History of Ecological Sciences, Part 51: Formalizing Marine Ecology, 1870s to 1920s

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This part is the fourth in a sequence of histories of ecological sciences that arose from the 1870s into the 1920s, the previous ones being on plant ecology, animal ecology, and limnology (Egerton 2013*b*, 2014*a*, *b*). However, since marine ecology is a part of oceanography as well as being an ecological science, its history is more complex than that of the other three, and consequently, this part is also much longer and more complex than the other three. None of the other three have international congresses on their history every few years, with resulting volumes of papers being published.

Marine ecology arose from three developments during the 1870s: founding of marine biological stations in Europe and America, voyages of research, especially H.M.S. *Challenger*, and plankton research, initiated at the University of Kiel. "Mac" McIntosh (1985:49–57) provided a bibliographical guide to the history of marine ecology. Eric Mills' *Biological Oceanography: An Early History, 1870–1960* (1989) is actually limited in scope to the history of plankton research. Marine ecology history is mostly embedded within the context of the history of oceanography, which has an extensive literature (including Herdman 1923, Idyll 1969, Schlee 1973, Ward 1974, Sears and Merriman 1980, Lenz and Deacon 1990, Vanney 1993, Deacon 1997*a*, Mills 2000, Benson and Rehbock 2002, Morcos and Zhu 2004, Groeben 2013). Of interest is John Murray, chapter 1. "A Brief Historical Review of Oceanographical Investigations" (Murray and Hjort 1912:1–21, with 12 portraits). A few small marine biology stations arose before 1870, but a major impetus for their development was the example set by Anton Dohrn founding his Stazione Zoologica in Naples in 1873. Voyages to explore marine life began in the 1840s, but were only occasional and of short duration until *H.M.S. Challenger*'s 3.5-year voyage, 1872–1876. The existence of plankton had been known before Victor Hensen named it and connected it to the fate of northern European fisheries; that connection made it seem worthy of sustained intensive research. The impetus of these three developments plus a decline in fish populations led to the founding in 1902 of the International Council for the Exploration of the Sea (ICES), which transcended European national Atlantic marine research limitations. ICES inspired the founding of the Commission Internationale pour l'Exploration Scientifique de la Méditerranée. Commercial fisheries science also progressed beyond Europe, and the American story is also discussed. However, rather than discuss the first part of the careers of William Beebe and Henry Bigelow here, both are deferred to part 58. Alister Hardy's career also extended beyond the 1920s, but with a briefer discussion than planned for Beebe and Bigelow, his account provides an ending for this part 51.

Marine stations: Europe

In 1910, two American zoologists, Charles Kofoid (1865–1947) and Chancey Juday (1871–1944), independently and apparently unaware of the other's project, published accounts of European aquatic biological stations, fresh and saltwater. Kofoid's is a book for which the U.S. Bureau of Education had provided a grant enabling him to survey Europe's marine stations, 1908–1909, which he did in preparation for planning such a station for the University of California (Goldschmidt 1951:127, Mullen 1973, Shor 1974, Burgess 1996:62, Day and Mills 2013:237–238). Juday's report is a 20-page article + 4 plates. Both are illustrated with photographs of station buildings. Since their accounts only extend to 1910, we also need to consult later guides. T. Wayland Vaughn edited and partly wrote *International Aspects of Oceanography* (1937), on oceanographic institutions. Homer Jack compressed a Ph.D. dissertation at Cornell (1940) into *Biological Field Stations of the World* (1945), with a few illustrations and references for almost all stations. Robert Hiatt compiled *Directory of Hydrobiological Laboratories and Personnel in North America* (1954) and *World Directory of Hydrobiological and Fisheries Institutions* (1963), both containing photographs of buildings, station grounds, and ships. C. M. Yonge (1956) published a brief world survey of marine stations. Patrick Scaps's *Histoire de la Biologie marine* (2005:73–88) has a chapter on early stations. Margaret Deacon (1993) has discussed foundation of marine stations in Britain during the later 1800s, from the standpoint of funding and other factors relating to their establishment and success. A few small stations opened before 1870, but most opened after 1870 (Yonge 1956, Benson 1988*a*, *b*, *c*, Dexter 1988, Maienschein 1988, Kohler 2002:42–44, Deacon 2003). Kevin Eckelbarger gave a recent very brief historical perspective (2007). Proceedings of international congresses on oceanographic history provide sketches of other stations (Sears and Merriam 1980, Lenz and Deacon 1990, Morcos and Zhu 2004). Johan van Bennekom (2013) discussed the history of European marine stations before 1900.

Professor of Zoology Pierre-Joseph van Beneden (1809–1894), University of Louvain, established the first marine research station in 1843 at Ostend, Belgium, on his in-laws' oyster farm, which he named Laboratoire des Dunes (Florkin 1970, Houvenaghel 1980:668–669, Ellis 2005:22, Scaps 2005:79, Chalier 2013:107). It attracted biologists from Belgium, France, and Germany. It was overshadowed in 1859 when Victor Coste (1807–73), from Collège de France, founded the first coastal station in France at Concarneau (Hiatt 1963:73). In 1883, Beneden's son, Edouard (1846–1910) founded another station at Ostend, which may have been where the elder Beneden's student, G. Gilson (1859–1944), began his studies about 1900 (Houvenaghel 1980:669). Later, Gilson became head of the Musée Royal d'Histoire Naturelle in Brussels, and in 1927, that museum took over Gilson's laboratory at Ostende and named it Institut d'Etudes Maritimes (Vaughn 1937:104–105, Hiatt 1963:15).

Surprisingly—since it is in far-eastern Europe—Ukraine (in the Russian Empire) developed one or two stations as early as 1871. Alexandru Bologa (2004:211) cited development of a station at Odessa in that year, initiated by three members of the Novorossiisk County Naturalists' Society (Alexander O. Kovalevskyi, Ilya Mechnikov, Ivan Sechenov), who attached it to Novorossiisk University; yet, Yuri Tokarev (2004:223) denied this claim, stating that the Sevastopol Biological Station (SBS) was the one established in 1871, attached to that university. The editors of both papers suggested that two stations may have been established in 1871. If so, however, the Sevastopol station overshadowed the Odessa one, which presumably faded away. It is also surprising that SBS's director in 1878–1888 was a woman, Sofia M. Pereiaslavtseva, who afterwards remained there as chief zoologist (Bologa 2004:211). The early goal of the station was simply to inventory the marine species of plants and animals. In 1890 and 1891, Nikolai Andrusov organized exploratory voyages to extend the inventory into deep seas. In 1892 the station came under supervision by the Russian Academy of Sciences. Sergei Zernov (1871–1945), who headed SBS in 1902–14, "created the Russian school of hydrobiology and established the chair in this domain at the Moscow Agricultural University" (Tokarev 2004:225). Zernov "extended the scope of the research from zoology to ecology and ethology" (Bologa 2004:211).

Kofoid began his country-by-country accounts with a detailed account of Stazione Zoologica, Naples, Italy (1910:7–32 + 8 plates), founded by German zoologist F. Anton Dohrn (1840–1909). Such attention was justified both because of its own scientific achievements and its influence on the building of other stations. Dohrn had studied at Jena under Gegenbaur and Haeckel (Vaughn 1937, Ward 1974:137–141, Oppenheimer 1978, 1980, Groeben 1985, Heuss 1991:35–36). In 1867 he visited David Robertson on Great Cumbrae Island in Scotland's Firth of Clyde, where he realized the advantage of residing on the coast to study marine life (Allen 1976:209). In 1868 he traveled to Messinia, Sicily and studied early development of crustacea in aquaria (Heuss 1991:74–79). In 1871 he settled in Naples and obtained city land in a park on Naples Bay, where he built a zoological station (Dohrn 1872, Juday 1910:1275–77, Heuss 1991:114–120). He had to raise money to build and maintain it, but coming from a wealthy family, and making it an international enterprise—even Darwin contributed books and money (Groeben 1984:61, Heuss 1991:212)—he succeeded in building the foremost marine zoology station in the world (begun in 1872 and opened in 1873) which attracted researchers from Europe and America (Herdman 1923:135–144, Ghiselin 2008, Slack 2010:63–69). It contained research tables that were for rent at the equivalent of U.S.$500 per year. Various governments and institutions rented them (Ebert 1985:173–174), and an account of Russian scientists who studied there (Groeben and Fokin 2013) is undoubtedly

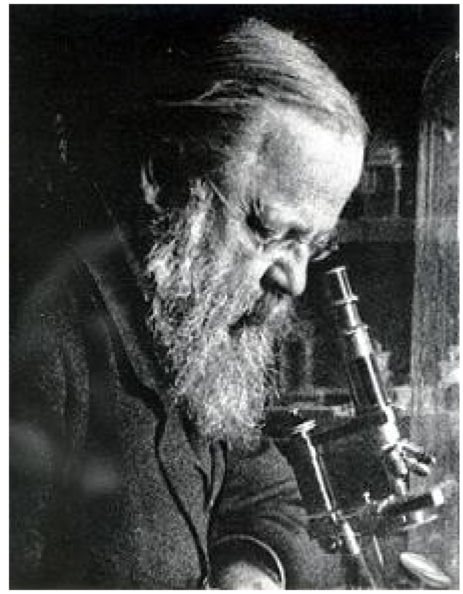
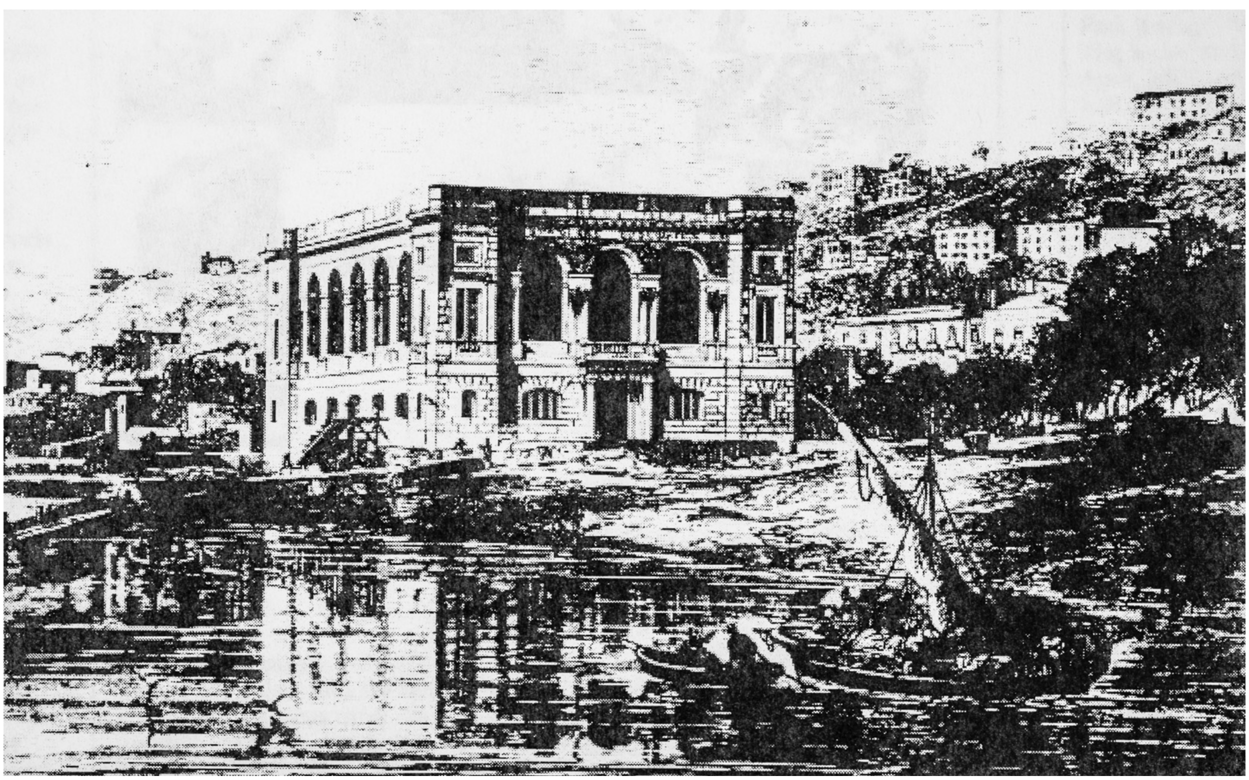


