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# The Plankton-Expedition and the Copepod Studies of Friedrich and Maria Dahl

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## 1 Introduction

> 15 July 1889 - 11 *o'clock—National* escorted from Kiel by four steamers, amid many cheers, kisses, and parting speeches by Admiral Illustrious. One of the steamers took the folk on board: *Geheimrat* Mommsen, and Meyer, Spee, Klein, et al.; the whole Professors' Club was already on the steamer—shaking of hands, emotional farewells, along with the tears of Heaven and the loud cheers of the students on the other steamers. Finally the Minister and the Governor boarded the *Stephan.* Again the students' ship came nearby, again a Hurrah! from our ship—and off we went (Dahl, diary).

So began the expedition which became to plankton research what the *Challenger* Expedition represents for oceanography in general. It is not the purpose here to compare that plankton expedition with the *Challenger* Expedition, even though some contemporary critics rejoiced in such comparisons; it was emphasized at once that the aims of each enterprise were different (du Bois-Reymond 1890). Neither expedition revolutionized techniques, but instead were broader applications of the achievements of an earlier period.

The cruise of the *National* was called the Plankton-Expedition, and something special might have been expected from an expedition that was named for a new world of living beings, rather than for its ship. Certainly no previous endeavor was worthy of that name. The recent discovery of the diary kept by Friedrich Dahl during the Plankton-Expedition prompted us to review the principal results and influence of those early investigations. The primary arguments against the expedition's methods and conclusions had been translated into English (Haeckel 1893). Unfortunately the responses to these criticisms were not translated. We

have therefore indicated something from both sides of this sharp controversy. Our discussion leads to the activities and contributions of Friedrich and Maria Dahl. Bischoff (1930) published a biographical memoir and a list of the publications of F. Dahl, emphasizing Dahl's work in terrestrial ecology. There has been no published account of M. Dahl's life and work.

## 2 The Plankton Expedition

What we would call applied marine ecology was expanded by government support in the glorious decade of 1870-1880. Beside the *Challenger* Expedition and its investigative structure which long outlasted the field effort, those years saw the beginning of similar science/government coalitions elsewhere, particularly the U. S. Fish Commission (1871) and the Kommission zur Wissenschaftlichen Untersuchungen der Deutschen Meere (1870) at Kiel.

The intellectual basis of the Kiel Kommission came from the joining of modern concepts of benthic ecology as outlined by Karl Mobius in 1865, and of economic zoology problems as outlined by Victor Hensen around 1868 (Hedgpeth 1957). In 1868 Mobius was named professor of zoology at the University of Kiel, while Hensen, who was already the director of the Physiological Institute in the Faculty of Medicine, was named professor of physiology. Hensen was sent to the Landtag in Berlin by the first Prussian election in Schleswig-Holstein, and he used his influence there to further a government fisheries research program. The Kommission was the outcome of Hensen's political activity, and both professors were among the Kommission's four charter members (Porep 1970).

Hensen's goal at the outset was to study the "productivity of the ocean" as a framework for maintaining or improving the fisheries. A war postponed field work until the first investigations of the physical, chemical, and biological conditions of the Baltic Sea in summer 1871. The report of this work contained the main ideas that later would become routine quantitative surveys of the ocean's drifting organisms. By 1887 the Kommission's numerous cruises had included the North Sea, and once even the adjacent Atlantic, and had revealed seasonal trends within the Baltic. These studies suggested that much could be learned from the relationship of the distribution and abundance of organisms to physical and chemical conditions, but only through a quantitative approach. Hensen then clearly stated the principles and methods of his investigations, and gave the drifting organisms the name plankton. Hensen believed that populations of some spawning fishes could be estimated from samples of planktonic fish eggs. And since fish larvae consume other plankton, the productivity of the fisheries must depend on plankton abundance. Further, he believed that in a sea area of uniform physical conditions, a sample from a vertically hauled fine-meshed net could give a dependable estimate of the quantity of plankton in that area. Hensen's problem of determining the quantity of all plankton in a stated volume of water remains unsolved, but methods introduced by him 100 years ago are still in use.

