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Pioneers of Plankton Research: Sheina Marshall (1896-1977)

Sheina Marshall (Fig. 1) is known to senior workers in the field as an important figure in plankton research. In the 1960's, the names of Sheina Marshall, and her long-time collaborator Andrew Orr, were said to be familiar to every worker in marine biology and fisheries (Yonge 1962) and that "Anyone attempting to study the biology of the marine plankton would not get far into the literature before becoming aware of the notable contributions made to this field by Sheina Marshall and the late A.P. Orr" (Dorsett 1966). Bruce Frost named a species of copepod for her, *Calanus marshallae* (Frost 1974). Recently, Gustav Paffenhöfer described Marshall as the "Queen of Copepods" (Paffenhöfer 2018). However, to the younger generation of plankton researchers, the work of Sheina Marshall may not be well known. This editorial aims to introduce her to them, and her substantial and varied contributions to plankton research. Marshall's work on plankton was mainly concentrated on copepods, thus explaining her being attributed the title "Queen of Copepods". However as will be shown here, Marshall early on did important work on a variety of other planktonic taxa such as diatoms, dinoflagellates, ciliates and larval fish. She also worked on the effects of artificial fertilization on plankton. A brief sketch of her life and career will be given and some of her 'notable contributions' to our field will be highlighted. The account here relies heavily on the biographical memoir by Frederick Russell, which includes a complete bibliography of Marshall's publications (Russell 1978), and on the short review of Sheina Marshall's life given in Coliss (2008).



Fig. 1. Sheina Marshall, in 1924, at age 28, Assistant Naturalist at the Millport Marine Biological Station.

Sheina Macalistar Marshall was born on April 20th 1896. Her early bent towards biology may have been influenced by her father, John Marshall. He was a medical doctor but also a naturalist, the founder of the Buteshire Natural History Society. She first attended Glasgow University in 1914, but with the outbreak of the First World War, left the university for a year to work in her uncle's factory, that manufactured luminous dials for the military. She returned to Glasgow University in 1916 earning a B.Sc. degree with honors in 1919. In 1920 she was awarded a Carnegie Fellowship to pursue research in biology under the guidance of John Kerr, a Professor of Zoology. As a Carnegie Fellow, she published her first paper in 1921 on the anatomy of an embryo of an anteater (Marshall 1921) and second paper on the freshwater hydrozoan *Hydra* (Marshall 1922). At the end of her fellowship, on the advice of Kerr (Coliss 2008), she took a job at the Scottish

Marine Biological Association's newly created Millport Biological Laboratory, on the small island of Great Cumbrae in the Firth of Clyde on the west coast of Scotland. Marshall began working as an Assistant Naturalist in 1923. She was the first of two permanent researchers; the second was Andrew Orr who began working as an Assistant Biochemist in 1924.

Research at the Millport Station was oriented towards fisheries, as was common in the marine laboratories in the United Kingdom at the time (Marshall 1945). According to the station report for the year ending 31 March 1923, "Miss S. M. Marshall naturalist began work in October. She has been studying the food of copepods, particularly *Calanus finmarchicus*, in view of its importance as fish food.' (Russell 1978). Her third publication, her first on plankton, was "The Food of *Calanus finmarchicus* in 1923" (Marshall 1924). She examined the gut contents of over 3000 specimens and recorded seasonal changes in prey consumed (Fig. 2.) She also recorded changes in feeding patterns, noting, for example, that in winter *C. finmarchicus* fed only at night. Remarkably, it would be the first of 50 papers and a book she published on *Calanus*. Her last paper on *Calanus* would appear 50 years later (Corner et al. 1974) when she was 78 years old.

