NEPTUNE'S REALM: EXPLORATIONS IN MARINE BIOLOGY

INAUGURAL LECTURE

delivered at the College
on 7th December, 1976

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Professor J. S. RYLAND
M.A. (Cantab.), Ph.D., D.Sc. (Wales)
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NEPTUNE'S REALM : EXPLORATIONS IN MARINE BIOLOGY

IT would indeed be surprising if a university institution, given a favoured location on the coast and Britain's maritime traditions, did not focus some of its attention on a study of the sea. In the University of Wales, this happened first in any major way at Bangor, through the perceptive initiative of the late F. W. Rogers Brambell, F.R.S., Professor of Zoology in the University College of North Wales. An advantageous situation, provided by the sheltered waters of the Menai Strait and the proximity of faunistically rich and varied intertidal habitats, led in 1953 to the establishment of the Marine Biology Station. Marine Biology was in turn brought to the University College of Swansea three years later when Dr. E. W. Knight-Jones, Deputy Director of the Marine Biology Station, was appointed first Professor of Zoology. Swansea, though exposed to marine conditions certainly different from those affecting the coasts of Gwynedd, is well placed for the study of intertidal and sublittoral life. Zoological research in these fields prospered, and this activity was reflected by the inclusion of a generous leavening of marine ecology in the zoological courses.

Research and teaching in marine zoology received a major boost in 1967 with the purchase, by the University College, of the 100-foot drifter-trawler *Ocean Crest* in support of the newly founded Sub-department of Oceanography. Meanwhile, outside the universities, the invention of the aqualung had focussed popular interest on life in the seas. The variety and beauty of marine animals became widely appreciated through the medium of television ; while many people came to understand the need to exploit rationally and non-destructively, for the good of mankind, the natural resources of the ocean. The expertise that had accumulated within the University College became formally linked to the developing interest outside it when, in 1975, an honours course in Marine Biology was introduced. As an "umbrella" to cover diverse fields of marine science, the University College established the Institute of Marine Studies in 1974. Through this organisation disparate interests are being co-ordinated and interdisciplinary facilities developed.

Against this background, I believe myself to be fortunate in being a zoologist whose interests lie firmly in the field of Marine Biology, and the time is propitious for an inaugural lecture in the College to be devoted to this subject. My own background of research, which has been divided between fisheries and some non-applied fields, is reflected at Swansea by our approach to the teaching of Marine Biology and will be apparent during this lecture. I propose to look briefly at some of the people, events and voyages that have led Marine Biology to its present state ; and I want to emphasize that transition from qualitative to quantitative and numerical methods of investigation that has characterized its development—a change that I hope is well appreciated by the aspiring marine biologists at present in the senior forms of our schools. My approach will be unashamedly insular : obvious constraints would make anything else an impossibility, but such was Britain's dominance during the infancy of Marine Biology that history will not, I trust, be too seriously travestied in this way.

The oceans are vast, for they cover seven-tenths of the earth. The huge extent of their surface inhibited the explorations of our ancestors, just as their colossal depth frustrates the inquiries of our contemporaries. The average depth of the ocean is 3800m, and much of the sea bed is abyssal plain 4000—6000m down. The great trenches descend to over 10,000m, so that their waters could cover Mount Everest with a kilometre to spare. Little sunlight penetrates much below 100m and the depths below 600m are essentially dark. Neptune's realm is difficult and dangerous to explore.

Study of the sea must be as old as the civilizations built on its shores. Sea routes were explored and developed by seafaring, trading peoples such as the Phoenicians, who are believed to have circumnavigated Africa in about the year 600 B.C. The Greeks too had their navigators, such as Pytheas, who reached the Shetland Islands, and possibly Norway or

Iceland, on his voyage around Britain in ca. 325 B.C. Greek mathematicians and astronomers discovered how to calculate latitude on the basis of daylength, and their philosophers were interested in the sea for its own sake. Aristotle theorized about the saltness of the sea and was acquainted with dozens of species of marine animal, while his knowledge of their anatomy remained unequalled for two millenia. Some of Aristotle's information, was of course, derivative in origin but that was far more true of Pliny. The Romans added less to our knowledge of the sea than the Greeks had done and Pliny's *Historia Naturalis* is a little more than a derivative compilation.

Centuries later interest in the oceans was still, Phoenician style, associated with geographical exploration and the development of trading routes. The latter part of the Renaissance was an age of exploration, exemplified by the voyages of Diaz, Columbus, Cabot, da Gama, and Magellan ; but the sailors of the fifteenth and sixteenth centuries were concerned for the safety of their ships and with navigational routes in coastal and ocean waters, not with marine biology.

Geographical discoveries, however, contributed to the awakening and flowering of the sciences which took place in Britain during the seventeenth century, particularly after the Restoration of the Monarchy (1660). This period will always be remembered for the inauguration by Charles II of the Royal Society in 1662. Now inquiry into the properties of the oceans was pursued by physical scientists such as Robert Boyle and Robert Hooke, while the British fauna and flora was described and catalogued by naturalists Francis Willughby (1635-72) and John Ray (1627-1705). Willughby, a founder Fellow of the Royal Society, and Ray, whose fame came later, together finding "the 'History of Nature' very imperfect . . . agreed . . . to reduce the several tribes of things to a method, and to give accurate descriptions of the several species from a strict view of them". Willughby was to describe and classify the animals and Ray the plants. However, Willughby's premature death left Ray to complete his friend's volumes on birds, fishes and insects. In 1690, Ray recast his earlier, alphabetically arranged *Catalogus Plantarum Angliae* into a systematical treatment in the *Synopsis Methodica Stirpium Britannicarum*.