Fig. 1. (a) Felix Anton Dohrn. Web. (b) Stazione Zoologica, Naples, about 1875. Groeben 1984:61.



a story which was similar for other countries. The station built a public aquarium that attracted tourists in Naples, who were charged admission (Heuss 1991:294–295). Dohrn succeeded in attracting a capable staff to assist researches, and as its popularity grew, he expanded its buildings and equipment (Hiatt 1963:104–105). Despite being named a zoological station, an active program in the study of micro- and macro-algae began four years after it opened (Tomas 1985); in 1888 Dohrn built a new building for a Department of Physiology (Ghiretti 1985). The station created three sets of publications to publish researches accomplished there: *Zoologischer Jahresbericht*, begun 1879, with annual summaries written by various specialists; *Mitteilungen aus der Zoologischen Station zu Neapel*, begun 1879, for less extensive researches on Mediterranean flora and fauna; and *Fauna und Flora des Golfes von Neapel*, with colored lithographs, 31 issues being published by 1908 (Kofoid 1910:20). The *Mitteilungen*'s name was changed in 1916 to *Publicazioni della Stazione Zoologica di Napoli* (Reidl 1980:4). The station also collected and exported specimens to marine biologists elsewhere, and it still maintains an excellent archive (Groeben 2002). Dohrn's report of activities during 1879–1880 included an account of his trip to Kiel to see and try out a scaphander for underwater exploration, and upon returning to Naples, he obtained one from the Italian Navy, which he and several assistants used to explore underwater during two years. However, as the Bay of Naples became polluted, his station confined its research to the laboratories (Reidl 1980:5–7).

For other stations Kofoid provided less information. The country with the greatest number of stations which he discussed was France (Kofoid 1910:48–143; also, Josquin Debaz's Ph.D. dissertation, 2005), and the largest of 19 French stations which he described was founded by zoology professor Félix-Henri de Lacaze-Duthiers (1821–1901), of the Sorbonne, in 1872, a marine laboratory at a fishing village, Roscoff, in western Brittany (Kofoid 1910:95–104 + 3 plates, Juday 1910:1268–70, Appel 1973, Théodoridès 1990, Matagne 1999:203–204), which later received a research vessel, *Le Dentale*, from l'Association française pour l'Avancement des Sciences. By 1880, it accommodated 17 biologists, and in 1881, the station became affiliated with laboratories of the Faculté des Sciences in Paris, and later was named Laboratoire Lacaze-Duthiers (Juday 1910:1268–1269, Jack 1945:46, Hiatt 1963:74–75). Upon Lacaze-Duthiers' death, he was succeeded by his associate at the station since 1878, Professor Yves Delagne (1854–1920), an experimental physiologist (Tétry 1971). The station grew under able leadership and could accommodate over 100 students and investigators by 1908. Lacaze-Duthiers was a cofounder in 1872 of *Archives de Zoologie experimental et générale*, which published many of the monographs produced at Roscoff. In 1881 Lacaze-Duthiers also established Laboratoire Arago Banyuls-sur-Mer on the Mediterranean coast (Hiatt 1963:72–73).

Kofoid devoted 10 pages to Monaco's Institut Oceanographique, on the Mediterranean (Juday 1910:1271–1272, Kofoid 1910:37–47, Herdman 1923:119–133, Jack 1945:53–54, 135, Hiatt 1963:135, Deacon 1971:382, 391, 392, Schlee 1973:132–137, Mills 2009:162–191). Prince Albert I (Honoré Charles Grimaldi, 1848–1922) served for a time in the Spanish navy, and in 1873 he bought a schooner, mastered navigation, and in 1885 began oceanographic research that lasted for the rest of his life (Petit 1970, Mills 1983:48–58, 1989:116–117). He enlisted the services of Scottish chemist John Buchanan (1844–1925), who had served on the *Challenger* Expedition, who became Albert's close collaborator until World War I (Kutzbach 1970, Carpine-Lancre and McConnell 2013). Albert conducted research from several vessels, beginning with *Princesse-Alice* (Doumenge 1997), and in 1887 he sailed to the Azores, where he met Afonso Chaves (1857–1926), who had a military career, but had become interested in sciences relating to the Azores; Albert and Chaves became fast friends for life (Martins 1997). In 1906 Albert attempted, unsuccessfully, to organize an international oceanographic congress to meet in Monaco (Carpine-Lancre 1980). In 1910 he opened the Musée Oceanographique de Monaco which displayed biological specimens (Mills and Carpine-Lancre 1992), and in 1911 he opened the Institut Océanographique in Paris for teaching and research. Its director, Professor Paul Portier (1866–1962), University of Paris, supervised over 100 Ph.D. dissertations (Monnier 1975:101, photo; Day and Mills 2013:250). Albert also founded two publications, an institute *Bulletin* and *Annales*. Although inspired by Dohrn's Stazione Zoologica, Albert was also responding to the slow development of oceanography and marine biology in France (Mills 1983:48–58, 2009: chapter 6).

In 1886, the Spanish Navy launched Spain's first oceanographic expedition, using "the outdated frigate *Blanca*" (Morcos et al. 2013:269). A doctoral student at the University of Madrid, Odón de Buen (1863–1945), became the expedition naturalist, and that experience changed the direction of his interests. He received his Ph.D. in 1887, and in 1889 he became Professor of Zoology at the University of Barcelona until 1911, when he returned to the University of Madrid as Professor of Natural History. While at Barcelona, he frequently visited Professor Henri de Lacaze-Duthiers' marine Laboratoire Arago at Banyuls-sur-Mer, France. The influence of Lacaze-Duthiers and his marine laboratory were important guidance for Buen when establishing the Laboratorio Biológico-Marino (1906) at Porto Pi, Majorca. In 1908, he began corresponding with Jules Richard, Albert's collaborator, who became head of Albert's Institut Océanographique (1911), and subsequently Buen also corresponded with Albert (Morcos et al. 2013:270–271).

Albert's example also inspired King Carlos I de Bragança of Portugal (r. 1889–1908) to study oceanography (Saldanha 1980, 1997, Carpine-Lancre and Saldanha 1992, Amorim 2009:53–55). He had earlier stayed informed about oceanographic explorations in or near Portuguese waters (Deacon 1997b). In 1896, he used his own vessel, *Amélia*, to begin oceanographic research in Portugal's coastal waters, and he later graduated to three more ships, all named for his queen, which enhanced his investigations. His scientific colleague was Albert A. A. Girard, of French ancestry, who had grown up

Fig. 2. (a) Albert I of Monaco (in white hat and shoes) and orca on his yacht. Web site. (b) Carlos I of Portugal. Web site (standing, in color).

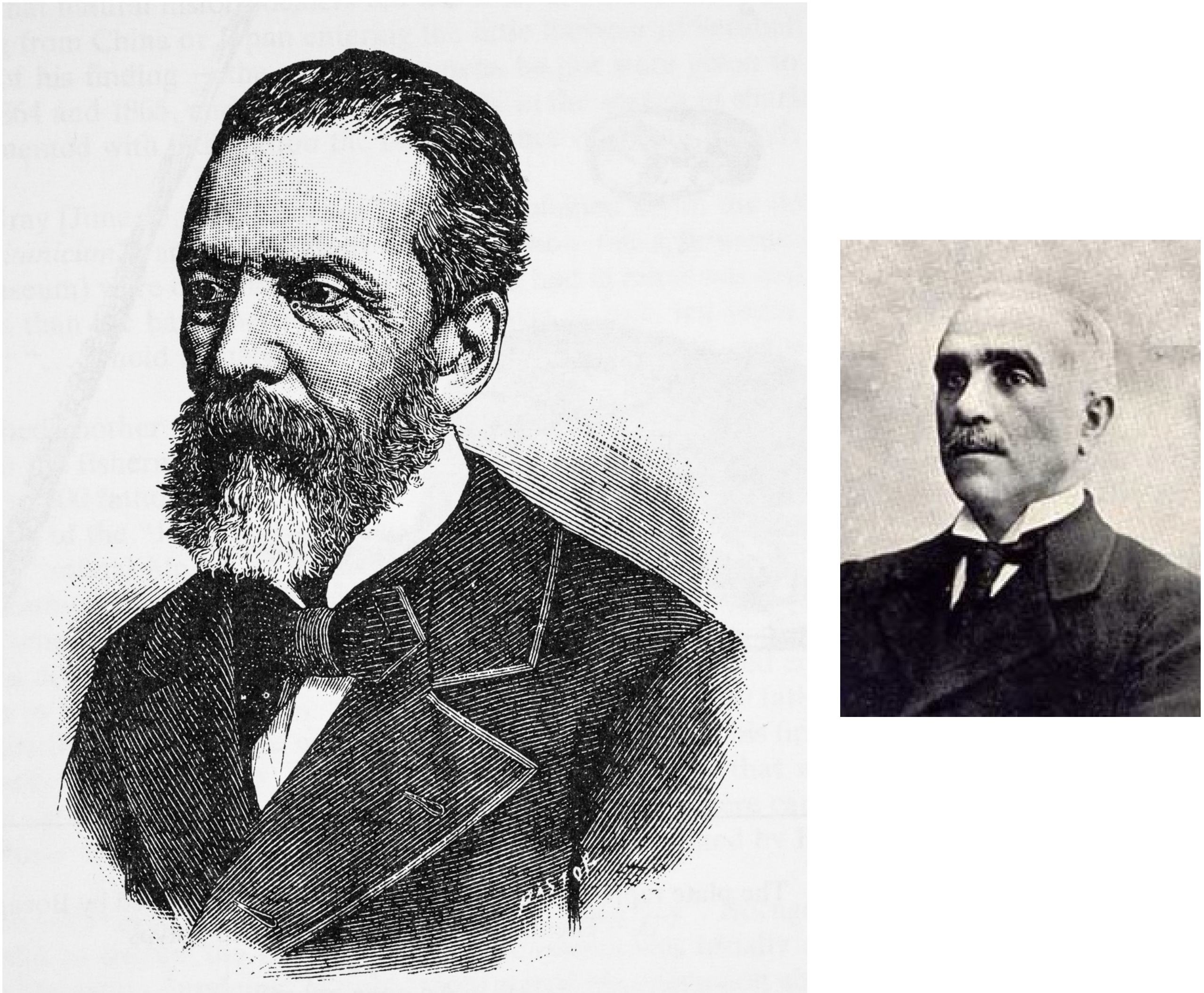


Fig. 3. (a) José Vicente Barboza du Bocage (1823–1907). Saldanha 1990:169. (b) Augusto Pereira Nobre. Web.

in Portugal and worked at the Lisbon zoology museum (Ramos 2006:180). Their biological collecting was accompanied by environmental measurements of ocean waters. Carlos was particularly interested in fisheries; a transition was underway from sailing to steam fishing vessels, with the latter having a greater harvesting potential. He studied the Portuguese tuna fishery by distributing questionnaires to owners of fixed nets in 1899 and published his findings. He also published in 1904 a monograph on sharks in Portuguese waters. His assassination prevented the publication of all of his findings, and he left no oceanographic tradition or institution. Portugal's most prominent zoologist of the time was not Girard, but José du Bocage (1823–1907), from the Atlantic island of Madeira, who had studied at the University of Coimbra, and became a professor at Lisbon Polytech, later renamed the Science Faculty, University of Lisbon and head of the Museum of Natural History (Saldanha 1990:169, Deacon 1997b:67–78). Bocage is most remembered zoologically for a controversy concerning a sponge *Hyalonema lusitanica* Bocage, which closely resembled a Japanese species. He also became a prominent statesman.