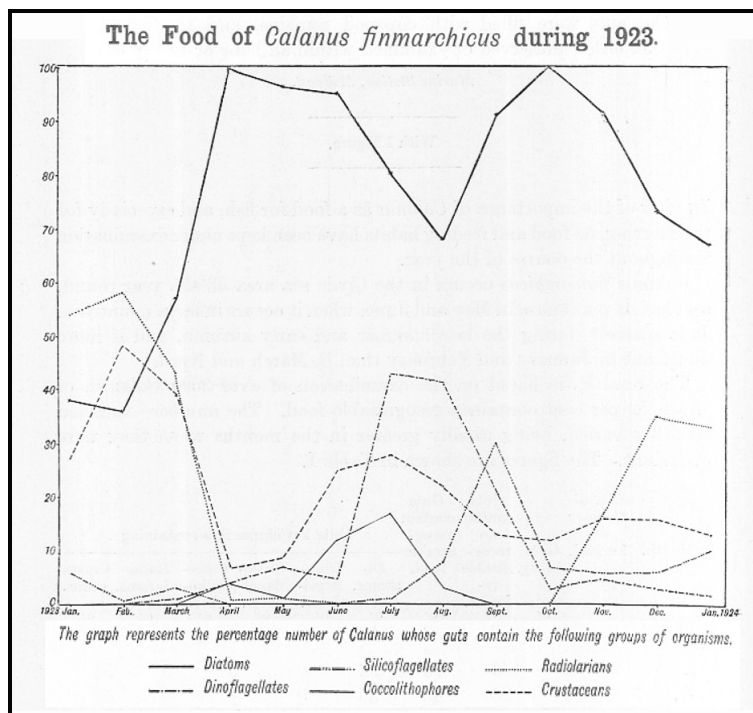


Fig. 2. From Sheina Marshall's 1924 publication "The Food of *Calanus finmarchicus* in 1923". She reported on seasonal changes in the composition of the prey items found in the gut tracts of the copepod. Note the inverse relationship in the occurrence of diatom and dinoflagellate prey that Marshall attributed to seasonal changes in the composition of the microplankton assemblage.

However, Sheina Marshall's work was not exclusively on *Calanus*. Her second publication as an "Assistant Naturalist" at Millport (Marshall 1925a) was a description of a new species of dinoflagellate, *Proterothropsis vigilans*, now

known as *Nematopsides vigilans* (fig. 3). She found it in water samples taken off the pier near the station and in highest abundances following diatom blooms. Her third publication on plankton concerned the seasonal changes in the composition of the microplankton in the Firth of Clyde (Marshall 1925b). Meanwhile, Andrew Orr was working on methods for the determining nutrient concentrations in seawater (e.g. Orr 1926). Marshall and Orr first published together in 1927, in a joint chemical and biological study, entitled "The relation of plankton to some chemical and physical factors in the Clyde Sea area" (Marshall and Orr 1927). They described regeneration of phosphorus from deep water and found that day length alone was insufficient to predict the occurrence of the spring diatom bloom.