In 1888 Hensen petitioned the Royal Academy of Science in Berlin for assistance in extending his plankton researches into the Atlantic high seas. "Two large expeditions [from England and Italy] having performed the investigation of pelagic animals in an extensive way, it was necessary to explore one of the three oceans intensively and with the aid of new methods and with new aims" (Brandt 1891). Hensen's proposal received the maximum support of the Academy's Humboldt Foundation for Natural Science and Explorations. This was followed by a larger royal grant, and some additions from the German Fishery Society and private sources.

The steamer *National* was chartered and equipped with the latest apparatus, including electric lighting. Hensen, the leader of the expedition, chose five other members from the University of Kiel: Karl Brandt (assistant leader and zoologist), Friedrich Dahl (zoologist), Franz Schutt (botanist), Otto Krilmmel (physical oceanographer), and Bernhard Fischer (bacteriologist and physician); a marine artist, Richard Eschke, completed the scientific staff. Their departure coincided with the end of the university semester.

The *National* touched the major biogeographic zones and current systems of the North Atlantic. Hensen's argonauts covered 16,000 miles in a large figure-8: from Kiel to the ice-laden currents of southern Greenland, through the Gulf Stream to Bermuda, across the Sargasso Sea to the Cape Verde Islands, beyond the equator to Ascension and the expedition's southernmost point, into the mouth of the Amazon at Para, and, with time running out, a speedy return to Kiel by November 7, via the Azores and the English Channel. More than 100 high sea stations were sampled with Hensen's quantitative net, towed vertically from 200 m, generally, to the surface. These primary collections were supplemented by samples from a large, coarse-meshed vertical net and an improved closing net of Hensen's modification (Krummel 1892).

From our distance this cruise of pre-eminent men has an idealistic glow. But these calculating collectors from Kiel were annoyed by events that vex us still: poor weather, equipment failures and losses, human failures, unexplainable accidents, groundings, official ceremonies, a crew reluctant to work on Sundays. Among the observations of the opening days, Dahl added:

> soon we felt the weak swells which made the ship roll slightly; and we had in consequence the first seasickness (Prof. Br.) . . . I could hear in the next room that those disagreeable movements also went badly for our Leader . . . I dressed lying on my bed, catching my things as they went gliding by .. . Breakfast was very slightly attended, only three came for it (Km., Hens., and myself) . . . One of our traveling companions did not come *up* until 1 o'clock (Dr. Sch.) . . . I am obliged to say that I felt somewhat uneasy.

Perhaps these frustrations had been blunted when Dahl wrote, with satisfaction, that the flies collected on board after leaving Bermuda were impaled together on a single pin! And there was continuous testimony to Dahl's excitement and awe in the variety and beauty of land and sea creatures from zone to zone. Previously known only from books if at all, their vivid descriptions filled his diaries. Yet there was room to record a full-dress traditional equator crossing:

> *Geheimrat* Hensen was invited to come down. He was smeared with soap, shaved with the large wooden knife, while his hair was cut with the big wooden scissors; this was followed with an appropriate jet from the steam sprayer.

No neophyte escaped Neptune's retinue; each was baptized with suitable ritual and personalized verse (Dahl, diary).

The Plankton-Expedition was Germany's first prominent oceanographic exploration (Brandt 1901), and this generated considerable popular enthusiasm. One month after the cruise, Krummel and Brandt presented preliminary findings to the Geographical Society, in Berlin (Brandt 1921). The expedition's official and published name dates at least from that meeting. Early in 1890 du Bois-Reymond, the secretary of the Academy of Sciences, and Hensen published the initial executive accounts of the Plankton-Expedition (Hensen 1891). The most important result was that quantitative investigations of oceanic plankton were possible and fruitful. It was reported that the planktonic plants and animals everywhere significantly exceeded in mass the well-known and easily seen larger organisms. The high seas were generally poorer in plankton abundance than the bays and river mouths. Furthermore, within the open ocean, the warm tropical seas essentially had much less plankton than the cold northern seas, in spite of theory and expectation. "Investigation of color, transparency, and plankton contents give parallel results, and all these show that the pure blue is the color of desolation of the high seas" (Schutt, in Krumrrel 1892). Without the quantitative sampling methods, this astonishing fact would not have been easily detected. Basking in the acclaim, du Bois-Reymond asserted that "our plankton voyage will take a position of its own within its modest limitation, by the novelty and the beauty of its well-restricted task." Unknowih to him and to Hensen, the critics were about to pounce.

