DEEP-SEA BIOLOGY: A natural history of organisms at the deep-sea floor

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1 Historical aspects

The history of the study of the populations inhabiting the interface of the floor of the deep ocean with the overlying water spans a short period of little more than the maximum lifespan of a blue whale (approx. 120 yr). We associate this with the remoteness of the deep sea and the resulting difficulties in studying this environment: our methods of study are inhibited by the need for our instrumentation and observation chambers to be encapsulated in the atmosphere of the surface, and strengthened against the crushing pressure of a water column several kilometres in height.

EARLY EXPLORATION OF THE FAUNA OF THE DEEP-SEA FLOOR

In the middle years of the nineteenth century, in his investigations by dredging for life on the bottom of the deep fjords of the west coast of his country, the Norwegian pastor/naturalist, Michael Sars, together with his son, G. O. Sars, had listed nearly 100 species of invertebrate living at depths greater than 600 m. Even earlier, in 1818, the British explorer John Ross made a fortuitous discovery of a many-armed basket star (Fig. 1.1) from a sounding line cast in a depth of more than 1.6 km during his search for the North West Passage. Later, James Clark Ross and J. Hooker on the exploratory voyages of the 'Erebus' and 'Terror' to the southern ocean in 1839–43 had obtained animals from the mud on the sounding lead in a depth of 1.8 km and described a 'teeming animal life' on the Antarctic continental slope. Such discoveries fuelled curious and adventurous minds in nineteenth-century Britain to speculate that life existed at the greatest depths being revealed by the sounding lead in surveying the oceans in order to route the new trans-oceanic submarine cables. Unfortunately for Victorian science, the collections were never adequately described and the prevailing opinion perceived the continuous darkness, lack of plant life, and water pressure of several hundreds of atmospheres as precluding the existence of living forms.