Another outstanding Portuguese zoologist at the time of Carlos I was Augusto Nobre (1865–1946), born into a wealthy family in Oporto, who was educated in Portugal, at the Sorbonne in Paris, and at the Station de Biologie Marine de Sète, University of Montpellier (Almaça 1997). In 1890 he returned to one of the places where he had studied in Portugal, the Oporto Polytechnic Academy, and in 1891 he organized a Department of Zoology and a university museum. In 1914 he established a Marine Zoology Station at Foz do Douro, and he published accounts of Portugal's marine invertebrates and fishes.

Northern Germany experienced a different organizational situation than elsewhere. Kiel is on Kiel Bay, joined by a canal between the North Sea and Baltic Sea. Kiel had Christian-Albrechts Universität, and in 1870, the German state founded there a Kommission zur wissenschaftlichen Untersuchung der deutschen Meere (Kofoid 1910:219–221, Mills 1989:14, 1990:20–21). This commission established observation stations that were used by zoologists on the university faculty. Details of this activity are discussed below under Plankton Studies. There were also other stations being established in Germany (Kofoid 1910:217–246, Roll 1990). The station at Helgoland (founded 1892) was particularly important for zoological, ecological, and fisheries research (Bulnheim 1990). Early directors were Friedrich Heincke (1892–1921) and Wilhelm Mielck (1921–33). The station began publishing Wissenschaftliche Meeresuntersuchungen in 1894. Other important research was conducted by the zoologists at the Naturhistorisches Museum at the University of Hamburg (Scheele and Hünemörder 1990). Stations Roll outlined were within Germany; however, the Berlin Aquarium opened a collecting station at Trieste on the Adriatic Sea in 1870, and, because of pollution, moved it to Rovinj in 1891, expanding its scope to include research (Zavodnik 1990). Like Albert I and Carlos I, Friedrich Alfred Krupp (1854–1902), monarch of a German industrial empire, used his own ships for biological exploration in the

Mediterranean Sea, from his villa on the isle of Capri (Müller 1990). Salvatore Lo Blanca (1860–1910), from Stazione Zoologica, published Krupp's findings.

England had shown great initiative in dredging from ships, but was slow to build marine stations (Deacon 1993). There was a successful International Fisheries Exhibition in London in 1883, and zoology Professor Ray Lankester (1847–1929), University College, London, deciding to strike while the iron was hot, began canvassing colleagues and the Royal Society to support a station. In 1884 a Marine Biological Association (MBA) of the United Kingdom was organized to bring the idea to fruition (Allen 1976:211–212, Mills 1982:6–8, 1983:62–63, 1989:190–199, Cushing 1988:191). Government land was allocated for a station beside the naval Citadel at Plymouth. Building at Plymouth began in 1886, and by 1887, the public had raised £10,000, and government contributed £5000 plus a promise of £500 a year for five years, with some strings attached. It opened in a fine building on 30 June 1888, while commercial fish stocks were declining (Juday 1910:1259, Hiatt 1963:192). The annual operating funds were modest, but "the early work at the laboratory was prolific and significant" (Mills 1989:195). Physician–zoologist William B. Carpenter (1813–1885) was a founder of MBA and a strong supporter of its Plymouth station (Thomas 1971). In 1895, Walter Garstang (1868–1949) began bringing university classes there for marine biology instruction, and in 1897 he became the Plymouth Laboratory Naturalist (with a meager salary). He had a degree in zoology from Oxford University and had studied an additional year at Owens College, Manchester (Hardy 1951, Holland 2011). Garstang showed that the total fisheries catch had in 1889–1898 increased only 30%, while trawler capacity had increased 300% (Cushing 1988:193). The Plymouth Laboratory was fortunate in having E. J. Allen (1866–1942), who had studied at Leeds, London, and Berlin, serve as its director, 1895–1936 (Kemp and Hill 1943, Mills 1989:203–206, Deacon 2004*a*). Devoting his life to the laboratory, Allen (a bachelor) was both a productive researcher and a capable administrator. The Kiel school had begun to lose its productive members even before World War I, and the school never regained leadership in plankton studies after the war (Mills 1989:174–186). The Plymouth lab assumed world leadership under Allen, doing much with modest funds (Mills 1989:189–257). It not only collected much diverse data, it could also achieve a meaningful synthesis of it (Mills 1989:258):

> *The Plymouth group's view of how the plankton cycle was controlled in the sea crystallized during the late 1930s and 1940s into a virtually paradigmatic qualitative model involving biological, chemical, and physical processes that took place mainly at temperate latitudes…*

MBA retained world leadership in plankton dynamics studies until 1958 (Ellis 2005:32). In 1892, two other fisheries laboratories opened, at Liverpool and at Port Erin, and later another at Lowestoft (Mills 1989:197–201).

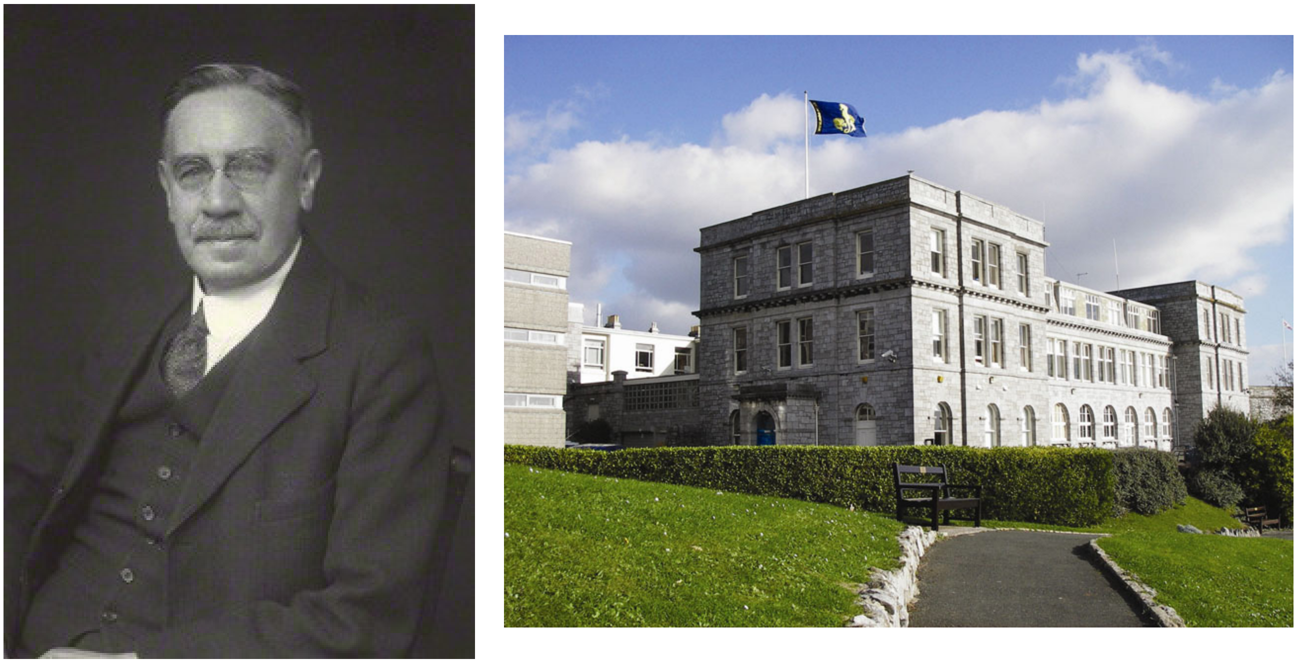


Fig. 4. (a) Edgar Johnson Allen. Web site. (b) Plymouth Laboratory of the Marine Biological Association. Web.

Cushing (1988:191) summarized European end-of-the-century station foundings:

> *In 1889, Petersen worked the Danish* Station*, a barge which could be towed from place to place. The Gatty Laboratory at S. Andrews started work in 1892, as did the Liverpool University laboratory at Port Erin in the Isle of Man. Hjort set up a laboratory at Drøbak on the Oslofjord in 1897. The Scottish Fishery Board came into being in 1882 and the Marine Laboratory was built in Aberdeen in 1898. Prince Albert constructed his Monaco laboratory in 1899.*

Vera Schwach (*personal communication*) provides some more precise details: The University of Oslo established the station at Drøbak, with Hjort as director (Sømme 2001); in 1897, the Kristianiafjord had not yet been renamed Oslofjord.

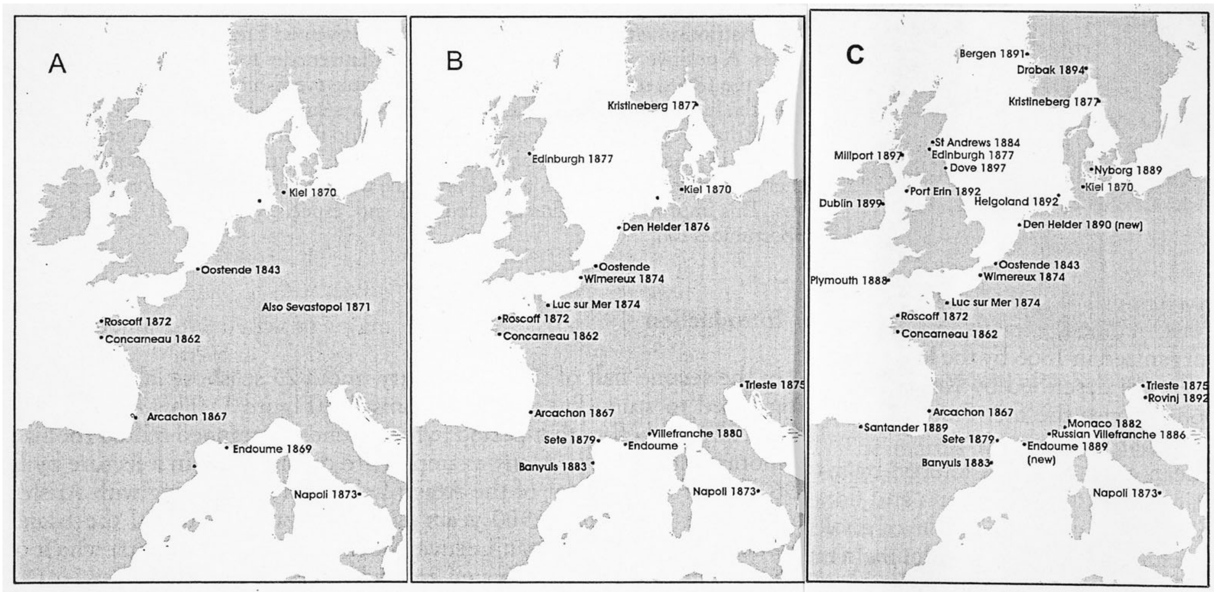


Fig. 5. Marine biology stations in western Europe. (a) 1843–1873. (b) 1874–1883. (c) 1884–1900. Van Bennekom 2013:126–127.

