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EDITORIAL

Pioneers of Plankton Research: Alister Hardy (1896-1985)

Alister Hardy is known among plankton researchers for developing and employing his Continuous Plankton Recorder (CPR). The CPR likely needs no introduction. Hardy used the first version of the CPR during the 1925-1927 *Discovery Expedition* to the Southern Ocean (Fig. 1). By the last count attempted, 30 years ago, there were already over 400 publications based on CPR data (Gamble & Hunt 1992). In more recent years, several reviews have been devoted to CPR studies (e.g. Planque & Reid 2002; Reid et al. 2003; Richardson et al. 2006; Baten & Burkill 2010). However, while the CPR is well known, many plankton researchers today are likely unfamiliar with the story of its genesis and its precursors, as well as the full breadth of Hardy's contributions to plankton research. Here I will attempt to provide an introduction to the plankton research of Alister Hardy. Summaries will be provided of his extensive plankton work, beginning with studies of the food of herring in early 1920's, and ending with his last article, published posthumously, on 'aerial plankton' in 1986. As the CPR studies of Hardy have received substantial attention, CPR development and the early surveys will be but briefly covered. The following account is based on both Marshall's biographical Memoire of Hardy (Marshall 1986) and Hardy's articles and books.

Alister Clavering Hardy was born on the 10th of February 1896 into a relatively well to do family. He attended a good preparatory school (Bramcote) followed by the public school Oundle, and in 1914 was admitted to Exeter College of Oxford University. Hardy's college education was interrupted by the outbreak of the First World War. Hardy first served as commissioned officer, an Acting Captain, in charge of a company assigned the duties of digging and manning trenches along the East Coast of England followed by service as an assistant camouflage officer in London. Hardy finally returned to Oxford in 1919 and there focused on zoology. It was an Honors Class on vertebrate zoology where he met his future wife, Sylvia Garstang. In 1920 (at age 24), Hardy was awarded an Oxford scholarship, the Christopher Welch Scholarship allowing him to work at the *Stazione Zoologica* in Naples for six months. It was a key event in Hardy's life as it was in Naples that he was introduced to marine plankton. Hardy graduated from Oxford in 1921, and interested in plankton, immediately went to work as an Assistant Naturalist at the Fisheries Laboratory in Lowestoft, charged with investigating relationships between plankton and fisheries.



Fig. 1. Alister Hardy aboard the *HMS Discovery* in 1925.

Hardy began at Lowestoft on August 1, 1921 and by the last week of August, he was already sampling the plankton during survey cruises searching for herring spawning grounds. In his first publication on plankton, he reported on swarms of pteropods off the East Coast of England found in August and September of 1921 (Hardy 1923). By March of 1922, Hardy was engaged in his massive study of the food of herring, from the larval stage to maturity, that he would publish in 1924 (Hardy 1924). He examined the contents of 11,656 adult herring and the gut contents of 2,330 larval and post-larval herring. He used his data, and the previous findings of Marie Lebour (see Dolan 2021), to construct the truly remarkable comprehensive vision of herring predator-prey relationships throughout the life history of a herring shown in Fig. 2. The work solidified Hardy's reputation as a plankton specialist. The original diagrammatic version of 1924 was used by Elton in his classic text "Animal Ecology" (Elton 1927), one of the first textbooks of ecology.