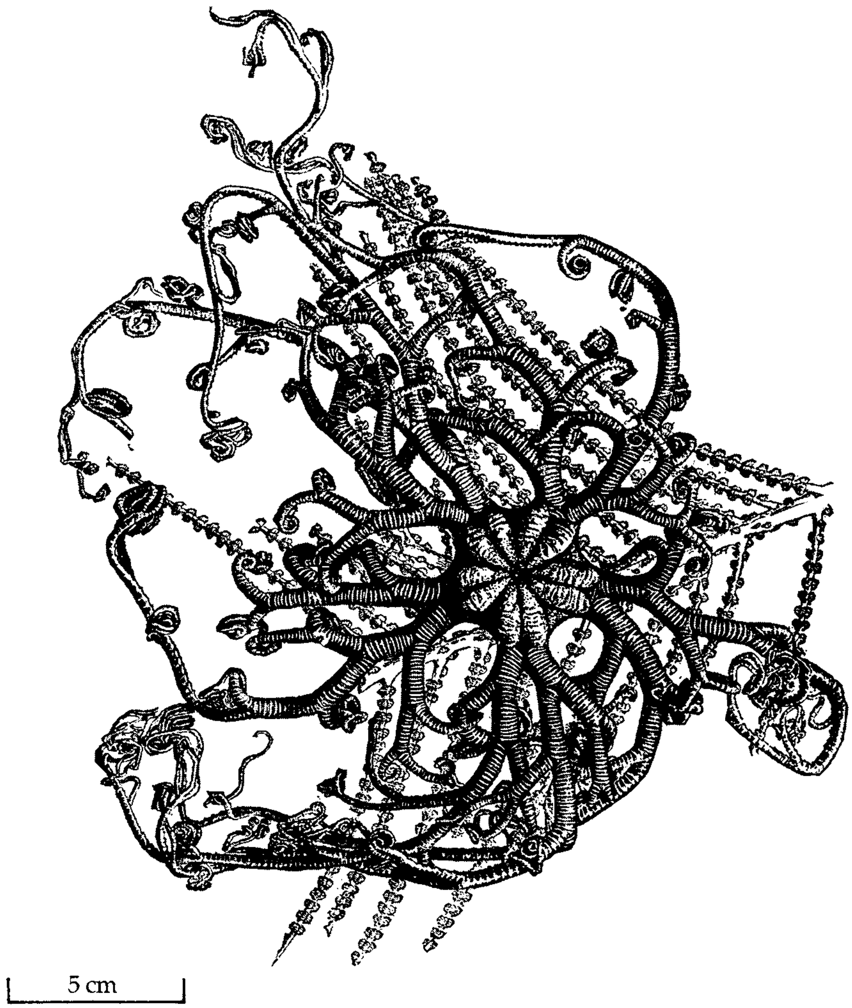

Fig. 1.1. Basket star *Astrophyton* entwined in its 'perch' on a gorgonian branch. In life, the finely branched arms are spread in a net to ensnare organisms carried by the current. (From Agassiz, 1888.)

CONCEPT OF 'ZERO' OF ANIMAL LIFE

Although his work served to reinforce the view that life would be absent at great depths, it was a young professor at Edinburgh University, Edward Forbes, above all others, who deserves credit for stimulating the early exploration of the deep sea. His concept of an 'azoic zone' below 0.6 km depth was derived from his dredging work in the Aegean (where later work has shown that deep-sea life is particularly sparse). His idea of a threshold for life was quickly challenged by others in the lively intellectual climate prevailing in Edinburgh at this time of publication of Darwin's work on the origin of species. Attempts to sample the greatest depths available offered the chance of perhaps finding there, still living, some of the archaic forms of life then being abundantly revealed to science as fossilized remains from sedimentary rocks. Charles Wyville Thomson, a later incumbent of Forbes' professorial chair at Edinburgh,

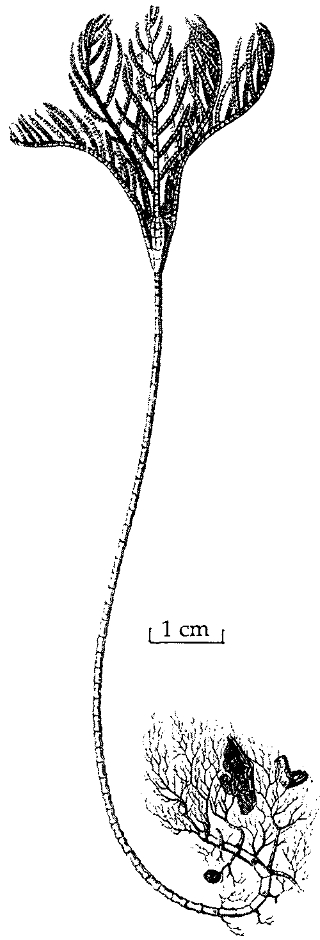

Fig. 1.2. The sea lily *Rhizocrinus lofotensis*. (From Thomson, 1874.)

visited Michael Sars in Norway in order to examine, at first hand, his collection of marine animals that he had collected from the deep Lofoten Fjord. These included specimens of the stalked sea lily, *Rhizocrinus lofotensis* (Fig. 1.2) which, as a member of a group of echinoderms hitherto only known from fossil remains, excited Wyville Thomson and led to a hope, long nurtured afterwards, that the deep sea has provided a refuge for all manner of forms of life thought to be extinct.

THE 'CHALLENGER' EXPEDITION AND THE ERA OF NATIONAL EXPEDITIONS

On his return, Wyville Thomson, together with an eminent friend, W. B. Carpenter, persuaded the Royal Society of London to get the British Royal Navy to help him organize a cruise in order to undertake the exploration of deep water. The cruises, first of H.M.S. 'Lightning' in the summer of 1868 and later of H.M.S. 'Porcupine' in the summers of 1869 and 1870, took place in the waters lying to the north and west of Britain and the

Iberian peninsula. These pioneering expeditions recovered new forms of life that were washed from the cold, clay-like ooze dredged from depths down to 4.289 km. Surprisingly, the muddy ooze was found to be almost entirely made up of the skeletal remains of innumerable tiny single-celled organisms falling from the planktonic populations at the surface.