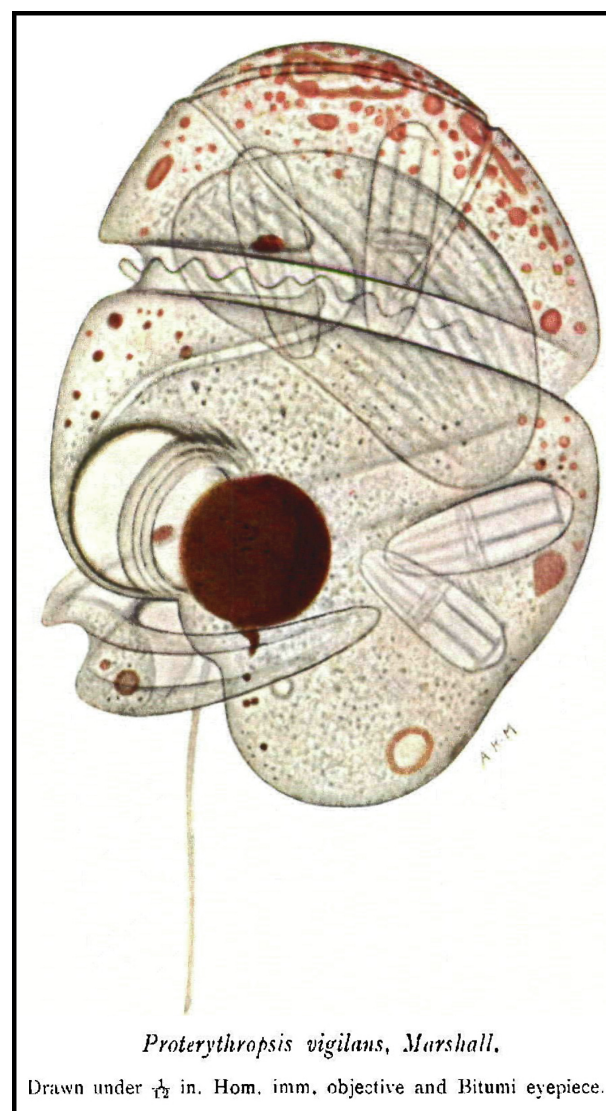


Fig. 3. The heterotrophic dinoflagellate species described by Sheina Marshall (1925a) as *Proterythropsis vigilans*, today known as *Nematopsides vigilans*.

Their second joint paper reported on a series of innovative field experiments focused on determining the role of light in controlling photosynthesis in diatoms *in situ*. In an extensive set of experiments, they suspended cultures of diatoms, and occasionally natural communities, in light and dark bottles at various depths (Fig. 4) and measured respiration and net photosynthesis through changes in oxygen concentrations in the bottles (Marshall and Orr 1928). They estimated a 'compensation point', a depth at which photosynthesis equals respiration, and recorded its temporal variability. Marshall and Orr also documented the photo-inhibition effect, showing that photosynthesis was lower in near surface waters compared to just 2 or 3 m of depth. Their experiments have been noted as among the first investigating the role of light levels in phytoplankton bloom formation and depth location, and in determining *in situ* the depths at which oxygen production via photosynthesis equaled oxygen consumption (Mills 1989).

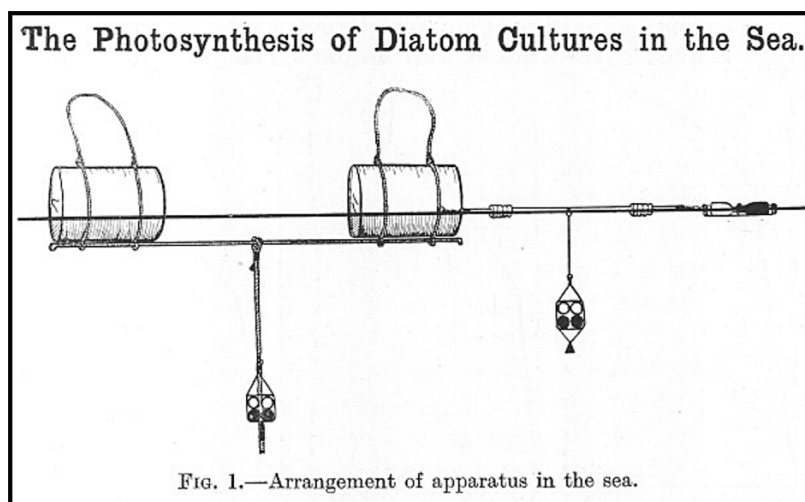


Fig. 4. Figure 1 from Marshall & Orr 1928. The figure showing how light and dark bottles were suspended at different depths from the sea surface along a cable suspended between buoys.

Shortly after the appearance of their paper on diatom growth in the sea (February 1928), both Sheina Marshall and Andrew Orr were recruited to participate in the Great Barrier Reef Expedition. The Scottish Marine Biological Association granted them a leave of 18 months. The Great Barrier Reef Expedition was a major and prestigious undertaking. It was a field study involving 20 scientists, mostly from the United Kingdom, working onsite for 13 months from a base camp on a small island. Sheina Marshall was charged with phytoplankton studies and Andrew Orr with studies of seawater chemistry. Together with Freddie Russell, charged with zooplankton studies, they formed the 'boat party' of the expedition (Morton 1992). The scientists departed the United Kingdom in May 1928 and returned in September 1929. Once back in Scotland, Marshall summarized the work done during the Great Barrier Reef Expedition, and her experiences, giving a paper to, fittingly enough, the society founded by her father, the Buteshire Natural History Society (Marshall 1930).