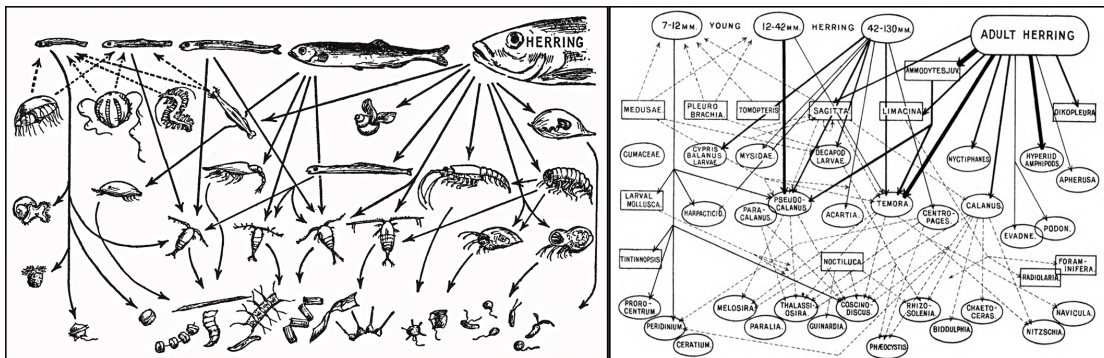


Fig. 2. The two versions of Hardy's illustrations of the trophic relationships of herring from larvae to adult. The right panel is the original diagram from Hardy's 1924 report "The herring in relation to its animate environment. 1. The food and feeding habits of the herring". It was based in large part on his examination of thousands of herring stomachs. The left panel is the 'cartoon version' from Hardy's 1959 popular book, "*The Open Sea. Its Natural History. II. Fish and Fisheries, with Chapters on Whales, Turtles and Animals of the Sea Floor*".

It was also, early on, in March of 1922 that Hardy made a discovery that would lead him to eventually developing the CPR. The March survey cruise aboard the *George Bligh* (Fig. 3) was to map the distribution of herring in the southern portion of the North Sea. Having completed sampling a day earlier than planned, Hardy decided to repeatedly sample a single station every 6 hours throughout last 24 hours of the planned sampling days. He found that variability among the 4 samples was greater than among all the stations sampled. According to Marshall's account of Hardy's life (Marshall 1986), it was this experience that convinced Hardy of the need to sample large areas quickly as possible to acquire a synoptic view of distributions, thus the need for a device continuously sampling young fish and plankton, documenting variability mile by mile. However, the CPR was not to be Hardy's first foray into designing new devices to sample the plankton. The first invention of Hardy was an instrument he called the "Plankton Indicator" and it was designed to be a fisherman's aide.



Fig. 3. The R.V. *George Bligh* of the Lowestoft fisheries laboratory.

Hardy had found, as had others before him, that copepods were scarce in waters with dense phytoplankton populations of diatoms or *Phaeocystis* and adult herring feed predominately on copepods. Presumably, herring would not be found in areas with few copepods such as those with dense phytoplankton populations. If fisherman could avoid fishing in waters with dense phytoplankton populations, they could avoid poor catches so a simple device allowing diagnosis of the phytoplankton of an area should be of some value. The Plankton Indicator was such a simple device, basically a small open torpedo with a removable filtering gauze (Harding 1926a). It was to be towed for a short period, retrieved, and the later the gauze inspected for signs of having sampled, or not, an area of dense phytoplankton populations. The first trials of the device by fisherman were in 1922 and 1923. His analysis of the retrieved filters and the catches of the fisherman led Hardy to conclude that a green or pale filter was negatively related to herring catch. However, to be used by the fisherman a smaller instrument, and one allowing on the spot diagnosis by the fisherman, was needed. Such a device would be developed, but many years later, as Hardy abandoned his post at Lowestoft to participate in the *Discovery Expedition* to explore the plankton of the Southern Ocean. Expedition work would occupy him for years to come.

It was in May of 1924 that Hardy started work on the *Discovery Expedition*. The expedition goal was to investigate the biology of the southern ocean whaling areas with a special focus on krill, known to be an important prey of whales. Stanley Kemp was named Director of Research and Expedition Leader. Hardy was named by Kemp "Chief Zoologist, Discovery Expedition". He was the first member of staff and was shortly joined by 3 other staff members (J.E. Hamilton, Rolfe Gunther, and H.F.P. Herdman). The five scientists of the Expedition worked in a room of the top of the colonial office in London, designing the laboratory and sampling equipment for the voyage. According to Hardy himself, it was then and there that he invented the first version of his CPR (Hardy 1967). It was formally introduced, along with some preliminary results from the expedition sampling, in a short article in *Nature* (Hardy 1926b). The complete, detailed description of the CPR version similar to the one used today (fig. 4), and the data gathered with it, finally appeared in 1936 in one of the many volumes of the *Discovery Reports* (Hardy 1936a).