Ernst Haeckel (1893) added insult to the investigation by condemning the results of the cruise of the *National,* and making Hensen the prime target in a war of polemics that brought to bear the considerable resources of both sides. Haeckel had been a student of Johannes Muller in 1854, at the very root of plankton research, though as a systematist/morphologist. Haeckel did not at all understand Hensen's quantitative/statistical approach to biology. Haeckel believed the opposite of Hensen's principal conclusions. And in this he was not alone, for the land-oriented notion of the rich tropics and barren north was well entrenched. Haeckel and' his associates implied that Hensen and his colleagues were imbecile swindlers;'and that Hensen's sponsors, presumably up to and including the Emperor, shquld be taken to task for squandering the largest sum ever available for biologidal research in Germany. Nullifying Hensen's judgment on tropical plankton, Haeckel emphasized his own extensive experience and observations of

> extraordinarily rich aihd valuable material . . . innumerable masses . . . fabulous wealth of life ...'immense swarms of pelagic life . . . inconceivable myriads ... complexity of composition ... I am convinced that the whole method employed by Hensen for determining the plankton is utterly worthless . . . How such work [plankton counting] can be carried through without the ruin of mind and body I can not conceive.

Haeckel had an imposing hold on his generation, both in and out of scientific circles (Goldschmidt 1956). Who could resist this onslaught? That Haeckel's treatise had a great impact can be seen from its additions to our vocabulary: *benthos, nekton, neritic, holoplankton, meroplankton.*

Hensen (1891) reluctantly picked up the challenge:

> So now Haeckel has called me to make my confession . . . He describes my studies as the most unnecessary, useless, unskilled, unsuccessful, and foolish ones in this world . . . Haeckel stresses my words that I am neither a botanist nor a zoologist, but only a physiologist, as if I had thereby renounced my right to join in the discussion . . . They say to me that I would make too many enemies by standing up against Haeckel's party—so be it! . . . The results of the Plankton-Expedition will represent the truth as true and clear at it can be within the ability of my co-workers and myself. This depends only on *facts,* facts as carefully determined as possible, on measurement, weight, and number. Against these, all opinions and suggestions will be blown away like dust.

And what followed *were* facts, which admirably answered each of Haeckel's criticisms within the observations and statistical tools of those times.

A more concise rebuttal was offered by Brandt (1891):

> Haeckel's attacks can be attributed partly to a lack of insight, partly to misunderstanding, and finally, partly to gross misrepresentations and irresponsible falsifications of the findings of other investigators.

Papers by Dahl and others injected the wealth of data being generated from the Plankton-Expedition. Books by Schutt (1892) and Apstein (1896) overwhelmed the opposition, but by then the main battle was over.

As usual in great controversy, both sides were correct on some points. Hensen did not anticipate the complex behavior and patterns in plankton vertical distribution (Currie 1972), nor were there yet statistical methods for proper analyses (Lussenhop 1974). And even within Hensen's camp, Lohmann admitted at first that the paucity of tropical plankton might only be an illusion, if the bulk was lost through the meshes of the nets. But over the next two decades, Lohmann's careful researches confirmed that even the abundance of nanoplankton, collected by centrifuging water-samples, followed the net-plankton distribution as revealed by the Plankton-Expedition (Brandt 1925).

Yet old ideas are not readily put away, especially since a number of rich tropical areas proved exceptions to the generality. These exceptions had to await an understanding of relationships between plankton, nutrients, and upwelling. So that as late as 1923, Herdman was obliged to consider as *still controversial* the "alleged deficiency" of plankton in the "genial warm waters of the tropics."

The detailed elaboration of the extensive Plankton-Expedition material demanded most of the working power of the Zoological Institute over many years. This ambitious task eventually embraced 36 scientists, some foreign, whose

monographs contributed to the everlasting usefulness and fame of the *Plankton-Expedition Results.* The magnificent illustrations by Werner and Winter and other superb lithographers have never been surpassed (Goldschmidt 1956). Even Haeckel would have had to admit that this was a suitable monument. The last of the *Results* appeared in 1926, ending but not completing the series which physically comprises a dozen large and beautiful volumes.

## 3 Friedrich and Maria Dahl

In the quantitative plankton investigations, Hensen gathered about him a number of men recently launched on their scientific careers. The names of his earliest coworkers are an honor roll of marine biology: Brandt, Apstein, Heincke, Lohmann, Schutt, and Dahl. Hensen gave room and responsibility to these devoted disciples, and his school was a true team effort from start to finish. Each had a role in the planning and execution of cruises, the development of results, and, ultimately, in the successful defense against detractors.