Russia had at least six biological stations founded before 1911, some of which were freshwater (Jack 1945:59–60). Russian Konstain Saint-Hilaire (1866–1941) was the son of zoologist Karl Saint-Hilaire (1834–1901), who had taught at the St. Petersburg's Main Teacher Institute (Goryashko and Fokin 2013). As a student and later, Konstain worked at various European biological stations, and in 1903 he became Professor of Zoology at Juriew University (now University of Tartu, Estonia). In 1911 he established a peripatetic marine station in the village of Kovda on the White Sea's Kandalaksha Bay. It lasted there for thirty years without ever having a permanent home. It nevertheless was the locus of both teaching and research. Juriew University was occupied by German troops in 1918, and the Russian Revolution was also disruptive of station activities. All of Saint-Hilaire's scientific papers and research were destroyed in German attacks during World War II.

Romania lacked a marine station until 1926, when Professor Ioan Borcea (1879–1936), who had a doctorate in biology from the Sorbonne (1905), and who taught at Alexandru Ioan Cuza University, founded a Marine Zoological Station on the Black Sea coast at Agigea (Serpoinau and Malciu 2002:273–

274, Bologa et al. 2013). Borcea died from septicemia at Agigea, but two years later Homer A. Jack visited the station (5 December 1938) and concluded that “this is an extremely successful zoological station and assuredly, it accomplishes its mission of being a leading station in the Balkans” (quoted in Bologa et al. 2013:175; Jack 1945:56).

Marine stations: United States

In the United States, where controversy raged over causes of decline in fisheries, Spencer F. Baird (1823–1887) got Congress to create the U. S. Commission of Fish and Fisheries, with him as Commissioner (with no pay beyond his salary at the Smithsonian Institution), in 1871 (Allard 1967:78–86, Smith 1994:44–47, Egerton 2011:156). The U.S. Commission of Fish and Fisheries was America’s first conservation agency (Hobart 1995:4). Baird sponsored research at Woods Hole, Massachusetts, where he took his family in summer to escape the humid heat of Washington (Allard 1967:64–65, Pauly 1988:128, Rivinus and Youssef 1992:141–151). Woods Hole had been a whaling port, from about 1815 to about 1860, and later was home of Pacific Guano Works (Galtsoff 1962:1–6). In 1871, Baird brought with him to Woods Hole Professor Addison E. Verrill (1839–1926) of Yale University, whom Baird asked to survey the animals and their distributions in Martha’s Vineyard Sound (Coe 1932, Hedgpeth 1957:4–5, Verrill 1958, Shor 1976, Dexter 1997*b*). His survey resulted in publication of a substantial report (Verrill 1873). In five or six years, Verrill collected there hundreds of thousands of specimens of over 2000 species (Verrill 1958:65–69, Rivinus and Youssef 1992:89). The Commission erected a fish hatchery at Woods Hole in 1882, with hatchery ship *Fish Hawk*, and in 1883 built a research vessel, *Albatross*, “which continued to serve science until 1921, [and] probably did more significant work in oceanic research than any other vessel” (Galtsoff 1962:38–50l, Allard 1967:340, Spencer 2002:288–290). (Schwach [*personal communication*] is skeptical of Allard’s claim for *Albatross*’ importance, if he meant worldwide, and research was done by scientists aboard, not by the ship itself.) The Commission built a Biological Laboratory at Woods Hole in 1885, influenced by Dohrn’s laboratory in Naples (Hiatt 1954:141–142, 1963:246, Schlee 1973:67–73). Although it was the northeastern fisheries crisis that prompted Baird’s actions, he knew that it had to be a national agency in order to win Congressional support, and he also sponsored a survey of the Great Lakes fishery (Allard 1967:107–109). After Baird died in 1887, fish hatchery activities overshadowed research (Galtsoff 1962:54). In 1916, a U.S. Fishery exploration trip discovered good quantities of tile fish and introduced the fishery to commercial fishermen and introduced it as a food to the public (Herdman 1923:309–310). The U.S. Bureau also persuaded fishermen to market dogfish sharks as gray-fish, which made them acceptable to the public.

The Marine Biological Laboratory (MBL) was founded at Woods Hole because the U. S. Biological

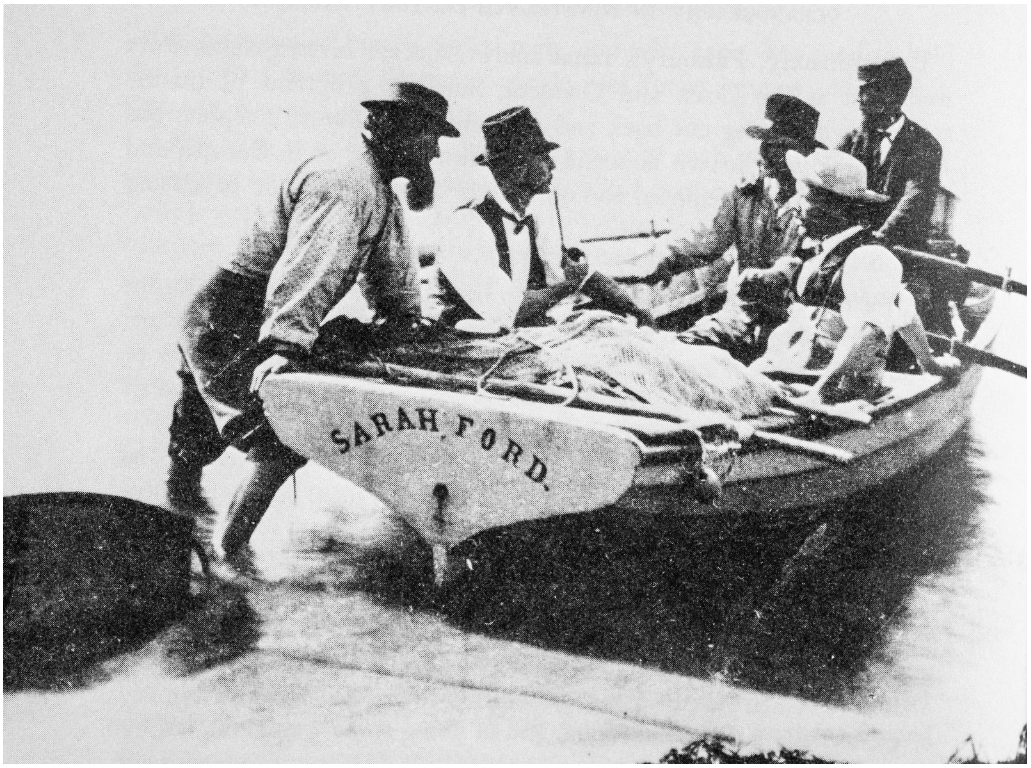


Fig. 6. (a) Baird supervising marine collections. (b) U.S. Fish Hatchery, Woods Hole. Schlee 1973:68, 71.

Laboratory was there. It was inspired by the example of the Naples Stazione Zoologica, though the importance of that example has possibly been over-emphasized by some historians (Benson 1988*b*). The sparkplug was a philanthropist making available Penikese Island with buildings, near Woods Hole, to Louis Agassiz (Egerton 2011:165–166) for a summer school for teachers of natural history, which opened in 1873 (Lillie 1944:15–22, Lurie 1960:379–381, Maienschein 1989:8–12). The school was a success, and among the 28 men and 16 women who attended were: Alpheus Hyatt, a founder of MBL; David Starr Jordan, later leading ichthyologist and president of two universities; and Charles Otis Whitman, a founder, and first director, of MBL (all three are discussed below).

Louis Agassiz died in December, 1873, and his son, Alexander Agassiz (1835–1910), who became America's foremost oceanographer (Murray 1911, Goodale 1912, Agassiz 1913:129–130, Dohrn 1913, Herdman 1923:99–118, Lane 1969:47–49, Dupree 1970, Ward 1974:152–167, Lurie 1999, Dobbs 2005:114–119), organized the school for summer 1874, though the double shock of having his father and his wife die a few days apart in December 1873 left him psychologically unable to run it. Alexander had been born in Switzerland, where his mother died of tuberculosis in 1848, and he had come to Boston in 1849, joining his father (Lurie 1960:152, 170). He spoke no English, but was nevertheless enrolled in the Cambridge High School to prepare for college (Agassiz 1913:14–15). His father taught natural history there, and physics and chemistry were also well taught. He entered Harvard in 1851, age 15. He graduated in 1855 and entered the Lawrence Scientific School and earned a master's degree in engineering (1857), and another master's degree there in zoology (1862). He worked at Harvard's Museum of Comparative Zoology with his father (Winsor 1991:134–146), but decided he could not raise a family on his salary. In 1866 he traveled with several Bostonians to the Upper Peninsula in Michigan to inspect two copper mines and then bought shares in them (Agassiz 1913:57–85). Those controlling the mines asked him to run them, which he did, 1866–1868, and eventually he became a millionaire. In 1874, he and a brother-in-law bought land on Narragansett Bay, Rhode Island, and built houses there; Agassiz's included a laboratory where he could study marine animals (Agassiz 1913:151–156).