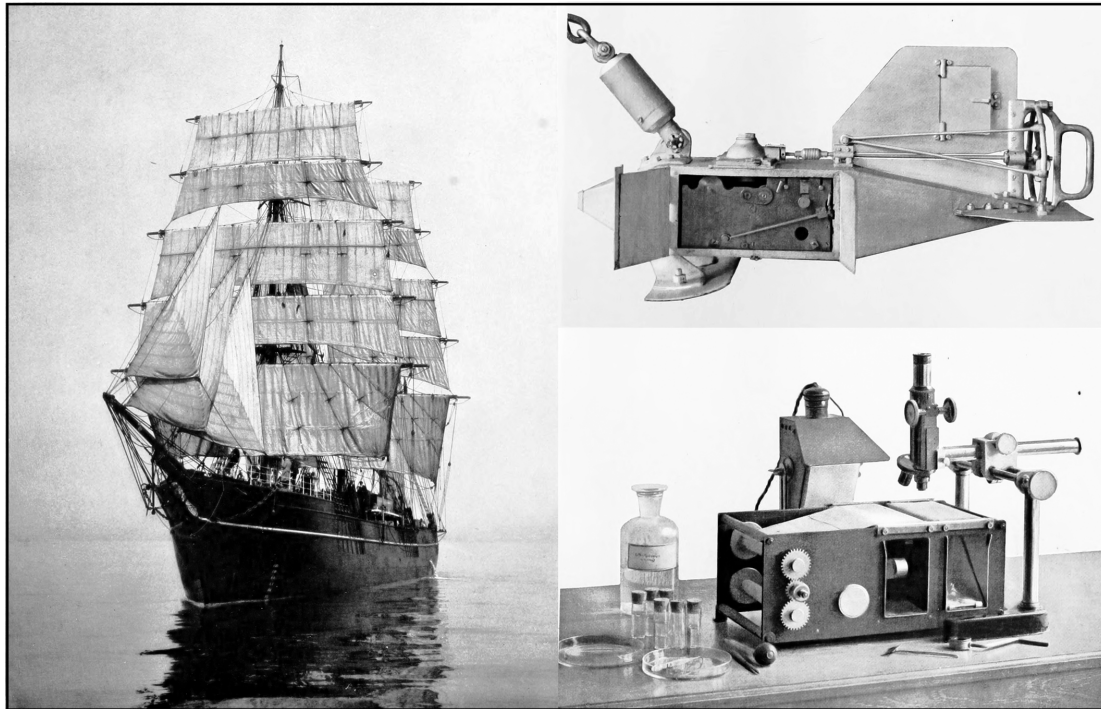


Fig. 4. The *HMS Discovery*, one of the two ships used during the Discovery Expedition of 1925-1927 (left panel). The right panels show one of the later versions of the CPR (relative to the one shown partly in Fig. 1) with the door open exposing the sampling core (upper right panel) and the sample core removed to allow examination of the CPR silk with a specially adapted microscope.

According to Marshall (1986) Hardy's major findings from the *Discovery Expedition* with regard to the ecology of the plankton in the Southern Ocean were: 1) that phytoplankton production removed phosphorus from surface layer. Consequently areas low in phosphorus had recently experienced dense phytoplankton population. 2) More importantly, phytoplankton production was negatively related to the concentrations of *Euphausia superba* and 3) *Euphausia* concentrations were positively related to the abundances of Blue Whales and Fin Whales. The positive relationship of the Blue Whale to its euphausiid prey and the negative relation of the euphausiids with dense phytoplankton populations thus resembled Hardy's previous observations concerning the herring, its copepod prey of *Calanus* and dense populations of diatoms or *Phaeocystis* in the North Sea. Hardy would later formally propose his "hypothesis of animal exclusion" to account for the negative relationships between the concentrations of phytoplankton and their grazers (Hardy 1935a, 1936b). In the meantime however, Hardy had a pressing need upon his return from the *Discovery Expedition* to find a job. He was soon to be married, having proposed by post during the Expedition, to Sylvia Garstang.