The "Genus Secundum. Plantae Submarinae" of this work in fact includes several of the less obviously animate fauna (sponges, hydroids and bryozoans). Another naturalist of this time was the physician, and correspondent of John Ray, Martin Lister (1638 ?-1712), who was elected F.R.S. in 1670. Lister's chief work was the *Historia sive Synopsis Methodica Conchyliorum* (1685-92), which included accurate figures of all shells then known. He is regarded as the father of British malacology. Despite the initiative of such naturalists, the scientific exploration of both shores and oceans really commenced only in the eighteenth century, when marine life began to be studied for its own sake almost for the first time since Aristotle. Count Luigi Marsigli was eminent in France during the first decades, and his *Histoire Physique de la Mer* (1725) was the first book on marine science. Marsigli had collected precious coral (*Corallium rubrum*) with a primitive kind of grab, and most scientists of the time accepted his claim that the coral polyps were its flowers. The realization by Jean Peyssonel, a Marseilles physician, that corals were animals was ridiculed at first, but the controversy was settled in mid-century by John Ellis (1710 ?-1776), in discourse to the Royal Society, and in his masterly *Essay towards a Natural History of the Corallines* (1755). This finely illustrated volume described many sessile British species now classified as hydroids and bryozoans. Ellis collected specimens on the shores of south-east England or obtained them from local fishermen, and he also received some from other naturalists. He kept them alive for study under the microscope and the *Essay* is a remarkable testimony to the accuracy and pertinence of Ellis' powers of observation.

Contemporaneously in Sweden, Carl von Linné was producing his great classifications of animals and plants, including that all-important landmark, the tenth edition of *Systema Naturae* (1759), recognized officially as inaugurating the binomial system for the nomenclature of animals. Ray and Ellis had been dependent on brief Latin diagnoses plus a vernacular name. In Britain Thomas Pennant (1726-98), popularly best known as the recipient of Gilbert White's letters from Selbourne, was preparing his *British Zoology*,

volume IV of which (1777) contained descriptions of many marine invertebrates (crustaceans, molluscs and worms) using binomial nomenclature. Following the Linnean example, the latter part of the century was characterized by a vigorous search for new animals and plants to name, describe, and classify.

Britain was, at this time, a major sea power : yet hydrographic survey was largely a neglected field. Consequently, when astronomers of the Royal Society decided that the transit of Venus between the earth and the sun, predicted for 3 June 1769, should if possible be observed from the southern Pacific, George III and the Admiralty were happy to provide a ship. The coasts of Australia and New Zealand could then be charted and search prosecuted for the supposed southern continent *Terra Austràlis Incognita* ; James Cook, an expert surveyor, was appointed captain. The voyage was seen also as the means of collecting many exotic animals and plants, and the Royal Society proposed that one of its Fellows, wealthy naturalist Joseph Banks (1743-1820) should accompany Cook. Banks' entourage included artists and servants, together with a professional biologist, Linnaeus' pupil Dr. Daniel Solander (1736-1782). Solander had come to Britain in 1760 bearing a letter of introduction to John Ellis, written for him by Linnaeus, who had described Ellis as "the main support of natural history in England". Solander evidently became friendly with Ellis and, after the latter's death, completed for him the important *Natural History of Zoophytes* (published, however, four years after he too had died). The historic voyage of the *Endeavour* which made both Cook and Banks famous, instigated an important tradition that naturalists should sail on voyages of exploration.

During the first voyage (1768-1771), Cook reached Tahiti in time to observe the transit of Venus, charted much of the New Zealand coastline and sailed up the eastern seaboard of Australia. Here he discovered the Great Barrier Reef in memorable and nearly disastrous fashion. During the early part of June 1770 he was heading northwards off the coast of Queensland, generally in deep water, past islands now recognized as constituting the southern or diffuse part of the Great

Barrier Reef. Further north he sailed past low wooded islands (reefs inside the outer barrier which have subsequently featured prominently in the scientific exploration of the region) without appreciating their essential nature. On 11 June *Endeavour* crashed into a patch reef off the site of present-day Cooktown. Having thus discovered the reef, Cook, with the *Endeavour* repaired, followed it warily northwards to Torres Strait and thence headed for home. Cook never returned to the reef, which was subsequently further delimited and charted by Matthew Flinders, with the patronage of Banks, in the voyage of H.M.S. *Investigator* (1801-1803).

Daniel Solander died before he could complete his study of the *Endeavour* collections. Banks meanwhile in 1778 had become President of the Royal Society—a post he held for a remarkable 43 years ; he was a generous patron of natural science and was made a baronet in 1781. It was he who encouraged the whaling officer William Scoresby Jr. to develop his interest in marine science. Scoresby twice journeyed to Edinburgh and studied Natural History under Robert Jameson. His voyages to the Arctic were amongst the most important of the early nineteenth century and led to a classic book, *An Account of the Arctic Regions* (1820).

A naturalist of some distinction in the early nineteenth century was John Vaughan Thompson (1779—1847). Born at Berwick-on-Tweed, he became an army surgeon holding various appointments until he was posted to Cork in 1816. Here he published his *Zoological Researches* (1828—1834) based on observations of notable originality. He is the first man to record using a plankton net (Memoir III, pp. 46-47, 1829), but his zoological fame rests mainly on his discovery of metamorphosis in Crustacea. He established that the zooea was the larval stage of the crab ; and that barnacles, then classified as molluscs and still supposed by the credulous to be miraculously transformed into barnacle geese, were crustaceans. He observed the attachment and settlement of the cyprid larva into an acorn barnacle (Memoir IV, 1830). In the same year (Memoir V) he distinguished the Polyzoa (or Bryozoa) as a new and distinct animal class.