Alpheus Hyatt (1838–1902), from Washington, D.C., studied under Agassiz at Harvard (Brooks 1909, Mayer/Mayor 1911, Gould 1972). He graduated in 1862 and joined the Union Army during the Civil War. Afterwards, he married (1867), and became part-time professor of zoology and paleontology at the Massachusetts Institution of Technology, 1870–1888. In 1870 he was also elected curator of the Boston Society of Natural History and remained its scientific head until he died. In 1877 he additionally became professor of biology at Boston University. In 1883, he helped organize the American Society of Naturalists and served as its first president. He conducted research on invertebrates, living and fossil (Dexter 1968). He studied bryophytes, gastropods, and evolution, and was an American cofounder of neo-

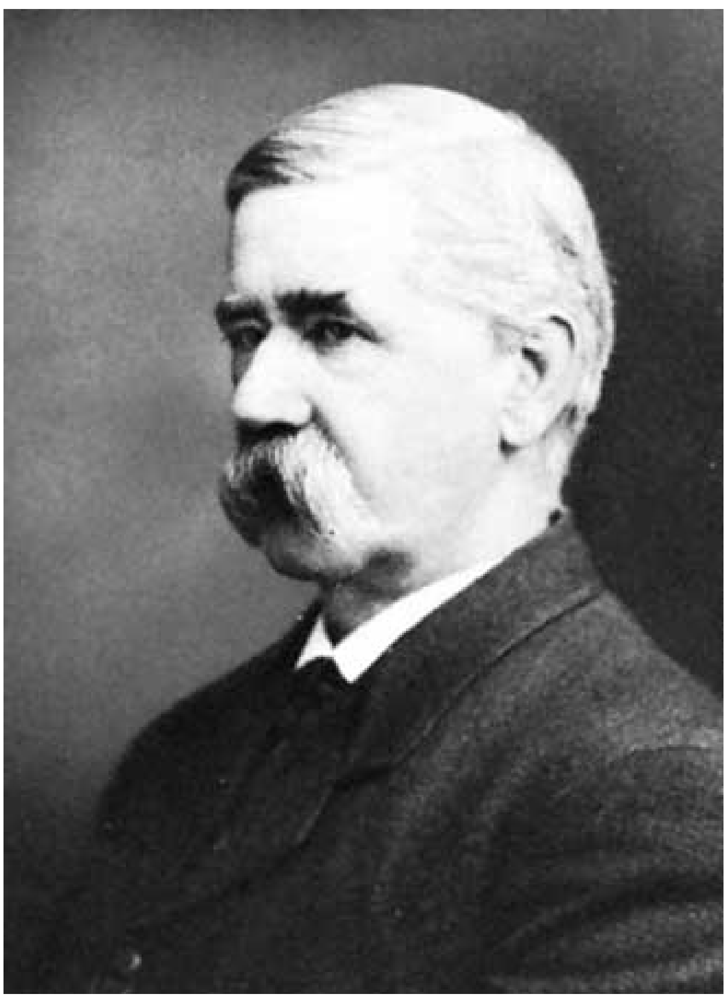


Fig.7. (a) Alexander Agassiz. Web page, middle age. (b) Alpheus Hyatt. Brooks 1909 or online. (c) William Keith Brooks. Conklin 1913:facing 25. Online.

Lamarckism. In 1879 he established a marine biological laboratory in his summer home at Annisquam on Cape Ann, Massachusetts (Dexter 1952, 1956), and in 1880 he had a schooner-yacht, *Arethusa*, built for collecting and studying animals along the shores of New England, Newfoundland, and Labrador, for himself and students (Hyatt 1954). In 1882 the laboratory moved to a small building at Lobster Cove, but there was some pollution there and Baird persuaded him to move it to Woods Hole in 1887, where it was reorganized into the Marine Biological Laboratory, Woods Hole (Lillie 1944:26–33, Hiatt 1954:95–96, Dexter 1980, Maienschein 1985, 1989).

William K. Brooks (1848–1908) graduated from Williams College in 1870, attended Agassiz's Summer School of Natural History on Penikese Island in 1873, studied under Alexander Agassiz, and received his Harvard Ph.D. in 1875 (Conklin 1913, Edds 1970). He then joined the faculty of Johns Hopkins University, founded 1876, where he served as head of the Biology Department, 1894–1908. He studied the morphology of marine invertebrates. He received university funds to run a summer Chesapeake Zoology Laboratory, 1878–1906, which was the first research marine station in America (Benson 1985:193). Despite its name, it moved in most summers from one place to another, from Massachusetts to Jamaica. This summer station was quite successful—15 major articles appeared on work done there in 1878–1880, and over 30 of Brooks' doctoral students worked in it (Benson 1985:194–197). Brooks founded several Johns Hopkins biological periodicals to publish such studies, and he also was influential on other periodicals.

Entomologist Alpheus S. Packard, Jr., a Louis Agassiz student discussed in part 45 (Egerton 2013:53–55), was an instructor both years at Penikese, 1872–1873, and he convinced the Peabody Academy of Science, Salem, Massachusetts to establish a six-week Summer School of Biology under his direction in 1876, costing students $10, plus $5 a week for food (Dexter 1957). It was limited to 15 students in 1876, but had 21 enrolled in 1877, with 10 others attending lectures. Its third summer, with a longer period and fewer students, was described beforehand in *Harper's Weekly* (13 April 1878). In the fourth summer (1881), Packard had left for Brown University, and the Summer School was supervised by Edward S. Morse (1838–1925), new director of the Peabody Academy. Plans were made for continuation in summer 1882, but the previous summers had satisfied the demand among Massachusetts teachers; only three students indicated interest and it was canceled. Yet, the idea still did not die.

Charles O. Whitman (1842–1910) was the first director at the Marine Biology Laboratory (1888–1908), which opened 17 July 1888 (Lillie 1944:35). He was the first American to work at Dohrn's station in Naples, staying there for six months in 1881–1882 (Morse 1912, Conklin 1944, Ward 1974:142–146, Mayr 1976, Maienschein 1985*b*:187, Pauly 1988:129–132). Whitman was also a pioneer in ethology (Kohler 2002:31, 45–47, Burkhardt 2005:19–33). He was a capable director, though MBL struggled with

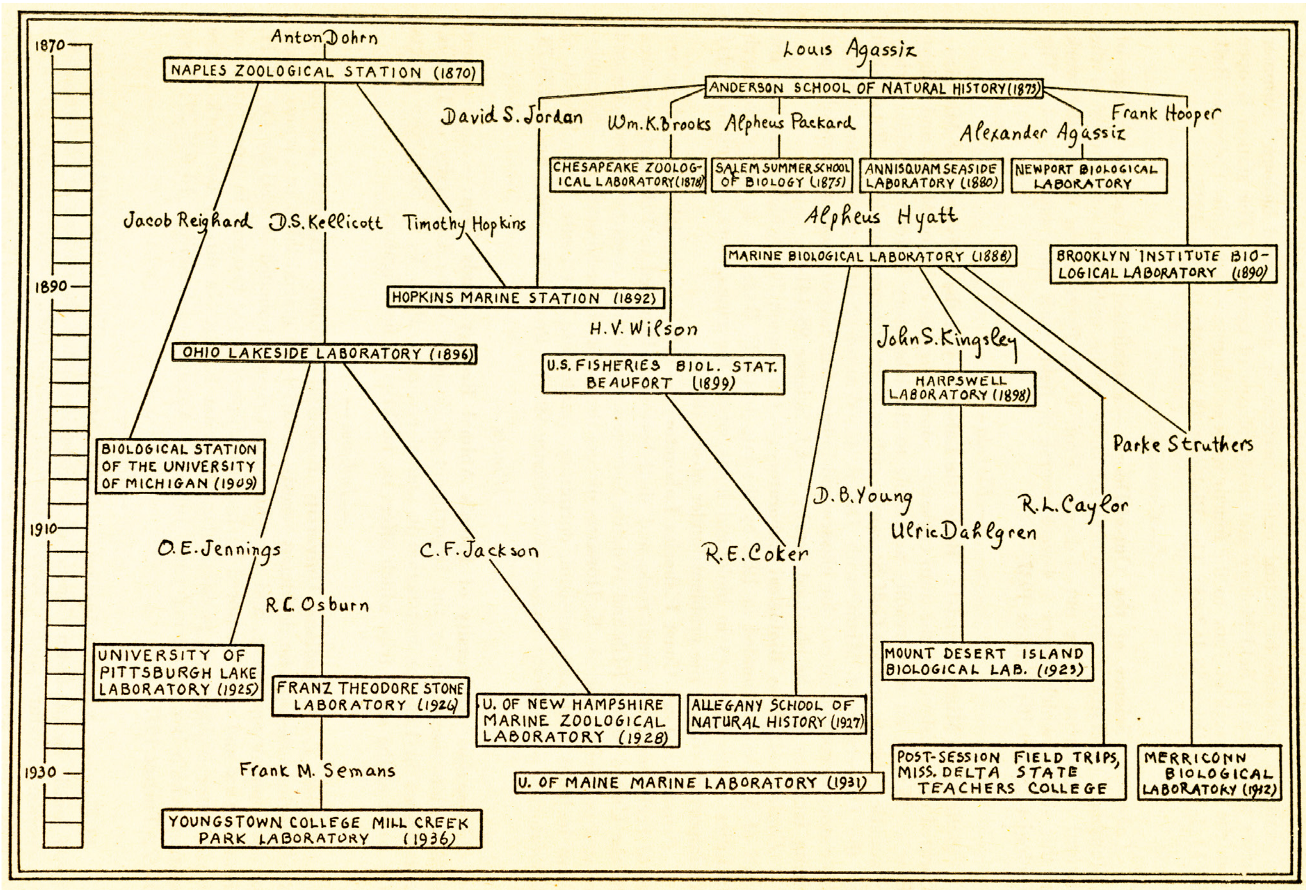


Fig. 8. Genealogy of United States Biological Stations. Jack 1945:64.

finances during Whitman's tenure (Maienschein 1985*c*). It did attract three years of funding from the Carnegie Institution of Washington (Lillie 1944:53–59, Ebert 1985:174–180). MBL began the *Biological Bulletin* in 1900—an outlet for research done at MBL—and its issues were traded for other biological journals published around the world (Lillie 1944:106–107, Russell-Hunter 1985). Frank Lillie (1870–1947) was a native of Toronto, and when he graduated from its university in 1891, he went to Woods Hole to work under Whitman (Watterson 1973). In the fall, he followed Whitman to Clark University, and in 1892, he followed Whitman to the new University of Chicago, where Lillie received his Ph.D. in 1894. Lillie taught at the University of Michigan and Vassar College before joining the University of Chicago faculty in 1902. Lillie succeeded Whitman as director of MBL in 1908 and as chairman of the Department of Zoology at the University of Chicago in 1910. He would be an important participant in the founding of the Woods Hole Oceanographic Institution (WHOI) in 1931.

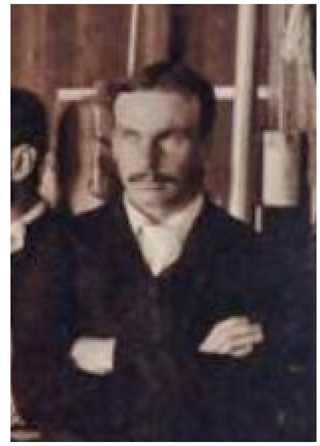


Fig. 9. (a) Charles Otis Whitman [Morse or Web] (b) Frank Rattray Lillie. Web [color]

Dr. Alfred Mayer/Mayor (changed spelling from Mayer in 1918, 1868–1922), was the son of a physics professor, and he earned an M.E. degree from Stevens Institute of Technology (1889) in physics and a Sc.D. degree from Harvard University (1897) in zoology (Stephens and Calder 2006:2–26). Because of his skill as an animal illustrator, he became an assistant to Alexander Agassiz at Harvard's Museum of Comparative Zoology, 1892–1900, after which he became curator of natural sciences at the Brooklyn Institute of Arts and Sciences, 1900–1904. He had collected marine invertebrates for the MCZ, and he urged the Carnegie Institute of Washington to establish a tropical marine station (Davenport 1926, Colin 1980, Stephens and Calder 2006:34–48). In 1898 he had chosen a site for one on Loggerhead Key in the Dry Tortugas Islands (now a national park; tortugas is Spanish for turtle, and loggerhead is the name of a turtle species that lays eggs on the key), Florida, 67 miles (110 km) west of Key West (Stephens and Calder 2006:14). A lighthouse was there, and obsolete Fort Jefferson was on nearby Garden Key. He published two notes in *Science* supporting his idea for that station (Mayer 1903*a*, *b*). Carnegie Institute agreed and offered him the directorship in January 1904 (Stephens and Calder 2006:48), and he had station facilities and a boat built during summer 1904. The boat, *Physalia* (=Portuguese-man-of-war), was built in Maine, and he sailed it to Loggerhead Key in the fall, collecting specimens as he sailed south. (It remained seaworthy only through summer 1910, then was replaced by a larger, more expensive

Fig. 10. (a) Alfred Goldsborough Mayer/Mayor at the helm of *Physalia*. (b) Two species of Scyphomedusae: *Rhopilema verrilli and Crambione cookie*. Mayer 1910:III, plate 74. From Stephens and Calder 2006:frontispiece or after 88.