In what Hardy described as most lucky coincidence, his return from the *Discovery Expedition* coincided with the opening of a new external college of the University of London in Hull (on the East Coast of England), University College Hull. Hardy was named Professor of Zoology in 1928 and profited from the university workshops in further developing both the CPR and a new version of

his Plankton Indicator. Hardy published the bulk of his work on the *Discovery Expedition* while at Hull where he remained until 1942. It was also while at Hull that the first CPR surveys were conducted (Hardy 1935b). These early efforts in CPR studies are relatively well known (e.g., Reid et al. 2003). However, during his time at Hull, Hardy's plankton work extended well beyond the CPR and this work is not well known as it has been overshadowed by the CPR studies.

During his Hull years, Hardy was involved in another historic expedition, the *Nautilus Expedition* of 1931. Harald Svedrup, who would later head the Scripps Institution of Oceanography, was the chief scientist. It was the first attempt to cross the Arctic by submarine. The United States Navy Department supplied a submarine, the *O 12*, which was modified for traveling under pack ice and rechristened the *Nautilus*. The modifications made turned out to be largely insufficient as the *Nautilus* was beset by a very large number of mechanical problems. A small example is that Hardy had supplied a CPR but it failed to function (Svedrup & Soule 1933). However, several samples of arctic plankton were collected using closing Nansen nets lowered through a sampling hatch, a modified torpedo hatch. The samples were obtained at 81°N, representing some of the first high latitude plankton samples. Hardy was entrusted with the plankton samples and sent aliquots to experts on various taxa but analyzed the microplankton components of the samples (diatoms and protists) himself. He found the diatoms and protists, mostly tintinnids, to be rather low in species diversity, representing no new forms but rather a subset of those known from previous arctic sampling at lower latitudes (Hardy et al. 1936).

Hardy also returned to his Plankton Indicator during his Hull years, designing and promoting a new version. As mentioned above, the first version he created while at Lowestoft, showed promise as a means of identifying waters likely unsuitable for fishing herring. However, it was somewhat unwieldy and most importantly, did not provide on the spot diagnosis, nor indication of waters promising, for fishing herring. The 'Improved Plankton Indicator' (Hardy 1936c), was first employed in the summer of 1930. The new version was small (56 cm long) and designed to provide easy, on the spot indication of the plankton for fisherman. The filtering silk, held between two rings, was be examined on board using a hand held magnifier and compared with photos of 'type samples' (Fig. 5). Unlike the CPR, the Plankton Indicator was patented by Hardy "... and marketed for commercial use by Messrs. V.D. Ltd., 54 Victoria Street, London, S.W.1, the inventor's royalties on commercial sales being devoted to further research for the benefit of the industry. Investigators who wish to use the instrument for research purposes may obtain it from Messrs. V.D. Ltd., at a specially reduced rate." (Hardy 1936c). Unfortunately, I could find no indication of the price of the device! The Plankton Indicator was a clever simple instrument. However, in stark contrast to the CPR, it can not be said to have been widely employed. I could find no documents attesting to any use by fisherman. With regard to use as a device for plankton research, other than some studies published in Hardy's own "*Hull Bulletins of Marine Ecology*", it appears that very few people have employed the "Plankton Indicator". I could find only 3 publications in which Hardy's Plankton Indicator was used (Gibbons 1937; Wiles 1951; Jones 1984), suggesting scant use by plankton researchers.