Thompson's research on barnacles provides a link with

Charles Darwin, author of the major work on them, *A Monograph on the Sub-class Cirripedia* (1854), and thus with another voyage, that of H.M.S. *Beagle* (1831—1836). Fixing longitude at sea had long proved a problem to navigators, and the purposes of this voyage were charting the coast of South America and developing the accurate fixing of longitude during a circumnavigation of the world. Darwin, selected as naturalist to accompany Capt. Robert FitzRoy, was inexperienced and newly graduated from Cambridge, though earlier a student of Jameson's at Edinburgh. That he was able to derive, develop and document from the voyage a thesis about evolution that has become an integral and central part of the fabric of modern biology is a clear measure of his genius. Certain parts of the voyage, however, also have additionally a more direct relevance to the development of marine biology.

In the spring of 1836 the *Beagle*, on the leg homeward from Australia, visited Cocos Islands in the Indian Ocean. Darwin had observed atolls from the *Beagle* in the Pacific and had been puzzling over their origin. During the voyage he had been reading Lyell's newly published *Principles of Geology* and had himself observed marine fossils high above sea level in South America : clearly, he reasoned, the relative levels of sea and land can change. Darwin deduced that an atoll would be formed if a coralgirt island was sinking slowly and steadily into the sea. At the Cocos Islands Darwin and FitzRoy made soundings, confirming that the atoll reef plunged steeply into the ocean and that living coral was found only near the surface. On his return Darwin published first his *Journal of Researches* (1839) and then *The Structure and Distribution of Coral Reefs* (1842) in which his theory was elaborated. It is a theory which has been much disputed, notably by John Murray. Murray's theory, based on his observations during the voyage of H.M.S. *Challenger* (described later), was that the summit of sea mounts might rise through the accumulation of mineral deposit of planktonic origin until, near the surface, reef building corals could become established.

Geological surveys at Eniwetok and Bikini atolls in the central Pacific, which followed their use for testing atomic bombs, included the drilling of deep borings. At Eniwetok these have shown that the atoll consists of a coralligenous limestone cap some 1200m in thickness resting on the flat basaltic top of a volcano. It seems that the summit of the volcano was above sea level early in the Tertiary period, and was eroded to a level platform by the waves. Coral growth evidently commenced 50 million or more years ago and has proceeded to the accompaniment of prolonged but discontinuous subsidence. These two atolls have formed in precisely the manner Darwin envisaged.

Other important voyages followed, such as those of James Clark Ross to the Antarctic with H.M.S. *Erebus* and H.M.S. *Terror* (1839—1843), with J. D. Hooker as naturalist ; and of H.M.S. *Rattlesnake* (1846—1850) with W. Macgillivray as naturalist and T. H. Huxley as surgeon. Huxley was particularly interested in the pelagic fauna and, in *The Oceanic Hydrozoa* (1859), established the coelenterate nature of siphonophores. But the shore animals were also being studied and popularized, above all by Phillip Henry Gosse in books such as *A Naturalist's Rambles on the Devonshire Coast* (1854) and *Tenby : a Seaside Holiday* (1856). Tenby was, in fact, fashionable with Victorian marine naturalists. Gosse was more than a popularizer though, and his *History of the British Sea Anemones and Corals* (1860), with its fine colour plates, was for long the standard monograph on the British sea anemones and corals. Later the Victorians' interest in the sea-shore waned, but by then the scientists had turned their attention to life below tidemarks.

Edward Forbes (1815—1854) was born in Douglas, Isle of Man, and grew up with a strong interest in natural history. After leaving school he attended Edinburgh University, ostensibly to study medicine ; however, he devoted most of his time to natural history, also studying with Professor Jameson. During the summers, from 1832 onwards, he started dredging the Irish Sea with the naturalists' dredge invented by O. F. Müller in 1799. In 1839 he joined John Goodsir in a dredging expedition to the Shetland Islands, the results from which were reported to the British Association meeting at Birmingham. These were so well received that a Committee "for the investigation of British marine zoology by means of the dredge" was formed to supervise shallow water collecting, which was then conducted enthusiastically all around the British Isles.

In 1841 Forbes was offered the position of naturalist on board H.M.S. *Beacon* for a voyage to the eastern Mediterranean and the Aegean. Dredgings were successfully completed to depths of 230 fathoms. In these Forbes observed an attenuation of both faunal diversity and abundance with increasing depth : this led him to speculate that the seas would be azoic below about 300 fathoms. Physical conditions in the eastern Mediterranean are somewhat unusual, the greater depths being affected by the outflow of anoxic water from the Black Sea. Neither Forbes nor anyone else appreciated this ; consequently, as a generalization, the azoic theory was of course duly disproved, but the efforts to support or negate the theory provided a great stimulus for research by deep dredging in the late nineteenth century.

Edward Forbes was greatly interested in biogeography and worked out the geographical elements constituting the British flora as well as of the marine fauna (the posthumous *Natural History of the European Seas*, completed by R. A. C. Godwin-Austen, 1859) ; he published important monographs, such as *A History of British Starfishes* (1840) at the age of 26 and, with Sylvanus Hanley, the four-volume *History of British Mollusca and their Shells* (1848—1853). The positions he occupied subsequent to the *Beacon* voyage indicate both his ability and adaptability : in sequence he was Professor of Botany at King's College, London, Palaeontologist to the Geological Survey and Professor of Natural History at Edinburgh. He died at the early age of 39 only a few months after the move to Edinburgh. Perhaps more than any other person, Edward Forbes should be remembered as the founder of British marine biology.