Anton Dorhn.) The Tortugas Marine Laboratory was the first tropical research station in the Americas. Mayer/Mayor invited young biologists or geologists of promise or established scientists with reputations. He was a productive invertebrate zoologist who set an example for the others (a good number of his publications are now online), and he also initiated the *Papers of the Tortugas Laboratory of the Carnegie Institution of Washington* (35 volumes, 1908–1942). His greatest work was *Medusae of the World* (three volumes, 1910), on jellyfish. However, he broke new ground in his quantitative ecological surveys of coral reefs (Mayer/Mayor 1918, 1924, Colin 1980:142), and the Tortugas Laboratory was the first station where systematic studies on living coral occurred (Fautin 2002:446–447). In June 1922 Mayor was ill with tuberculosis, but nevertheless went to the station, where he fainted and drowned (Stephens and Calder 2006:147).

The second head of the Tortugas Marine Laboratory was ichthyologist William H. Longley (1881–1937), born in Paradise, Nova Scotia, who earned his B.A. degree at Arcadia College (1901). He went to Yale University for his M.A. and Ph.D. (1908, 1910). He taught at Goucher College, Baltimore, beginning in 1910. One of his interests was the significance of color and color patterns in tropical reef fishes. He published "Life on a Coral Reef" (1927), and he first published underwater color photographs (8) of fish in their natural habitat (Longley and Martin 1927).

On the Pacific coast, David Starr Jordan (1851–1931) was America's foremost ichthyologist (Hubbs 1964:50–52), a former president of Indiana University, and in 1892, first president of Stanford University (Jordan 1922, Burns 1953, Hays 1953, Shor 1973, Geiger 1999), when he, along with ichthyologist Charles Henry Gilbert and Oliver P. Jenkins, opened the Hopkins Marine Station at Pacific Grove, California (Jack 1945:62, Hyatt 1954:125–127, 1963:216–217). It was the first such station on the Pacific Coast. Jordan ensured his place in history by writing a two-volume autobiography (Jordan 1922, 710 and 906 pages).

The University of California wanted its own station (Raitt and Moulton 1967:5–17, Walsh 2004:56–57, 63–65). Wisconsinite William E. Ritter (1856–1944) had studied under Alexander Agassiz at Harvard and became Professor of Zoology at the University of California, Berkeley (Sumner 1944, Pursell 1973, Ward 1974:146–149, Burgess 1996:92–93, Jackson 1999, Pauly 2000:201–212). On his honeymoon in 1891, Ritter and bride traveled to San Diego and met Dr. Fred Baker, physician and amateur conchologist (Raitt and Moulton 1967:9–10, Mills 1993:10–11). Baker suggested that San Diego would be a good location for a marine station. Ritter investigated several other locations first, to gain a perspective on where was best (Ritter 1912:148–155). In 1900 Ritter invited CharlesKofoid to move from Illinois to the University of California, Berkeley, and in 1901 Ritter obtained his assistance

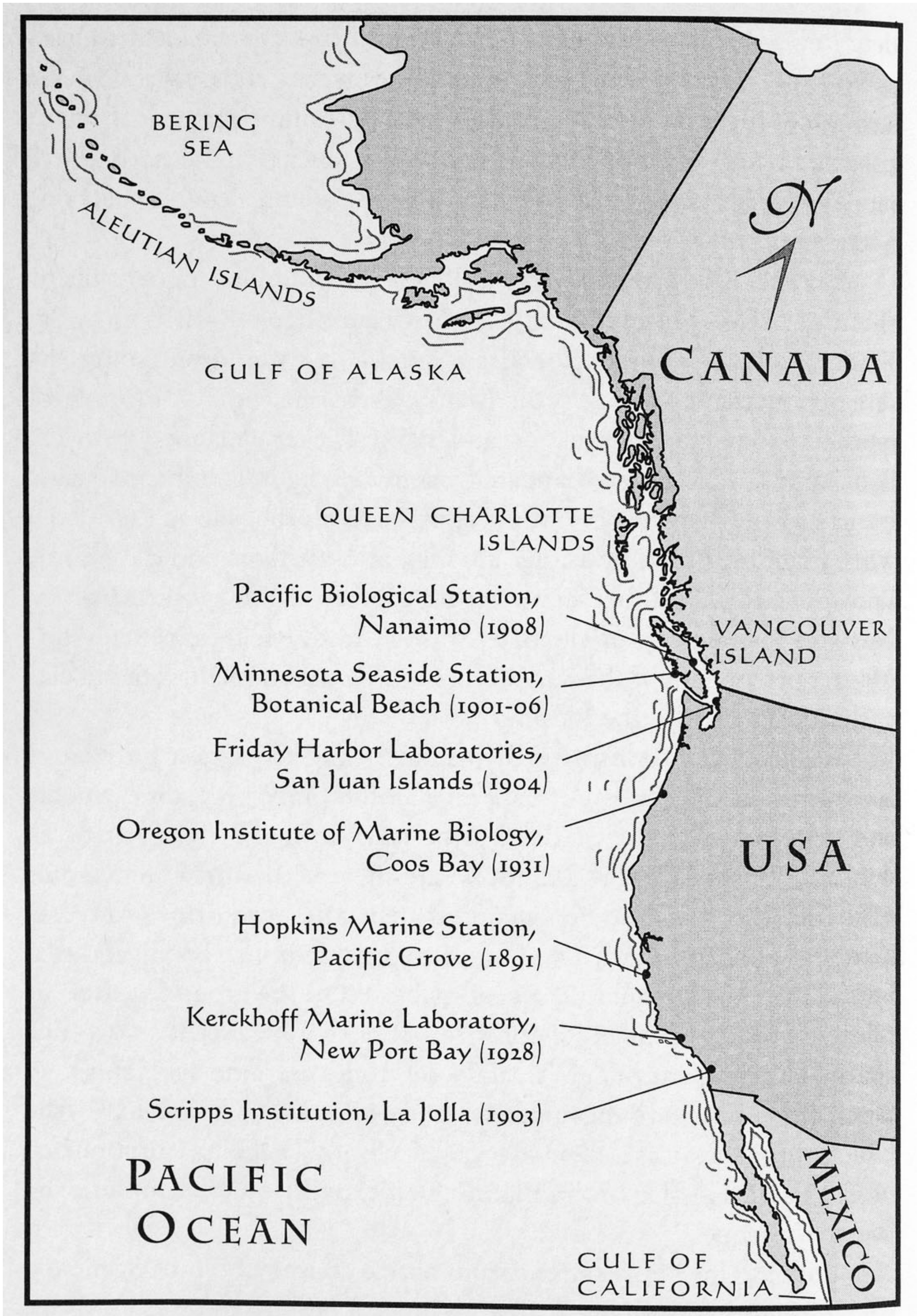


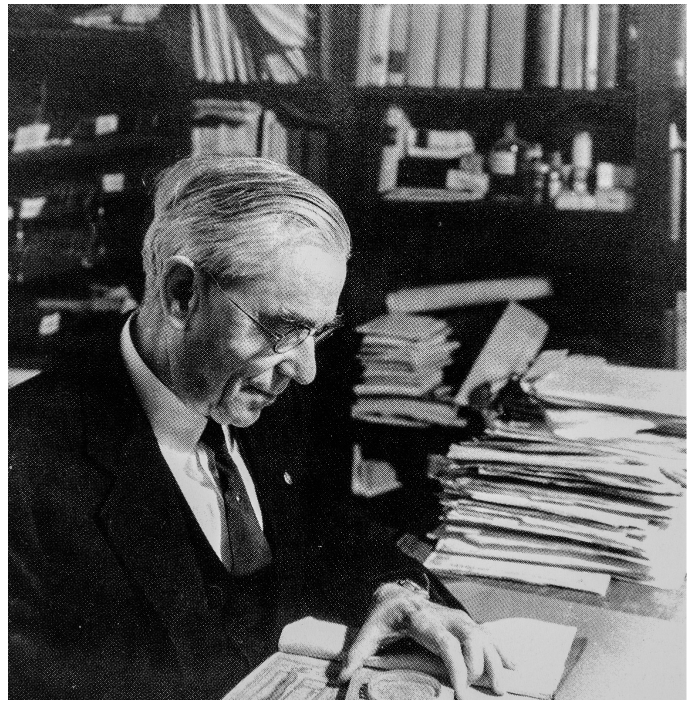
Fig. 11. Pacific Biological Stations and dates of founding. Tamm 2004:52.

in organizing a marine research program for that summer (Goldschmidt 1951, Mullen 1973, Shor 1974, Spiess 2002:8, Day and Mills 2013:236–237). In 1903 Baker arranged for Ritter to use a boathouse as a summer station. The Marine Biological Association of San Diego was established to support it. In 1904, Kofoid went to the boathouse a month before Ritter in order to arrange for the summer's work (Spiess 2002:9). In 1905 the Biological Association built, under Kofoid's supervision, a small laboratory at La Jolla Cove, and in 1907 the laboratory obtained a sailing ship, *Alexander Agassiz* (Ritter 1912:158–191, Raitt and Moulton 1967:50, Mills 1993:12–13). During that summer, Ritter met Edward W. Scripps and his sister, Ellen B. Scripps, and both became patrons of what would become the Scripps Institution for Biological Research (1912), which Ritter and Kofoid envisioned as having a team research orientation, including physical sciences, modeled on ICES (discussed below; Mills 1993:26–27, 2009:195–201). Ritter retired in 1923, and in 1925 the institution became the Scripps Institute of Oceanography under Wayland Vaughn (Vaughn 1937, Hiatt 1954:163–167).

While Kofoid was in Germany, Ritter wrote to him on 18 October 1908: "while we are greatly interested in oceanographic problems as such, we must not, as I see it, ever let these rise to the place of primary importance. Biology is our main interest…" (quoted in Benson 2002:311). After building the station, Ritter explained achievements from there under these headings: a "speaking acquaintance" with fauna (survey), abundance and mode of life, morphology and physiology, reproduction and development, adaptations of organisms, natural selection, animal behavior, the water, and topography of sea bottom (1912:192–209). Ritter had broad interests in biology and philosophy, indicated in his bibliography in his posthumous *Charles Darwin and the Golden Rule* (1954:381–392).