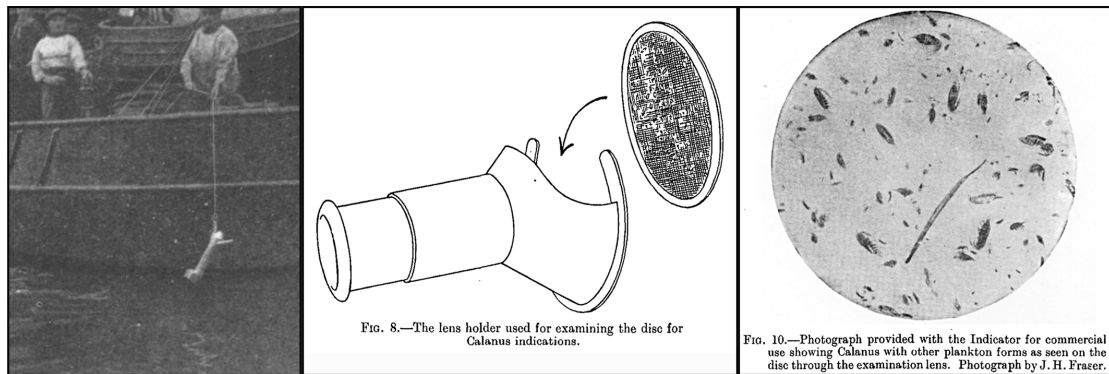


Fig. 5. Illustrations from Hardy 1936c on the new version of the Plankton Indicator. The left panel shows the Plankton Indicator being deployed on a fishing vessel. The middle panel is an illustration of the hand-held magnifying device, the lens holder, allowing on the spot examination of the filter removed from the Plankton Indicator. The right panel is a photograph of a filter towed for 1 km through waters promising for herring fishing as several *Calanus* copepods are evident. The booklet supplied with the device and lens holder contained images of several filters from desirable, and less than desirable, waters with regard to probabilities of good herring catches.

The Hull years of Hardy was also when he conducted pioneering work on "Aerial Plankton", the organisms transported passively by currents in the atmosphere. His interest in atmospheric transport of organisms was sparked by seeing masses of locusts transported by the winds during the Discovery Expedition (Marshall 1986). His first samplings were apparently aboard the *George Bligh* from Lowestoft where Hardy began his plankton studies. He deployed plankton nets from mast or attached to a kite when the ship was on station during a survey of the southern North Sea. He collected fairly large numbers of insects using nets of about one or two meter diameter and concluded that the numbers suggested that large populations of 'aerial plankton drift over the seas' (Hardy & Milne 1937). The next study was a land-based sampling using closing plankton nets brought up to heights of hundreds of meters with large kites suspended on piano wire (Fig. 6). Hardy and Milne found a large variety of insects with a preponderance of forms with large wing surface area relative to body mass and also suggested that aerial transport of insects could be responsible for the dispersal insect pests (Hardy & Milne 1938a). This later publication was followed a substantial article in the *Journal of Animal Ecology* entitled "Studies in the distribution of insects by aerial currents: experiments aerial tow netting from kites" (Hardy & Milne 1938b). Alister Hardy's last scientific publication, published posthumously in 1986, was entitled "Studies in the distribution of insects by aerial currents. III. Insect drift over the sea" and was based sampling using nets suspended from the masts of ships traveling from Scotland and England to destinations in Germany and Nordic countries (Hardy & Cheng 1986).

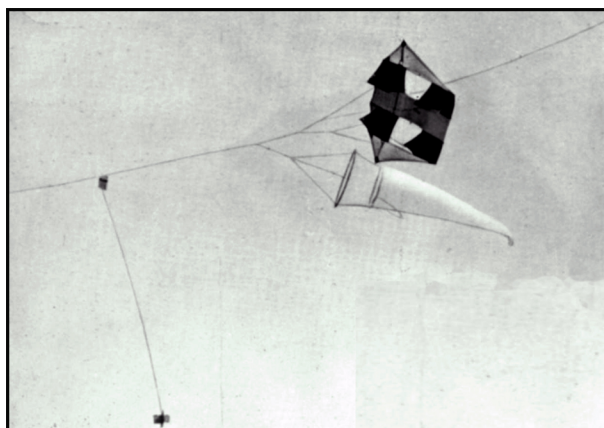


Fig. 6. An image of the aerial plankton net designed and used by Hardy and Milne to sample organisms transported by atmospheric currents (from Hardy & Milne 1938b).