The first published report of the Dredging Committee (and the only one prepared by Forbes himself) was presented, appropriately, at the Edinburgh meeting of the British Association in 1850, and listed the fauna (particularly the molluscs and echinoderms) dredged off the Isle of Man, off North Wales, in the Bristol Channel, off the south coast of England, in the Firth of Clyde, and among the islands of the Hebrides, Orkney and Shetland. Other reports were presented, by subsequent chairmen, to the annual meeting in many of the years between 1856 and 1875. These covered dredging activities off Belfast and Dublin, among the Shetland Islands, off Northumberland and Durham, and off the coasts of Devon and Cornwall. Thus it was through the dredging activities which Forbes had initiated that a remarkably complete knowledge of the marine fauna surrounding the British Islands was assembled. This was reflected in the production of many magnificent monographs on marine animals, most of which survive as standard works of reference to the present day : they include Spence Bate's *History of the British Sessile-eyed Crustacea* (1863, 1868), Gwyn Jeffreys' *British Conchology* (1862-69), T. Hincks' *History of the British Marine Polyzoa* (1880) and Francis Day's *The Fishes of Great Britain and Ireland* (1880-84).

John Gwyn Jeffreys (1809—1885), who became a famous conchologist, was a native of Swansea. Educated at Swansea Grammar School, he trained as a solicitor and practised in Swansea for many years before moving to London in 1856. He was an active naturalist, associated particularly with the British Association and, together with Rev. A. M. Norman, spent most of his summers in the period 1860—1870 dredging the shallower waters of British seas.

Charles Wyville Thomson (1830—1882), like Forbes, was sent to Edinburgh to study medicine but found natural science more to his inclinations. After Edinburgh, which he left without a degree, he held various posts including first the chair of Geology and then the chair of Natural History at Queen's College, Belfast. In this city Thomson became established as both a palaeontologist and a marine biologist of repute. He was particularly interested in the crinoids (feather stars) and was greatly excited by the news that Michael and G. O. Sars had obtained a stalked crinoid, very like the fossil forms with which he was familiar, from 450 fathoms in the Lofoten fjords. Animals had also by this time been found adhering to submarine cables raised from well below 300 fathoms. Thus it seemed to him that not only was there life in the deep sea but that such depths might provide a refuge for

archaic forms. Thomson, with the aid of his more senior colleague, W. B. Carpenter, persuaded the Royal Society to approach the Admiralty for a vessel with which to undertake deep dredgings to resolve the matter.

As a result of this approach Thomson and Carpenter, together with Gwyn Jeffreys and other colleagues, were provided first with H.M.S. *Lightning* and then H.M.S. *Porcupine*. The results were startling, shattering two widely-held misconceptions. Dredgings from as deep as 2500 fathoms came up containing animals, whilst the deep-sea thermometers registered temperatures down to 0 °C. (Even in 1868 it was still widely held that the coldest water in the deep ocean would be 39-40°F, a completely false conclusion from the established fact that *fresh* water reaches its maximum density at that temperature.) Moreover, dredging west of the Shetland Islands, they found one type of bottom fauna in water at 0°C but, not far distant, a different community in water at 8°C. Some years later it was established that a submarine ridge, to be appropriately named after Wyville Thomson, separated the water masses of Arctic and Atlantic origin. These researches brought Thomson considerable fame and, in 1870, sixteen years after Forbes' death, he in turn was appointed to the Chair of Natural History in Edinburgh. The discoveries resulting from the cruises of the *Lightning* and *Porcupine* were reported in a famous book *The Depths of the Sea* (1873).

Carpenter and Thomson, with the important support of Captain G. H. Richards, Hydrographer of the Navy, through the British Association, the Royal Society and the Admiralty, now pressed the government to undertake a major voyage of scientific discovery and circumnavigation. Britain's dominant role in marine science was threatened by developments in other countries : Louis Agassiz and his son Alexander in the United States were making an outstanding contribution to biology and oceanography, with men such as L. F. de Pourtalès and A. E. Verrill exploring the bottom fauna off the eastern seaboard as Forbes and Jeffreys had done around the British Isles. And the Germans were planning their North Sea expedition (that of the S.S. *Pomerania*, 1871—1872). Moreover a surveying voyage was seen as providing information about the sea bed vital for the laying of submarine telegraphic cables needed to link the countries of the Empire. The idea of a single, high prestige venture appealed to the government of the day, and thus was the great *Challenger* expedition conceived. Captain G. S. Nares was appointed to command and Wyville Thomson headed the scientific team of three naturalists (John Murray, H. N. Mosely and R. von Willemoes-Suhm) and a chemist (J. Y. Buchanan).

The objectives of the expedition were unambiguous : to study (1) the physics and chemistry of sea water at all depths, (2) the nature of the bottom deposits, and (3) the distribution of life, especially in the deep ocean. H.M.S. *Challenger*, a 226 foot corvette, sailed on 21 December 1872, not to return until 24 May 1876. In this time she sailed 68,890 nautical miles and worked 362 stations generally some 200 miles apart. She had sounded a maximum of 4,475 fathoms in the Mariana Trench and dredged animals in depths in excess of 3000 fathoms.

