephenson & Stephenson 1949). For his beautifully illustrated volumes on the British sea anemones he included vignettes depicting a naked sea nymph prancing in the surf or reclining on the rocks. She is clearly his wife Anne. Sadly the librarians at his University inked out the vignettes as they might induce a prurient interest in sea anemones.

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Stephenson, T. A. & Stephenson, A. (1949) The universal features of zonation between tide-marks on rocky coasts. *Journal of Ecology,* **37**, 289-305.

Stephenson, T. A. & Stephenson, A. (1950) Life between the tide-marks in North America 1. The Florida Keys. *Journal of Ecology,* **38**, 354-402.

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