In 1942 Hardy left Hull for Aberdeen University to occupy the Regis Chair of Natural History and but a few years later was named Professor of Zoology at Oxford. Hardy's plankton research after leaving Hull was dominated by studies of vertical migration among metazoan zooplankton carried out first at the Millport Marine Station, and later at the Plymouth Marine Laboratory. Some of the results from the first investigation (Hardy & Paton 1947) suggested that migratory behavior might be influenced by the different pressures encountered at different depths. In the second study, pressure effects on behavior were examined. While the copepod *Calanus* showed no effects of pressure on behavior, crab larvae did show an effect on behavior suggesting that decapods may have some sort of unknown pressure receptor (Hardy & Brainbridge 1951). In the last paper on vertical migration, a device for tracking the activities of individual organisms was used, it was likely the first such device. General relationships concerning vertical migration, based on observations made on a large variety of both marine and freshwater taxa, were proposed. These included that movement of the animals is directed, including downward migration (rather than passive sinking), and that upward migration is a positive taxis toward low light intensities and not a negative geotaxis. The 1954 paper describing the work (Hardy & Bainbridge 1954) is still regularly cited today. Interestingly, during this last period of scientific work, Hardy was still concerned with the patchy distribution of plankton he first saw in 1922 working in Lowestoft. He published a paper using data from consecutive, nearly overlapping net samples, taken during the *Discovery Expedition* in 1927. While steaming at about 4 km h^{-1} , a net was deployed for 10 minutes and while being recovered another was deployed, over a 20 km transect. The data clearly showed very considerable horizontal patchiness at the scale of 100's of meters, a patchiness pointed out by Hardy to be undetectable by his CPR (Hardy 1955). Alister Hardy's last paper on marine plankton concerned light production by planktonic organisms (Hardy & Kay 1964). Hardy had started working on luminescence in the ctenophore *Bolinopsis* in the early 1950's and in natural populations of dinoflagellates and the euphausiid *Meganyctiphanes* in the early 1960's.

Although not concerned with plankton, it would be remiss in an essay on Alister Hardy, to omit mention of two articles he published in 1960 that became famous, or notorious, depending on one's point of view. Both appeared in the magazine the *New Scientist* in March 1960, based on a lecture Hardy had given to British Subaquatic Club. The first article (Hardy 1960a), "Was man more aquatic in the past?" raised the hypotheses that *Homo sapiens* evolved as an inhabitant of the seashore, exploiting fish and shellfish of shallow depths. As supporting evidence Hardy cited diverse lines ranging from existence of a layer of fat underlying the skin in humans similar to that of marine mammals, to our general attraction to the seashore. The article has been cited hundreds of times. In the second article, appearing the following week (Hardy 1960b), "Will man be more aquatic in the future?" Hardy prophesized that humanity would necessarily, in 100 years time, return to the seashore through aquaculture and fishing. Needless to say, Hardy's views provoked reactions (Rozwadowski 2022).

Following his retirement as Professor of Zoology at Oxford in 1963, Hardy's focus broadened to a long-time preoccupation of his, as a deeply spiritual man, the subject of religious experiences. He responded to an invitation to give a series of lectures on the subject, Gifford Lectures, which formed the basis of two books Hardy published. The first was "*The Living Stream: a Restatement of Evolution Theory and its Relation to the Spirit of Man*" (Hardy 1965). In it Hardy proposed the hypothesis that having religious experiences was a favorable characteristic of awareness in the evolution of humans (e.g. Hay 1994). The second book was "*The Devine Flame: an Essay toward the Natural History of God*" (Hardy 1966) which concerned in large part accounts of religious experiences (Marshall 1986). Alister Hardy used the royalties from the sales of the books to fund, in part, a research institute housed in Oxford, the Religious Experience Research Center in 1969. Today it still exists as the Alister Hardy Religious Experience Research Center at the University of Wales with an associated journal, the *Journal for the study of Religious Experience*.