After the expedition Thomson completed a two volume work, *The Voyage of the Challenger : the Atlantic* (1877) in which he was able to present a first evaluation of their achievements. The greatest effort at the sampling stations had been expended on the sea bed. At each one the depth was sounded, samples of sediment and bottom water were recovered, the temperature above the sea bed was recorded, and a faunistic sample was collected by the trawl. The topography of the ocean bed was revealed by the soundings to an extent never before achieved (though the American oceanographer M. F. Maury had earlier prepared the first bathymetric map of the North Atlantic). The characterization of the sediments and the mapping of their distributions represent a major and fundamental achievement of the voyage (and, incidentally, at one point led directly to the discovery of the valuable Christmas Island phosphate deposits which have repaid the costs of the expedition many times over). Zoologically it established not only the existence but the nature of the abyssal fauna, and demonstrated its essential similarity throughout the worlds' oceans. Pelagic life was also collected, and Buchanan contributed a major study on surface salinity. Sir Maurice Yonge recently described the results from the *Challenger* as "the greatest

single contribution to scientific knowledge of marine life since Aristotle had begun this over 2000 years previously".

Wyville Thomson was able to draft only the first volume of the *Challenger* reports, for by then his health was failing. If the great mass of data and discoveries were to be presented to the scientific world, his responsibilities would have to be assumed by a successor.

John Murray (1841—1914) was a Scot born in Canada. Like Forbes and Thomson before him, Murray entered Edinburgh University to study medicine. He remained there for many years, a scholar of several sciences who never took any examinations ! He was still there in 1870 when Wyville Thomson moved from Belfast to take the Chair of Natural History, and was thus on hand when the latter was selecting assistants for the *Challenger*. His particular interests on the voyage became bottom deposits, coral reefs and plankton. When Thomson's ill health forced him to resign both the Chair at Edinburgh and the Directorship of the *Challenger* Expedition Commission in 1881, Murray succeeded him as Director and editor of the expedition reports. These—fifty huge volumes—steadily appeared in the years that followed, the work being concluded in 1895. Murray himself remained active as one of the leaders of marine biology and in 1910, at the age of seventy, spent four months on the Norwegian vessel *Michael Sars*. From this cruise Murray, in collaboration with Johann Hjort and others, produced another classic, *The Depths of the Ocean* (1912).

The *Challenger* scientists with small pelagic nets had established that animal life was present in the middle waters of the ocean. Murray and Hjort on the *Michael Sars* studied this fauna thoroughly using vertically hauled closing nets which would sample only between precisely determined depths, and by the simultaneous horizontal towing of several nets set at a series of depths. In these ways reasonably quantitative data were obtained on the depth range and abundance of many pelagic animals. They discovered that in the surface waters (0—150m) fish and some invertebrates were mainly blue, while fish larval stages and other invertebrates were transparent ; a zone of middle waters (roughly 150—500 m, now termed "mesopelagic") was characterized by small silvery or greyish fishes with large eyes ; and below 500m ("bathypelagic") the fish were black, the crustaceans mainly red (and thus black when illuminated only by blue light), and other invertebrates were violet, dark-brown or black. Thus the life zones of the open ocean were largely discovered and characterized on this North Atlantic voyage.

The success of the *Challenger* expedition led scientists in many other countries to mount similar voyages of scientific exploration, while in Britain ocean research lay temporarily in the doldrums. This same period, however, saw the introduction here of a major innovation, the marine station. Most people do not live by the sea, and the study of marine life is too vital to be left solely to those fortunate enough to do so. Even the latter require aquarium facilities, microscopes and, nowadays, a wealth of sophisticated apparatus. To meet this need marine stations had been opened in France, at Concarneau (1859) and Arcachon (1863). But the real stimulus in Europe came from the German Zoologist Anton Dohrn (1840—1909). In 1867 Dohrn had visited David Robertson, an amateur naturalist living at Millport, to study crustaceans. The following year he was in Sicily, searching for a site to build a marine station. However, no doubt influenced by Professor Carl Vogt who had wanted to establish a marine station at Naples, it was Naples that Dohrn chose.

Dohrn obtained grants of money from the German and Italian governments, raised voluntary contributions in England and elsewhere, and provided the rest himself. The foundations of the famous Stazione Zoologica di Napoli, situated in a strip of parkland on the sea front, were laid earlier in the very year that H.M.S. *Challenger* sailed on her historic voyage : the formal opening took place in February 1874. Dohrn remained director for over 30 years and established the Stazione's international character. Expenses were met partly by receipts from the public aquarium but also from the rental of "tables" (laboratory space with concomitant facilities) by universities and other research institutions from all over the world.

In Britain there was increasing awareness of the importance

of food fishes and the fisheries dependent upon them. The first fisheries organization in the United Kingdom was the Fishery Board for Scotland, established in 1809, but given a research commitment in 1882. In the latter year also Professor W. C. M'Intosh (1838—1931), a practising physician besides being Professor of Natural History at St. Andrew's University, started to use the zoological laboratory for marine research, particularly the early development of fishes. In 1884 a grant from the Fishery Board facilitated the equipping of a wooden building near the harbour, and the St. Andrews Marine Laboratory thus became the first in Great Britain. A generous donation from Mr. C. H. Gatty in 1892 made possible the construction of a permanent building.