The results of the expedition were published as '*Scientific Reports of the Great Barrier Reef Expedition*' over a long period of time (1930-1968), similar to publication of results of large oceanographic expeditions. Among the first studies to appear was one by Marshall and Orr on the effects of sediments on coral growth (Marshall and Orr 1931) and a study on oxygen production in coral planulae (Marshall 1932). These first studies appear to have been outside of the official charges of Marshall and Orr to study phytoplankton and seawater chemistry. However, soon following was a report on the physical and chemical conditions in the waters of the reef by Orr (Orr 1933) and a report on the production of microplankton in the reef region by Marshall (1933). In this later study, in addition to documenting temporal and spatial variability of the microplankton in the reef areas, Marshall compared the sizes of the standing stocks of diatoms in the tropical reef waters to those of productive temperate seas, showing dramatically the differences (Fig. 5).

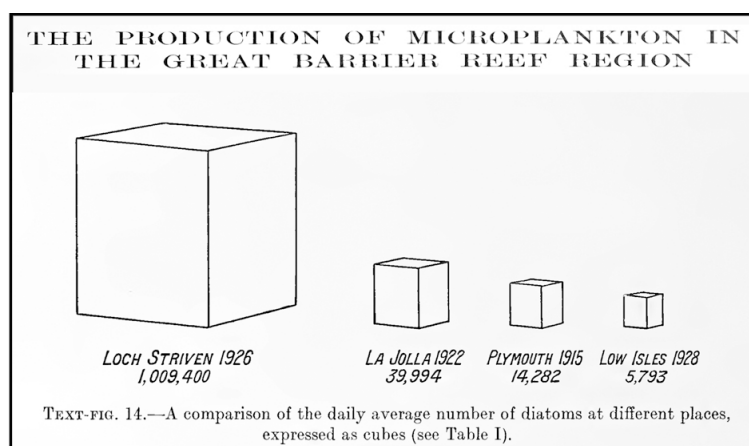


Fig. 5. Marshall's figure from her study of the microplankton of the Great Barrier Reef waters (Marshall 1933) showing the low concentrations of diatoms in the Low Isles of the reef compared to Plymouth on the west coast of England, La Jolla in southern California (USA), and Loch Striven on the east coast of Scotland.

Sheina Marshall also produced a taxonomic monograph on the silicoflagellates and tintinnids of the plankton found in the reef seas (Marshall 1934a). The monograph included detailed depictions of silicoflagellates and the description of new taxa of tintinnid ciliates (Fig. 6.) Although rarely said to be a taxonomist, one of Marshall's last publications would be a return to tintinnid taxonomy with her 1969 contribution to the plankton identification guides of the ICES, the 70 pages of the eleven tintinnid ciliate sheets (Marshall 1969).