However, in the latter years, Hardy's activities were not limited to studies of religion. He was also a veritable proponent of plankton research through popular books in which plankton studies were prominent and the beauty of plankton shown using his own striking watercolors. The first was "*The Open Sea Its Natural History: The World of Plankton*" published in 1956. It was reviewed very favorably, with comments on the beauty of Hardy's artwork, in both *Science* (Hedgpeth 1957) and *Nature* (Marshall 1957). A second volume followed in 1959 "*The Open Sea. Its Natural History. II. Fish and Fisheries, with Chapters on Whales, Turtles and Animals of the Sea Floor*". The volumes were illustrated with Hardy's artwork including 24 color plates, 17 of which showed the organisms of the plankton (e.g. Fig. 7). The second popular work of Hardy was his book on the *Discovery Expedition*, based upon his own journal notes and artwork from the voyage, *Great Waters* (Hardy 1967). While the main focus was telling the tale of the expedition he included several color plates showing not only the plankton of the southern ocean but also the plankton of the tropics encountered during the voyage (e.g. Fig. 8).

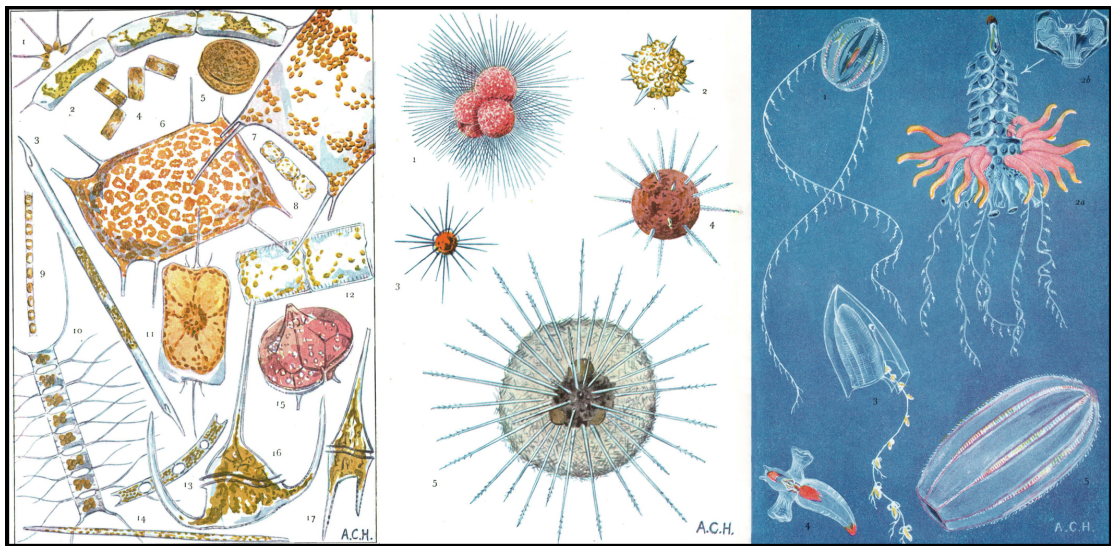


Fig. 7. Examples of Hardy's plankton artwork showing (from left to right), phytoplankton, microzooplankton, and gelatinous organisms from his popular 1956 book "*The Open Sea Its Natural History: The World of Plankton*" (Hardy 1956).



Fig. 8. Examples of Hardy's plankton artwork from his popular 1967 book on the *Discovery Expedition*, "*Great Waters*". The left panel is a plate showing the organisms he observed during transits through tropical waters. The right panel is a plate showing organisms from the Southern Ocean, *Euphausia superba* at the top and organisms from deep plankton tow in the bottom square.

Alister Hardy was a pioneer, a promoter, and a populariser of plankton research. His first studies revealed the complex food web of the plankton supporting the herring fishery. Hardy early on began developing sampling devices to reveal patterns of the distributions of planktonic organisms, and among them, the CPR has proven invaluable. Less well known is that Hardy also worked on "aerial plankton" making valuable contributions to our knowledge of atmospheric transport of insects and conducted several studies examining the vertical migrations of zooplankton as well as bioluminescence in the plankton. Nearly throughout his career, Hardy made efforts that today would be characterized as 'outreach': from lectures such as 'Plankton Ecology in the Service of Man' (Hardy 1943) to his popular books in the late 1950's and 1960's. Hopefully, with this essay, the present generation of plankton researchers will know a bit about the man of the CPR and the full range of his plankton work.

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