Also a reflection of the attention being paid to fisheries at this time were the fisheries exhibitions ; although the main incentive for these was commercial, to stimulate trade and provide entertainment. The first had been held at Arcachon, but similar exhibitions were subsequently staged in Britain : in Norwich (1881), Edinburgh (1882) and London (1883). The surplus profits from the 1882 exhibition were made available to the Scottish Meteorological Society to found a marine station. In 1884 John Murray converted a barge into a floating laboratory, calling it the *Ark*, mooring it at Granton, near Edinburgh, in an old quarry open to the Firth of Forth. In the following summer a shore laboratory was opened at Granton and Murray had the *Ark* towed through the Forth-Clyde canal to Millport, Great Cumbrae, where it was beached and subsequently supervised by David Robertson. Murray also brought his steam yacht *Medusa* to the Clyde, from which base he and his colleagues explored the hydrography and fauna of the Western Highlands' sea lochs. A permanent station was opened at Millport in 1897 but the *Ark* was destroyed in a storm three years later. The Scottish Marine Station at Edinburgh never received support from the Fishery Board and duly closed, but the Board established its own laboratory at Aberdeen in 1898.

The Millport laboratory was managed by the Marine Biological Association of the West of Scotland, which became the Scottish Marine Biological Association in 1914. The

S.M.B.A. remained at Millport until the late nineteen sixties, gradual transference to new laboratories at Dunstaffnage, Oban, being completed in 1970. Millport has now become the University Marine Biological Station, administered by the universities of Glasgow and London.

The fisheries exhibitions led to an appreciation that organized fisheries research in Britain lagged behind that in other European countries. An anonymous writer in *Nature* (vol. 28, 1883), pleaded that "the extraordinary contrast afforded by the British and Foreign exhibits . . . may lead to an effort on the part of the constituted authority to imitate in some way the action of foreign governments . . . in retaining the services of competent zoologists for the purpose of continually acquiring new knowledge in regard to fishes, and in particular of devising new ways of increasing and protecting the annual yield of fishes in the market." Consequent upon this situation T. H. Huxley, W. B. Carpenter, Ray Lankester, H. N. Moseley and other leading zoologists of the time met in March 1884 and founded the Marine Biological Association of the United Kingdom. The profits from the 1883 Exhibition had been otherwise committed, but the M.B.A. was promised a treasury grant, administered through the Fishery Research Board of Scotland, for the pursuance of "researches upon questions relating to the life-history and habits of food fishes". The famous M.B.A. journal first appeared in 1887, while the laboratory, finely situated on the Citadel at Plymouth, was opened in June 1888. The English fisheries laboratory at Lowestoft commenced work in 1902, as an offshoot of the laboratory at Plymouth. It is interesting to note that the Conseil Permanent International pour l'Exploration de la Mer (I.C.E.S. to most people), the co-ordinating body for fisheries research and legislation in Europe, was founded in the same year.

In 1885, at the time of the removal of the *Ark* to Millport, the Liverpool Marine Biological Committee was formed by the joint action of a group of professionals, led by W. A. Herdman, Professor of Oceanography at the University College of Liverpool, and amateur naturalists. At first the Committee conducted its field work from borrowed vessels, but the fauna

near the Mersey was unexciting and the need for a laboratory in North Wales was recognised. This was met by the loan in 1887 of the disused Dock Board Signalling Station situated on the seaward point of Puffin Island (Ynys Seiriol), off the northeast corner of Anglesey. Herdman initiated and edited the *Reports on the Fauna of Liverpool Bay and Neighbouring Seas* that are so well-known to all those that have conducted faunistic work in North Wales. In 1892 the activities of the L.M.B.C. were transferred to a pair of small stone buildings on the shore of Port Erin Bay in the Isle of Man, and the Puffin Island station was taken over by the University College of North Wales, though it was later closed.

After nine years at Port Erin the buildings became inadequate to accommodate the number of visitors, and a further move was made in 1902 when the original building of the present station complex was opened. Ownership was transferred to the University of Liverpool in 1919. Since then the Marine Biological Station has undergone many alterations and additions, and it is surely appropriate that the Isle of Man, birthplace of Edward Forbes and locale of his early dredgings, should now support this flourishing centre of marine research.

Marine Biology was restored to the University College of North Wales in 1949, largely through the initiative of the late Professor F. W. Rogers Brambell. After a serious early misfortune, the death of the first appointee, Dr. Fabius Gross, the vacancy was filled by the appointment of Dr. D. J. Crisp as Director of the Marine Biology Station. A building in Menai Bridge, on a site commanding a good view of the Strait, was purchased in 1953 and added to in 1958. In the two ensuing decades expansion and development have created an impressive building complex and established the Marine Science Laboratories, as they became, as one of the major marine institutions in the United Kingdom.

Turning again to the progress of marine biological science, important developments in the study of plankton were taking place outside Britain, particularly at Kiel, in Germany. Here Victor Hensen (1835—1924) and his colleagues were experimenting with vertically hauled nets carefully designed to filter completely a column of water of known cross-sectional area. This enabled the number of organisms in the plankton below a known surface area to be calculated. In turn this facilitated, for example, the assessment of the size of a fish population from the computed number of eggs present above the spawning grounds. But it also started to reveal that plankton was very unevenly distributed, such that a pair of nearby hauls might differ substantially in the composition of the catch. Expeditions such as the S.S. *National* (1889) for Germany and, later, the *Thor* for Denmark extended the observations from west European waters into the Atlantic and Mediterranean. Today most studies on marine life are essentially quantitative, and it was Hensen who pioneered this approach.

We shall see how, a few years later, problems associated with the unevenness of plankton were of particular interest to A. C. Hardy who, in 1921, started to study the herring at the Lowestoft Fisheries Laboratory. In particular he noticed the patchy distribution of herring larvae and also realized that adult herring were absent from areas of dense phytoplankton. To record such variable distributions Hardy devised his first continuous plankton recorder : this essentially was a device towed behind a ship to obtain an unbroken record of the plankton over a distance of several miles.