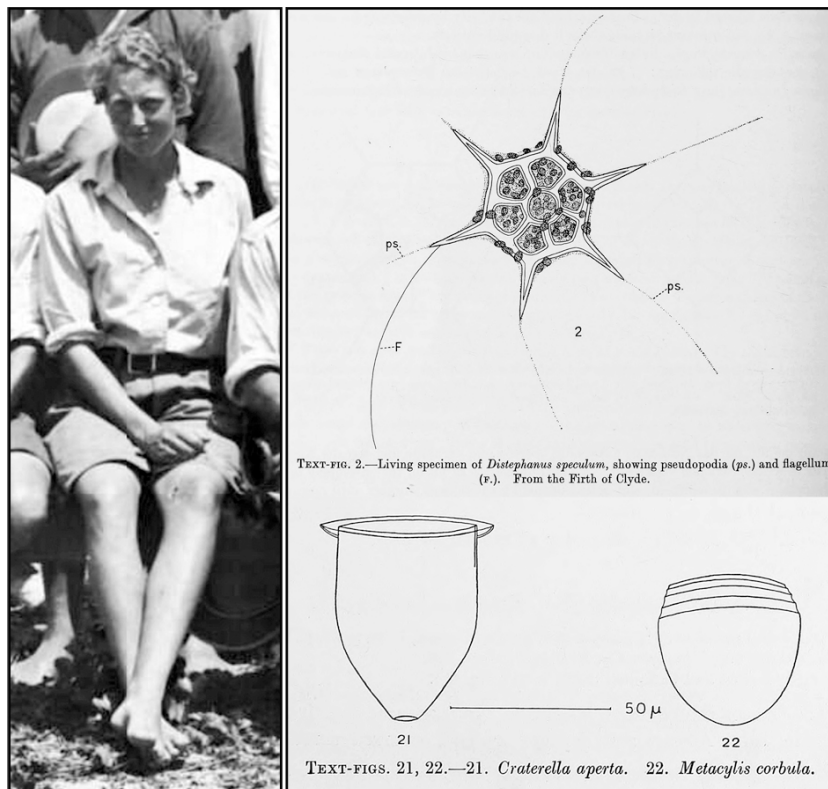


Fig. 6. Sheina Marshall from a group photo of the staff of the Great Barrier Reef Expedition of 1928-29 (Russell 1978) and illustrations from Sheina Marshall's monograph on the silicoflagellates and tintinnid ciliates of the Great Barrier Reef waters (Marshall 1934a). The tintinnid shown as *Cratella aperta* was described as a new species. It is now known as *Niemarshalliella aperta*, named in honor of both Marshall who first found the species and a Chinese taxonomist Nie who created a new genus for the species (Corliss 1960).

In 1934 Sheina Marshall was awarded her D.Sc. degree by Glasgow University. Her thesis was entitled "On the conditions influencing diatom growth in the sea" underlining the fact that her research interests extended beyond copepods. However, 1933, before her thesis on diatoms was submitted, marked the beginning of the appearance of a remarkable series of papers on *Calanus finmarchicus*, which would represent her lasting legacy. The series "On the biology of *Calanus finmarchicus*" consists of 13 papers, each substantial and most with Sheina Marshall as first author, published between 1933 and 1966. The papers total over 300 pages and have been cited over 1,500 times. Due in large part to these papers, *C. finmarchicus* is likely the best studied of any organism of the marine zooplankton. The papers formed the core of the well-known book "*The Biology of a Marine Copepod*", issued in two editions (Marshall and Orr 1955; Marshall and Orr 1972). Interestingly, the papers were published more or less regularly from 1933 to 1935 and from 1952 to 1961. The 'gap' of 1936 to

1951 did not represent a period of inactivity for Marshall, but rather a shift of major focus to fish.

Sheina Marshall and her co-workers (Nichols and Orr) made detailed studies of the occurrence and feeding biology of herring larvae and young stages. In this work they found that feeding was generally on the available zooplankton, but found some evidence of selective feeding and diurnal cycles as well with feeding maximal in the early evening (Marshall et al. 1937, 1939). During the years of the Second World War, a large applied science project of the Millport laboratory was directed towards fish farming as a possible strategy to improve local food production (Marshall 1945). An entire sea loch was periodically fertilized with nitrate and phosphorus additions over 2 years and small young fish caught in open water released in the fertilized sea loch (Gross 1944). Marshall tracked the changes in the plankton and found that microflagellates appeared to be the group most affected by the nutrient additions but showed only a short-term increase in concentrations (Marshall 1947). Interestingly, she concluded that the fertilization mostly profited the seaweeds, as it did not lead not to large changes in the plankton but rather marked and unexpected increases in seaweed biomass. The little known sea loch fertilization experiment appears to have been a precursor to the whole lake experiments of the 1960's that were used to examine the effects of eutrophication on the entire ecosystem (e.g. Schindler 1974); it was likely the first large-scale experiment to examine the effects of fertilization on a marine system.