Karl Friedrich Theodor Dahl (Fig. 1) denied tradition by becoming a zoologist rather than accepting the family farm at Rosenhofer Brok (Holstein), where he was born in comfortable circumstances on June 24, 1856. He was thus a Danish citizen until Prussia annexed Schleswig-Holstein in 1864. After four years at the Gymnasium in Eutin, and an additional year for military duties, Dahl attended the University of Leipzig in 1877 where, like Brandt and Apstein, he was a student of Rudolf Leuckart. After additional studies at the Universities of Freiburg and Berlin, Dahl went to the University of Kiel in 1881, and there obtained a doctorate in 1884 with a thesis on the form and function of insect appendages. Dahl's 200-plus publications began in this period, the first papers treating insects, spiders, and their mimicry and feeding.

Dahl joined the Zoological Institute of the University of Kiel in 1886, and began working with marine invertebrates from the *Kommission's* collections. He also participated in some of the Baltic cruises. In 1887 he became a Privatdozent for zoology.

Supported by the Kommission and the Royal Academy of Science, Dahl investigated the invertebrates of the Lower Elbe in 1888-1889 (Dahl 1893). Using surface net- and dredge-samples, Dahl demonstrated the dependence of the fauna upon salinity, substrate, current, tide, and temperature. This study was also notable in that it was the first time that the principles of Hensen's quantitative surveys were applied to benthos. Dahl systematically sifted ½ to 4 $m^2$ areas, to estimate organism numbers per $m^2$. Though these standing stock data were not measurements of productivity, they were prerequisites to Hensen's long-range goals of estimating the productivity of the sea. In this study, Dahl was also the first to use the experimental device of test squares, to determine the rate of settling of communities on hard substrates (Hedgpeth 1957).

Dahl's direct contributions to the Plankton-Expedition were mainly in the analyses of the abundance and the horizontal and vertical distribution of the


Figure 1. Friedrich Dahl (1856-1929), Kiel, ca. 1892.

common zooplankton, particularly Copepoda. His timely reports supplemented the earliest results from plankton volumes. Using five species in the copepod genus *Copilia,* Dahl (1892) presented the first detailed specific information on distribution and abundance of oceanic zooplankton, and demonstrated the possibilities inherent in quantitative data. Dahl (1894a) was especially intrigued by the distribution of copepods in the Amazon estuary, and saw parallels with his earlier studies on the Lower Elbe. He outlined four faunal districts in a classic pattern related to salinity: freshwater, true brackish, marine coastal, and oceanic. With species in other copepod genera, Dahl (1894b) provided a quantitative

basis to zoogeographic regions described qualitatively by earlier workers: arctic (and its southern extensions), temperate, subtropical (with the Sargasso Sea as center), and tropical (the equatorial currents and their extensions). Coastal and oceanic divisions, as well as surface, intermediate, and deep zones related to food conditions, were described within each region. Within subregions, Dahl showed a generally high uniformity of numbers over large areas. The details of this work were not surpassed until the cruise of the *Meteor* in the late 1920s.

Dahl also published several descriptive papers on copepods. He planned a comprehensive work on copepods, and also expected to work on the Plankton-Expedition amphipods, but other commitments precluded both projects. Dahl's other direct contributions to the Plankton-Expedition were his reports on marine insects, marine vertebrates, and land fauna, mostly collected by himself.

Three years were needed to complete the sorting and counting of the major taxonomic groups from the Plankton-Expedition collections. Since 1887 when Mobius became director of the new Zoological Museum in Berlin, Brandt had been professor of zoology and director of the Zoological Institute at the University of Kiel. In 1890, to assist with the sorting and illustrating of the collections, Brandt employed a young lady who had just come to Kiel from Russia. Maria Johanna Grosset (Fig. 2) was born in Boromlya, near Kharkov in the Ukraine, on July 26, 1872, into a family that had fled from the French revolution the previous century. Maria was an honor graduate of the Girls' Gymnasium in Kharkov, and expected to become a medical student. Germany's medical schools were open only to men, so her family's migration to Kiel ended Maria's academic hopes. Maria combined beauty with intelligence and artistic skill, and it is not surprising that Friedrich Dahl found her to be as interesting as his plankton collections. However, Dahl was also attracted to Berlin, lured by Mobius and a continuing interest in terrestrial arthropods. Dahl began to divide time between the Berlin Zoological Museum and Kiel. He made the final break with the Kiel group in 1896-1897, when he was supported by the Museum and the Royal Academy of Sciences to collect in the Bismarck Archipelago. Most of that work was with terrestrial organisms, but Dahl made a year-long collection of quantitative plankton samples, used by Brandt to strengthen the contention of low tropical plankton volumes. Dahl joined Mobius' museum in 1898, as the curator of spiders. When this position became permanent early in 1899, Friedrich Dahl married Maria Grosset.