Sir John Murray's death in 1914 had brought an era to its end. With the *Challenger* reports completed, and the main marine stations in operation, the early years of the twentieth century constituted a relatively uneventful period in British marine biology. Just at this time, however, the attention of our marine scientists was being focussed on an entirely new enterprise. The nineteenth century had seen the elimination from the North Atlantic, through rampant overfishing, of first the right whales and then the faster swimming rorquals that successively formed the basis of the European whaling industry. Then, at the turn of the century, its total demise was prevented by the discovery of enormous rorqual stocks in the Antarctic. At this time, before the days of factory ships, whales were towed by the catchers to shore stations for flensing, and the government levied a tax on the oil extracted. Scientists were aware of the danger to the Antarctic whales : rapacious exploitation on the northern pattern would soon reduce even

these great stocks to the level of near extinction (as indeed it has). It was thus concern partly for the whale stocks, but also for the future of the Falkland Islands' Dependencies (now British Antarctic Territory) that led to the establishment of a rather unusual government committee. The Report of the Inter-Departmental Committee on Research and Development in the Dependencies of the Falkland Islands was presented to Parliament in April, 1920.

The Committee proposed that the oil revenues should be used to promote and finance a scientific study of whale biology and research into hydrography and plankton of the type which had successfully been developed by the I.C.E.S. countries in Europe. The Committee recommended the equipping of a vessel for oceanographic research in southern waters and the *Discovery*, which had been used by Capt. R. F. Scott on his 1901-03 Antarctic expedition, was purchased. The planning committee, thenceforward known as the *Discovery* Committee, recognized the need for a second ship, designed as a whale-catcher and trawler. This was built and appropriately named *William Scoresby*. Dr. Stanley Kemp was appointed Director of Research and Leader of the Expedition : his first member of staff was A. C. Hardy. There is neither the need nor the opportunity to retell the story of the first *Discovery* voyage (appropriately described in 1928 by Sir Sidney Harmer as "the largest and most important scientific expedition that has left our shores since the time of the *Challenger*"), or those of the R.R.Ss. *William Scoresby* and *Discovery II* which followed. While they did not prevent the decimation of the southern whale stocks, they did obtain a vast amount of information about them and their environment which has been presented in the *Discovery* Reports. The interested reader is referred to Sir Alister Hardy's personal account in *Great Waters* (1967).

The first *Discovery* voyage (1925-27) provided Hardy with an opportunity to give the prototype of his continuous plankton recorder a thorough testing. With this experience, upon his return to England and appointment to the Chair of Zoology at the University College of Hull, Hardy was able to perfect the design of his invention. The continuous plankton recorder is a torpedo-shaped machine incorporating a diving plane, stabilizing fins and rudder. When towed on a set length of warp behind a ship at steady speed, it dives to a constant depth of 10m, automatically sampling the plankton. A propellor, rotated by its passage through the water, steadily draws a band of silk plankton netting across the through-flowing stream of water, and winds it into a container of preservative. In this way a continuous record is obtained of the composition and abundance of plankton along the ship's path.

By 1931, with the co-operation of ship owners, Hardy was ready to instigate trials across the North Sea, using a recorder which has since been little modified. Six years later the routes were extended into the northern waters of the North Sea and a new laboratory was opened at Leith. By the outbreak of war in 1939 some 90,000 recorder miles had been completed, and the *Hull Bulletin of Marine Ecology* (later simply the *Bulletin of Marine Ecology*) started publication. The war, inevitably, curtailed development and the Leith laboratory was closed : but a new method of exploring the sea of great potential value had been invented and successfully brought into use.

Hardy moved to Aberdeen in 1942 and then to Oxford, as Linacre Professor of Zoology and Comparative Anatomy, in 1946, remaining Honorary Director of the Recorder Scheme. Then, in 1950, the entire organization was transferred to Edinburgh to become the Oceanographic Laboratory of the S.M.B.A. New routes were added, in particular reaching westwards to the ocean weather ships and then right across the Atlantic, each route being traversed once a month. One result was the discovery of great numbers of larvae of the redfish (*Sebastes*)—an important food fish little esteemed in Britain—to the southwest of Iceland. The American government, through the Office of Naval Research, started to contribute to the operational costs in 1961. By 1973 the recorders were being towed 120,000 miles annually, and the Director (Mr. R. S. Glover) and staff of the Oceanographic Laboratory published *A Plankton Atlas of the North Atlantic and the North Sea*, a compendium of nearly 300 maps showing the comparative abundance of planktonic organisms at a depth of 10m. The first practical achievement of the scheme is thus an outstanding

contribution to marine biogeography, establishing the spatial distribution of many species.

The compilation of quantitative data on the spatial distribution of species is important particularly in that it provides the baseline for monitoring future changes. Hardy himself was well aware of this potentiality and of its contribution to the study of meteorological conditions and effects of major climatic trends which control the distribution of plankton. Some of such trends were discussed in the 1974-75 Annual Report of the Institute of Marine Environmental Research (which organization assumed responsibility for the Oceanographic Laboratory from the S.M.B.A. in 1970). The report notes the high degree of coherence in patterns of variability over the sea area covered, indicating large-scale climatic change affecting much of the northern hemisphere. A long-term decline in zooplankton biomass has been observed (exemplified by the decreasing abundance of the copepod *Pseudocalanus elongatus* in the North Sea), coupled with a progressive delay in the onset of the spring phytoplankton bloom. A related phenomenon is the change in spatial distribution of planktonic species, featuring a southerly shift in the area occupied. An example is provided by the mid-water oceanic fish *Stomias boa*, the larvae of which have disappeared from the deep water to the west of Ireland but are now plentiful in the Western Approaches to the English Channel. These changes appear to be correlated with the existence of high atmospheric pressure over Greenland during the nineteen-sixties.