On the basis of these cruises, Wyville Thomson was satisfied that life would be found on the bottom in the greatest depths. Their intriguing observations on discontinuities in the temperature of the deep-sea water mass opened up controversies on ocean circulation. These considerations, together with the interest of the Royal Navy in surveying routes for submarine telegraph cables, helped in the organization necessary for the subsequent circumnavigating voyage of H.M.S. 'Challenger' from 1872 to 1876. This pioneering voyage was largely organized, and later led, by Wyville Thomson. The results of this cruise without doubt laid the foundation, not only for our present knowledge of the life of the deep-sea floor, but also provided a quantum leap for the infant science of oceanography. Animal life was found from dredgings to 5.5 km below the surface, but no 'living fossils' were discovered. Instead, what appeared to be a rather cosmopolitan fauna was found which showed signs of being highly diverse (although a proper appreciation of this extraordinary diversity in animal life was delayed right up to the 1960s when fine-meshed dredges and sieves came into general use). The biological results of the subsequent studies of the samples obtained fill 34 large volumes which, together with the results of other national expeditions from other European countries and from the U.S.A. that followed, remain an indispensable source of descriptive information to this day. The names of these expeditions commemorate the ships that bore them: the 'Travailleur' and the 'Talisman' from France under the direction of the great Alphonse Milne-Edwards and the 'Hirondelle' and 'Princess Alice I' and 'II' under the personal direction of, and financed by, Prince Albert I of Monaco; the 'Ingolf' from Denmark, and the 'Michael Sars' from Norway; the 'Valdivia' from Germany, and the 'Blake' and 'Albatross' from the U.S.A. This era was effectively closed by the voyages of the Swedish 'Albatross' in 1947–48 in the Atlantic and the Danish round-the-world voyage of the 'Galathea' in 1950–52. It was on the latter expedition that the last frontiers in the quest, started in the mid-1800s, for life at the greatest depths were successfully overcome; the 'Galathea' recovering animals from the depths of the Philippines Trench (10.19 km).

MODERN QUANTITATIVE STUDIES GENERATE NEW ECOLOGICAL CONCEPTS

In the 1950s, a great expansion in deep-sea investigation was undertaken by Russian biologists, who also successfully sampled the varied benthic fauna of the deepest trenches and, following on from beginnings made by the 'Galathea', engaged in a programme of quantitative sampling of the sediments of the Pacific and other oceans with modified forms of the grabs used in coastal surveys. Their results established general 'laws' on the geographical and bathymetric distribution of benthic biomass in the deep sea.

In the 1960s and 1970s, ecological research into the life forms of the deep-sea bottom have been dominated by American work, particularly by lines of research initiated by Howard L. Sanders and Robert R. Hessler at the Woods Hole Oceanographic Institution and the latter later at the Scripps Institution of Oceanography. Their findings of unexpectedly high species diversity in the previously virtually unsampled small fauna, retained using fine-meshed screens, stimulated much theorizing by population ecologists on how high diversification could be maintained in such a food-poor and seemingly hostile environment. The advent of box-core samplers, derived from devices used by geologists, have provided, for the first time, unbiased samples of the sediment community comparable in quality to those from inshore sediments, whilst observations from deep-diving submersibles have provided not only intrepid (though cramped) observers with a wealth of data on the lifestyles of the larger fauna previously known only from the trawl or from seabed photographs, but a means to set up ecological experiments directly on the ocean bed.

MULTIDISCIPLINARY PROGRAMMES

The 1970s and 1980s have seen an international proliferation in research programmes; many having a multidisciplinary make-up and a regional focus. Oceanographers have, for the first time, monitored the organic flux from the surface, and measurements and samples have been taken at fixed stations over periods of several years. Discovery of unexpected seasonality in reproduction and respiration have challenged earlier assumptions of extreme constancy in the tempo of life on the deep-sea floor. Discovery of rich 'oases' of life depending not on sun-driven production at the surface of the ocean, but on sulphur oxidizing and methanotrophic bacterial production in emissions from hydrothermal vents and hydrocarbon seeps, and of populations of giant-sized amphipods and other scavenging animals attracted to baited traps, have shown that our understanding of the nature of life in the depths remains far from complete.