For the Dahls, the years before World War I were happy and productive. Friedrich published a large number of papers on insects, terrestrial isopods, and spiders. Most of these articles had a definite ecosystems approach, and several were strictly ecological, dealing with animal behavior and distribution. Perhaps it was inevitable that Dahl would be the first to apply Hensen's quantitative techniques in sampling terrestrial arthropods (Dahl 1898, Remane 1940). At the Zoological Museum, Dahl assisted with the distribution of the Plankton-Expedition materials. But he regretted the inability to honor his earlier commitments to Hensen's group. Dahl's burdens were not eased by his mentor's echoing words: "I venture to say that if only the collaborators remain faithful, then the Plankton-


Figure 2. Maria Grosset [Dahl] (1872-1972), Kiel, ca. 1896.

Expedition itself will become distinguished through the very thorough utilization of its results" (Hensen 1895). Around 1907 Friedrich encouraged Maria to pursue the work he had begun on the corycaeid copepods. To augment the considerable Plankton-Expedition and Bismarck Archipelago material, the Dahls obtained corycaeids from Farran, Steuer, and Vanhöffen. So that, of large regions, only the eastern Pacific was not represented. New descriptions, illustrations, and distribution data were given for all known species (36), including three which were previously unknown. Working at home, caring for her four children, and discussing progress during meals, Marie Dahl (1912) completed a monograph of excellence, one part of a planned series. There are few copepod references that equal the geographic coverage, organization, illustration, and potency of this

timeless record of duty and perseverance. We mourn the unfinished series, a victim of war's deprivation, sickness, and death.

After World War I, Friedrich Dahl was again at the Zoological Museum, joined shortly by Maria, now also engaged in arachnid research. Dahl recognized a need for a comprehensive zoological treatise on the fauna of Germany and adjacent seas, to serve students and specialists alike. Such a work would enable determination of species, and would also outline behavior, life-histories, and distributions. Dahl's dream was realized in 1925 with *Die Tierwelt Deutschlands,* of which he was the founder, author of the first three volumes, co-author with Maria Dahl of the fifth volume, and editor of 15 volumes. After Friedrich's death on June 29, 1929, Maria Dahl continued as editor of this distinguished zoological series until 1968. She died on January 6, 1972, a few months before her hundredth birthday.

## 4 Influence of Hensen's School

The achievements of Hensen's school were immense. In an age of description and descendence theory, this group introduced quantitative sampling of natural populations, and gave definite forms to the ideas of ecosystems and production. A few influential scientists ridiculed these developments. Others, like Friedrich Dahl, perfected them, and transmitted them to different disciplines and other countries. One branch of Hensen's school led through Lohmann and Brandt to nanoplankton, the determination of nutrients, and the relationship of production processes to hydrography. Another aspect, with a stronger element of biogeography and application to fisheries, influenced Petersen (Denmark), Gran (Norway), and Caullery (France). Except for Kofoid and C. D. Marsh, investigators in the United States did not respond readily to Hensen's techniques. Hedgpeth (1957) suggested that this was a result of the one-sided translation of the Hensen-Haeckel controversy. However, Reighard (1898) appraised Hensen's methods optimistically and fairly for the U. S. Fish Commission. And a review by Brandt (1901) was translated and widely circulated. Therefore there must have been other reasons for the delayed acceptance of quantitative plankton methods in this country. A fauna less well-described, an academic emphasis on embryology, and a scientific fisheries establishment oriented mostly toward fishing and fish-hatcheries, all contributed to this postponement of plankton ecology. It was not until after 1910, with Bigelow, that serious marine plankton surveys were undertaken in the United States.

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