An outstanding biologist whom Ritter recruited for the Scripps Institution was Francis B. Sumner (1874–1945), with Ph.D. from Columbia University (Child 1948, Burgess 1996:102–103). Sumner had held a variety of zoological positions before joining Ritter's organization in 1913. Most immediately, he had conducted a survey of life in the bay at Woods Hole and then another survey at San Francisco Bay (Sumner 1945:192–197). After Ritter retired, Sumner was acting director of the Scripps Institution, 1923–1924, and after Scripps became Scripps Institution of Oceanography with geologist-marine biologist Vaughan (discussed above) as second director (1924–1936), Sumner left in 1927 for the Carnegie Institution in Washington. Sumner published an obituary of Ritter in 1944 and his own autobiography in 1945 (without illustrations, bibliography, or index), the year in which he died.

Pacific University, Forest Grove, Oregon, announced in *Ecology* (4 [1923]:91) its new station at the mouth of the Columbia River, near Astoria, but apparently it did not long persist.



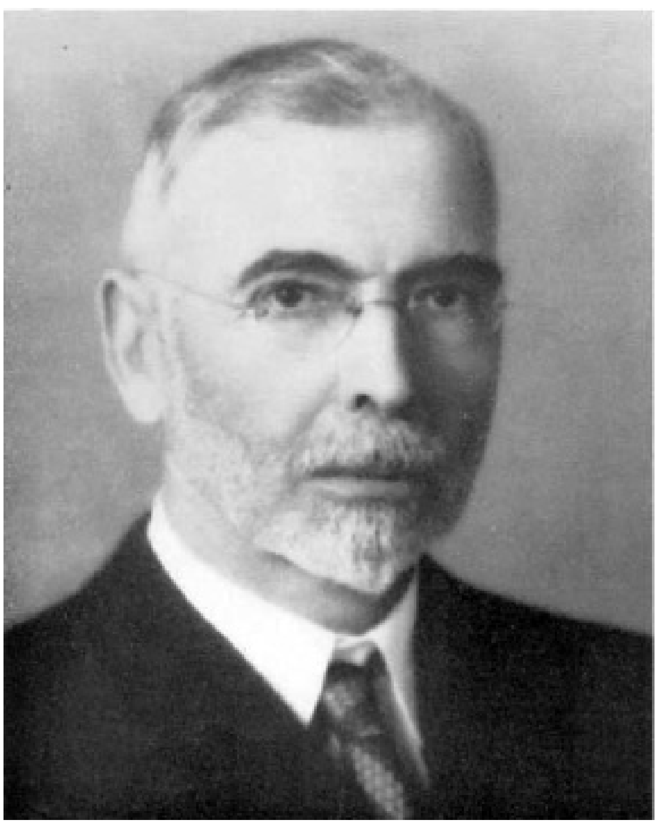


Fig 12. (a) William Emerson Ritter. (b) Charles Atwood Kofoid. Mills 1993:10, 25. (c, left) Francis Bertody Sumner. Child 1949:146. Online.

Research stations: Canada

Canada's concerns for the future of its fisheries arose parallel with such concerns in the United States, which led to some parallel developments, one of which was the construction of a biological station for research on fisheries. Zoologist Playfair McMurrich (1859–1939) earned his B.A. and M.A. degrees from the University of Toronto (1879, 1881) and Ph.D. (1885) from Johns Hopkins University (Johnstone 1977:24). At Johns Hopkins he conducted research at its coastal Zoology Laboratory, and he later suggested that Canada's Department of Fisheries establish marine stations in Nova Scotia, the Gulf of St. Lawrence, and on Vancouver Island. However, since McMurrich taught in U.S. colleges and universities, 1884–1907, he was not in a good position to push his idea. In 1892, Rev. Dr. Moses Harvey read a paper to the Royal Society of Canada urging "the desirability of establishing a Biological Station for the study of Ichthyology and Marine Biology in all their branches" (Johnstone 1977:25). The Society appointed a committee to investigate, but no report emerged. However, the suggestion may have influenced the Canadian government, which in 1893 appointed English zoologist E(dward) E(rnest) Prince (1858–1936) as Commissioner and General Inspector of Fisheries. He had been educated at St. Andrews, Edinburgh, and Cambridge universities. He soon recommended that the Canadian government establish a marine station, and the Royal Society of Canada pondered the matter again. Since the British Association for the Advancement of Science was to meet in Toronto in 1897, a BAAS committee was appointed in 1896 to report on the matter at that meeting. Prince was chairman of that committee, and the outcome was that the BAAS recommended to the Canadian government in 1898 that a floating station be established on the St. Lawrence River for five years (following the example of Petersen's portable Danish station). In summer 1899 the station opened under Prince's supervision, not along the St. Lawrence, but at St. Andrews on the New Brunswick coast, across the St. Croix River from Maine. A small group of researchers investigated different topics (Johnstone 1977:33–34).

> *R. R. Bensley studied the food of fishes and B. A. Bensley concentrated on the relation of the sardine industry to the herring industry, the decline of which was attributed to the taking of the young for sardines. Stafford began his study of the clams and the clam industry. His report and that of B. A. Bensley appeared in the first issue of* Contributions to Canadian Biology *in 1901. [Joseph] Stafford also began a study of the fauna of the region, which would continue along the coast as the station was moved to new locations. Knight joined the team later and began an investigation of the eggs and larvae of pelagic fishes and the morphology of the lobster. Macallum also arrived to study the chemistry of the Medusae, and both Bailey and Dr F. S. Jackson of McGill came to the station, though the extent of their studies was not reported.*

After two summers at St. Andrews, the station was towed in 1901 to Canso, Nova Scotia, which was the largest fishing center on the east coast, where zoologists could obtain specimens from commercial

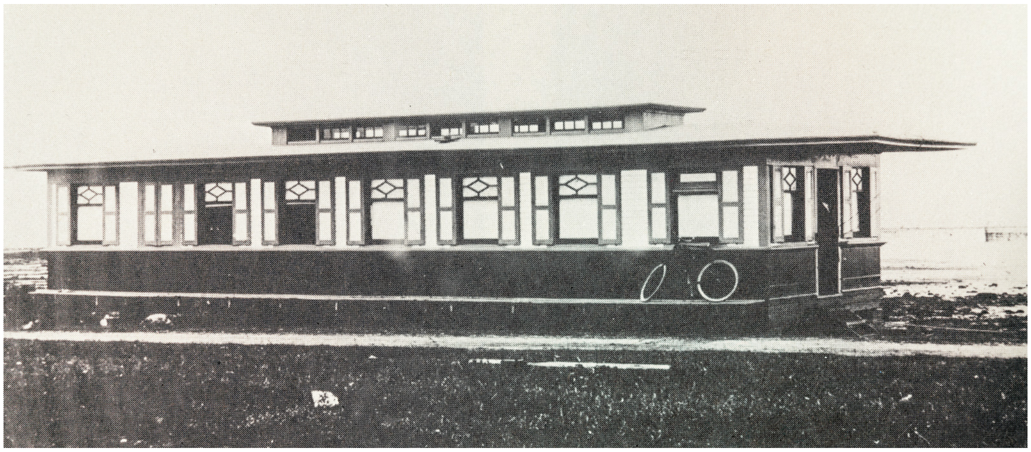
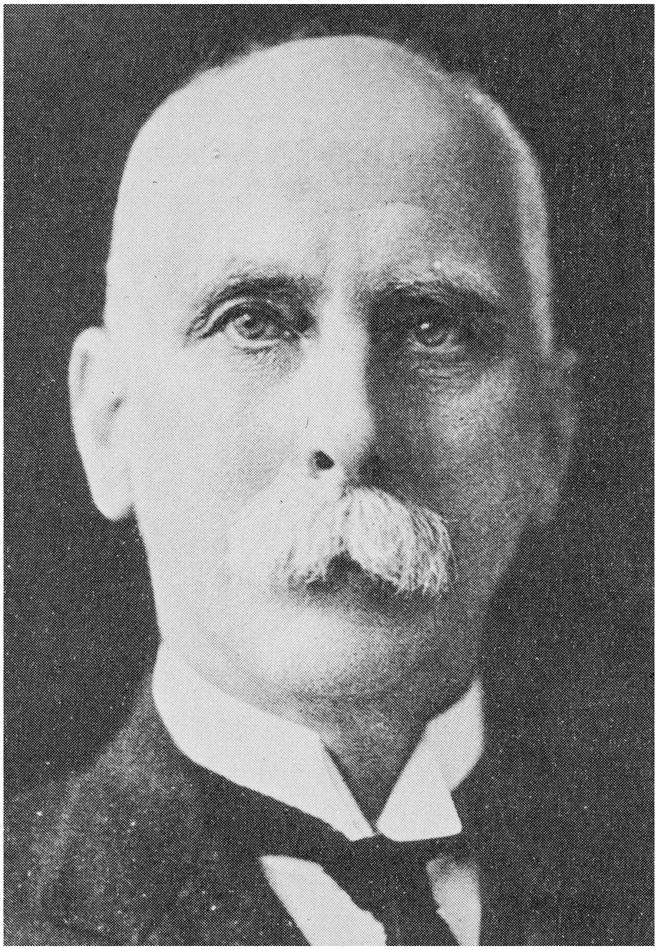


Fig. 13. Canada's first (moveable) Marine Biological Station, 1899–1906. Johnstone 1977:34.

fishermen, and the Whitman Brothers, fish merchants, allowed zoologists free use of its steam tug (Johnstone 1977:36). The third site to which the station moved was Malpeque, Prince Edward Island, center of an oyster fishery. In 1907, the station was to be towed to Seven Islands in the Gulf of St. Lawrence, but the scow on which it was placed leaked and it was abandoned. The attic of a fish house was rented instead. Kenneth Johnstone provided biographical sketches and photographs of eleven of the station's investigators (1977: sketches, 41–45, photographs, 30–33). The second station established by the Canadian Minister of Fisheries was the freshwater Georgian Bay Biological Station, previously discussed (Egerton 2014b:146).

Canada's first Pacific marine station was on Vancouver Island, established by Josephine Tilden (1869–1957), from the Botany Department, University of Minnesota, Minneapolis, operating in 1901–07; the only Canadian known to have worked there is McLean Fraser, in summer 1903 (Johnstone 1977:63). The University of Washington also had a marine station on San Juan Island, near Victoria. Those two stations motivated Canadians to build their own. Englishman George W. Taylor had done museum work before immigrating to Canada in 1882 (Johnstone 1977:61–69). He soon decided he needed two careers, and he became a parish clergyman in the Church of England without giving up his collecting of insects and marine animals. In 1905 he became a member of the British Columbia Fisheries Commission, which recommended establishing a biological station to the Canadian Marine Biological Board. In April, 1907, the Canadian Parliament voted funds for an Atlantic and a Pacific station, both of which were begun in 1907 and opened in 1908. The Atlantic station was built at St. Andrews (Hachey 1965:141–143, Johnstone 1977:52–53, Mills 2014:13–14). Professor McMurrich, who had returned from USA to the



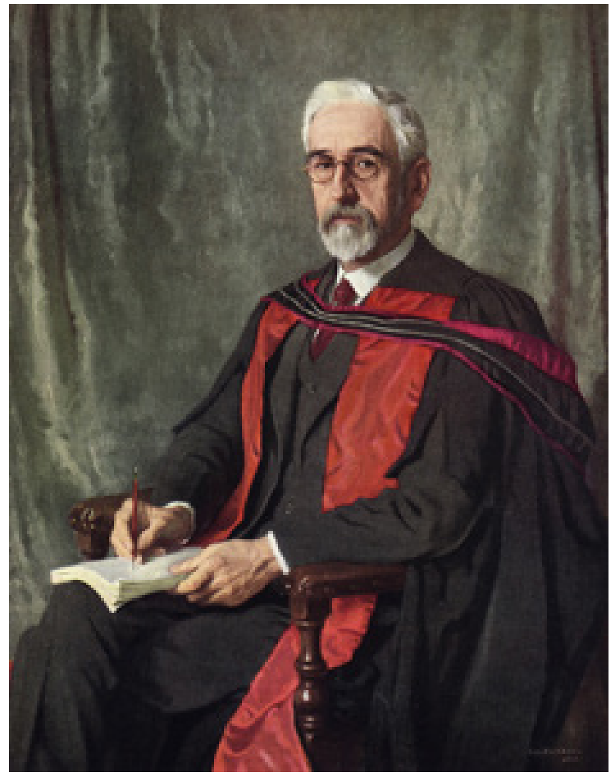


Fig. 14. (a) Edward Ernest Prince. (b) J(ames) Playfair McMurrich. Johnstone 1973:30, 31. (c, left) Archibald Gowanlock Huntsman. Johnstone 1977:89.