The survey also yields results that are clearly related to either the understanding or development of fisheries. One example is provided by Dr. J. M. Colebrook and Mr. G. A. Robinson in a series of papers devoted to variations in the seasonal cycle of phytoplankton production as indicated by the greenness of the recorder silks. These revealed that, moving from the Atlantic Ocean through shelf-edge areas into coastal waters, the biological season lengthens because the spring phytoplankton bloom develops progressively earlier (peaks in June, May and April respectively). All these areas show a subsidiary peak in autumn. The North Sea is unusual in that the autumn (October) peak is of as great or greater magnitude than that of the spring outburst. The increase in the number of copepods, which graze the phytoplankton, and their seasonal abundance, essentially follows the phytoplankton production curve. Thus copepods are extremely scarce in oceanic waters between January and March. The young stages of copepods (nauplii and copepodites) on which many fish larvae depend are therefore most abundant at somewhat different seasons in the various sea areas.

It has for long been known that herring stocks in the various sea areas spawn at different times of the year, ranging from early in the autumn through winter to spring. Dr. D. H. Cushing, of the Fisheries Laboratory, Lowestoft, has pointed out that there exists an important correlation between the season of spawning of the herring and the timing of the spring phytoplankton bloom. In general terms, autumn-spawning herring are found in the central North Sea, winter spawners are located in coastal waters, and spring spawners are found in more oceanic waters of the shelf. In the North Sea the production cycle is prolonged by high autumn productivity, implying that copepod young stages will provide the herring larvae with food from September to November. The winter herring are spawning in the English Channel and off the south-east of Ireland. Their larvae will need food in February, by which time the production cycle is well under way. Finally, the spring spawners of our western coasts will have larvae in the sea coincidentally with the production outburst in late spring. It thus seems that the annual biological cycle of the herring, which not only differs in phase around the coasts of the British Isles but determines the timing of the fishery, can be related to the seasonal production cycle of phytoplankton and, hence, copepods.

My final example concerns the discovery of stocks of the Blue Whiting (*Micromesistius poutassou*) in the Rockall Bank area. The presence of larvae of the little-known blue whiting over extensive areas of the North Atlantic had been established by Johannes Schmidt during the Danish *Thor* expeditions (1908-10), but it was the continuous plankton recorder survey that revealed the astonishing abundance of these larvae and their localization in specific areas. Members of the Oceanographic Laboratory have published a number of papers in the *Bulletin of Marine Ecology* showing that the blue whiting larvae are most abundant over deep water in an area south-east of Rockall ; that there they are by far the most abundant fish larvae in the plankton ; and that there is a very short period of peak abundance, with eighty per cent of the larvae being recorded during April. (It will be noticed that appearance of the larvae coincides with the period of most rapid increase of phytoplankton and copepods in shelf-edge oceanic areas.) Numbers of larvae expanded during the decade 1955-64, but there has been subsequently a shift in the spawning area southwards towards the Porcupine Bank (120 miles west of Ireland). A Russian echo-sounder plus trawling survey located spawning concentrations of fish on the Porcupine Bank in March 1965.

Such a superabundance of blue whiting larvae indicated a very large fish stock and this, since the early sixties, has been thoroughly investigated by scientists from the Marine Laboratory at Aberdeen. In 1967-69, when the continuous plankton recorder surveys were revealing a substantial movement of the spawning stock from Rockall to the Porcupine Bank, quantitative egg surveys in the former area indicated a minimum of 1.05 billion (10^9) and a maximum of 7.23 billion spawning females or a total stock biomass of 0.205—1.65 million tonnes. The fish are in deep water and concentrated only for a short season, but there is clearly the potentiality of obtaining a very substantial catch from this newly-discovered stock.

In this brief survey we have looked at only a few of the more important people and significant events in the development of marine biology in Britain. This started with the collector naturalist on board an Admiralty vessel making what was essentially either a voyage of exploration or a hydrographic survey. Contemporaneous were the activities of the shore naturalist, who in due course took to the shallow sea with townet and dredge. We have seen how these two lines of investigation converged to produce voyages specifically for scientific inquiry, of which the first and greatest was that of H.M.S. *Challenger*.

As the study of marine animals became more penetrating, it demanded the availability of live specimens, the facilities of a well equipped laboratory, and access to a specialist library. So the marine stations were founded, soon to diversify into fisheries and pure research laboratories. The study of our marine fauna ceased being essentially either taxonomic or morphologic, but was orientated towards answering the questions where ? why ? how ? and (in particular) how many ? I have discussed one example, showing the increasingly quantitative nature of plankton research : but several others could equally well have been chosen.

Contemporary marine biology has become, in the *Challenger* tradition, what is known as "big science" and government financed (through the Natural Environment Research Council), whether concerned primarily with fisheries or with background studies. It is heavily dependent on costly ocean-going vessels and teams of skilled scientists, while the back-up work is often labour intensive ; although opportunities remain for the contributions of smaller groups and individuals. Indeed, ultrastructural research, genetical taxonomy, and experimental ecology and physiology remain essentially the preserve of university departments ; such investigations complement, and in many ways support, the systems ecology and ocean research of government institutions. The combined programmes help slowly to assemble the complex jigsaw of life in the sea and so continue man's preoccupation with explorations in marine biology.

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