Following the end of the war, Sheina Marshall's focus returned to copepods. The availability of radioactive isotopes allowed the development of new methods to estimate processes such as primary production (Steemann Nielsen 1952). Marshall and Orr early on used radioisotope labeling of phytoplankton to track the fate of phytoplankton ingested by *Calanus finmarchicus*. According to Marshall, it was Orr who had the idea of using ^{32}P to label algal prey and follow ingestion and metabolism of the prey items in *C. finmarchicus* (Marshall 1963). They used both ^{32}P and ^{14}C labeled phytoplankton in probably the first uses of isotopes to examine ingestion and metabolism in zooplankton (Marshall and Orr 1955b, c; Marshall et al. 1961). Some of these experiments were done at Woods Hole Oceanographic Institute (Fig. 7).



Fig. 7. Sheina Marshall and Arnold Orr in Woods Hole in 1958. Their work with Robert Conover using ^{32}P -labeled phytoplankton was published in 1961 (Marshall et al. 1961). The photo was first published in a newspaper article on their visit to Woods Hole (Russell 1978) raising the possibility that the photograph was staged for the article explaining the formal attire of Marshall and Orr.

It would be remiss to omit mention of all the books authored or edited by Sheina Marshall and Andrew Orr (Fig. 8). The first book, the 1953 "Essays in Marine Biology", they edited. The second and the others following, they authored. As noted above, *The Biology of a Marine Copepod* was published in two editions. The original edition published in 1955, based largely on the work published as the articles I through VIII in the series 'On the biology of *Calanus finmarchicus*'. The second 1972 edition was a reprint of the 1955 edition with only the addition a bibliography of studies published between 1953 and 1971. In 1965 "*Seashores*", a book on marine biology for young readers was published, authored by Marshall and Orr. Orr had died in 1962, so it is unclear what his contribution to the book

represented. In 1969 "*The Fertile Sea*" appeared as authored by A.P Orr and S.M. Marshall. The book was assembled by Marshall from Orr's notes on a series of lectures, basically an introduction to biological oceanography, which he gave in 1957.

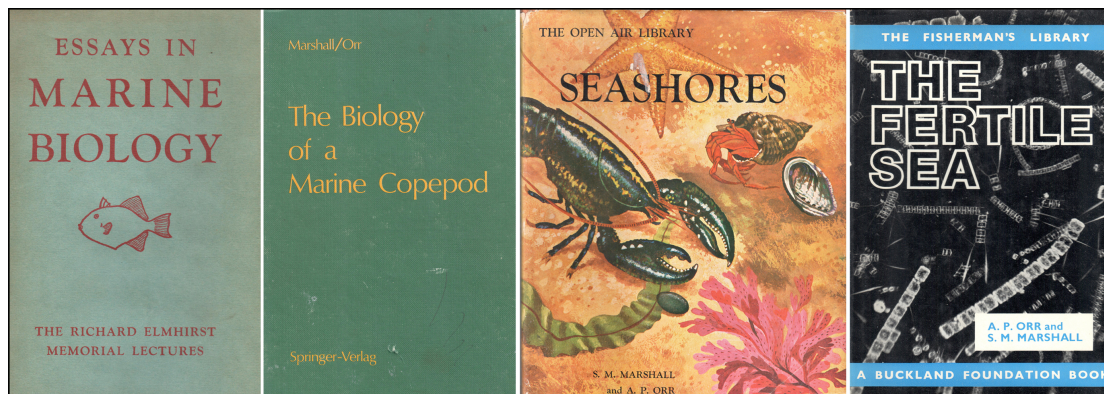


Fig. 7. The covers of the books authored or edited by Sheina Marshall and Andrew Orr. They were the editors of "Essays in Marine Biology". They authored "*The Biology of a Marine Copepod*" (2nd edition shown) published in 1972; "*The "Seashores"* in 1965 and "*The Fertile Sea*" in 1969.

Sheina Marshall was a remarkable figure in plankton research. Although officially retired in 1966, she continued to work until the day before her death. Her work then stretched over 54 years. While most famous for her work with Andrew Orr and others on copepods, her contributions ranged widely from the taxonomy of dinoflagellates and tintinnid ciliates to photo-biology of diatoms and the effects of fertilization on plankton. Although it has been about 25 years since her passing, her works continue to be cited. She certainly deserves the title "Queen of Copepods" but should also be recognized for her other important contributions to plankton research.

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