University of Toronto, arrived there first in summer 1908, to study sea anemones and cephalopods. Others soon followed, to study a variety of species, especially fish (Johnstone 1977:55–60). The Pacific station was built at Departure Bay, near Nanaimo, Vancouver Island, headed by Taylor, who brought along his own scientific library. There is a half-century history of scientific research at Nanaimo (Needler 1958; also, Hachey 1965:143–145).

Ontario native A(rchibald) G(owanlock) Huntsman (1883–1972) earned two bachelor's degrees from the University of Toronto (1905, 1907) and then spent his career there (Hubbard 1997, 2006, Mills 2014:14). In 1908, after the new station opened at Nanaimo Harbor, British Columbia, he spent two months there collecting and studying marine animals and returned in summer 1909 to continue (Johnstone 1977:67–68). In 1911, he began his long association with the St. Andrews station, serving as curator, 1911–1919, then as director, 1919–1934. In 1914–1915, at Prince's invitation, Norwegian fisheries biologist Hjort went to Canada and organized the Canadian Fisheries Expedition of 1915. "Hjort's influence on Huntsman was immense" (Mills 2014:14). An ESA member, Huntsman soon began other expeditions along the eastern coast which were more comprehensive than previous Canadian studies, which lasted until 1923 (Johnstone 1977:87–90). In addition to being director of the St. Andrews station, Huntsman agreed to also direct a Technological Laboratory at Halifax for the Fisheries Research Board of Canada (Johnstone 1977:113–114). However, Huntsman was stretched rather thin, and only published his findings in 1954. Huntsman obtained funds in the late 1920s to hire a physical oceanographer at the St. Andrews Station, Harry Hachey, who helped publish Huntsman's report (Mills 2014:16). By late 1920s, marine ecology was being equaled in Canada by physical oceanography.

Marine stations: Latin America

Latin America was rather slow in developing marine stations. Martín Doello Jurado (1884–1948), Director of the Argentine Museum of Natural History, established the Hydrobiological Station of Port Quequén in 1928, which was "the first oceanographic station in South America" (Sanchez 2002:149). As of 2002, it had not been able to expand beyond its original modest building, but

> *The range of research activities carried out is very wide, encompassing catalogues on the fish and molluscs of the region, embryological and trophic studies on echinoderms, marine parasitology research, studies on the distribution of water masses through plankton indicators, investigations on phytoplankton organisms producing toxic blooms, etc.*

Research voyages

British marine biology, which Edward Forbes and Philip Henry Gosse had advanced (Egerton 2010), retained its momentum, seen in the dredging work of John Gwyn Jeffreys (1809–1885), William Carpenter (1813–1885), Wyville Thomson (1830–82), and Alfred Norman (1831–1918), all providing a context for the *Challenger* Expedition (Herdman 1923:8–10, 37–68, Lane 1969:45–46, Deacon 1971:306–332, 2004*a*, *b*, Thomas 1971, Heppell 1973, Schlee 1973:94–103, Ward 1974:95–107, Thomas 1976, Mills 1980*b*, 1983:7–10, Rice and Wilson 1980:378–384, Vanney 1993:208–211, Rice 2004). That expedition was an early example of "big science," which means a big commitment of government support (Burstyn 1968*b*:665).

The immediate stimulus for the voyage of the *Challenger*, December 1872–May 1876, was the zoological success and temperature records from deep sea dredging during the summers 1868–1871 by Carpenter and Thomson, using British naval vessels, in waters near the British Isles (Lane 1969:46, Linklater 1972:13–14, Schlee 1973:99–103, Mills 1975:5–6, 1983:10–18, Deacon 1997:333–334, Rozwadowski 2005:35, 152–162). Forbes had provided logical arguments for why marine life could not exist more than 300 fathoms deep, which won general acceptance, until actual live specimens began to be dredged up from much deeper depths (Ward 1994:98–102, Saldanha 2002:235, Egerton 2010:182–183, 188). Thomson summarized their discoveries in *The Depths of the Sea* (1873). Thomson and John Murray also prodded the Royal Society with a letter (1871) stating that Germany, Sweden, and USA were planning deep-sea expeditions (Tomczak 1980:189). It was a giant step from summer dredging around Britain to a 3.5-year voyage around the world, covering 68,890 miles. Strong backing from the Royal Society of London, in an age when transoceanic cables were being laid, provided the British Government with the incentive to support an expedition that could collect information on characteristics of the sea floor (Burstyn 1968, 1972, Mills 1975:6–12, Rozwadowski 2005:6–13). Thomson, who had become Professor of Natural History at the University of Edinburgh in 1870, was appointed Director of the Civilian Staff. Captain George S. Nares and most of his 23 officers on the *Challenger*, 2300 tons and 240 men, were highly experienced from previous surveying voyages (Rozwadowski 2005:161–170).

Canadian-born John Murray (1841–1914), at age 17, immigrated to his parents' homeland, Scotland, where he went to high school and the University of Edinburgh (Herdman 1923:69–98, Merriman 1972*a*, Burstyn 1974, Ward 1974:113–136, Ashworth and Mills 2004, Price 2004). He studied medicine, but never earned a degree. While residing in Edinburgh, he was a last-minute recruit for *Challenger*, yet in the long run he was as important a naturalist as Thomson, since Murray saw the 50-volume report through the press after terminally ill Thomson resigned in late 1881.

The civilian staff on the *Challenger* voyage, besides Thomson and Murray, included biologist–anthropologist Henry N. Moseley (1844–1891), who afterwards became Professor of Anatomy at Oxford (Bourne 1892, Desmond 1977:452–453, Corfield 2003:113–14); chemist John Buchanan (1844–1925),

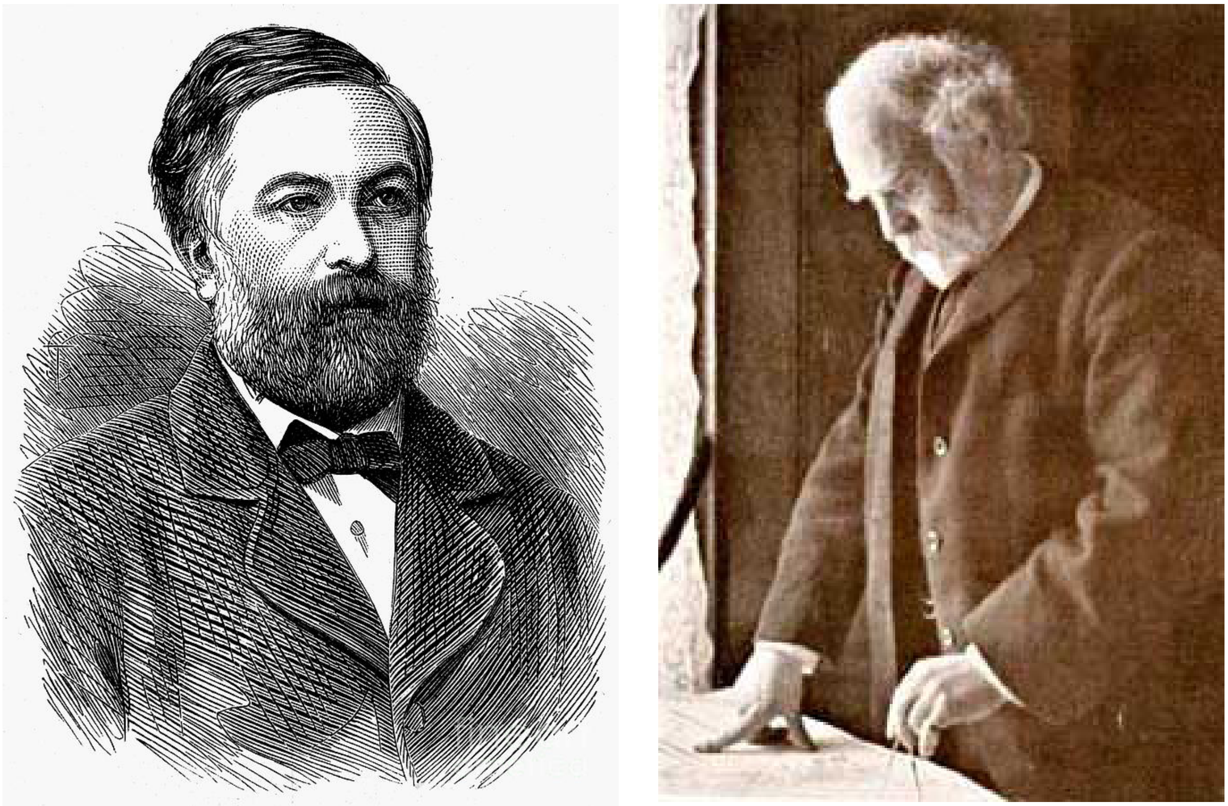


Fig. 15. (a) Charles Wyville Thomson. Web. (b) John Murray. Web.

who afterwards continued in oceanographic research (as mentioned under Albert; Kutzbach 1970, Corfield 2003:15–16, 251); German invertebrate zoologist Rudolph von Willemoes-Suhm (or Willimoes-Suhm, 1847–75), who was highly regarded but died of erysipelas during the voyage; and Swiss artist John James (Jean Jacques) Wild (b.1824), who was also Thomson's secretary, and afterwards wrote *Thalassa: an Essay on the Depth, Temperature, and Currents of the Ocean* (Wild 1877, Deacon 1997:357) and *At Anchor, a Narrative* (1878). Wild's drawings illustrated several volumes of the *Challenger Report*.

Willemoes-Suhm sent reports during the voyage to his former professor, Carl von Siebold, who published them in his *Zeitschrift für wissenschaftliche Zoologie*. He also wrote letters to his mother that were published in 1877 and in 1984. Daniel Merriman translated extracts from his letters (1971:22–28), which show that he was a happy colleague, enthusiastic about their discoveries (2 February 1873, Willemoes-Suhm 1984:42, translations in Merriman 1971:24):

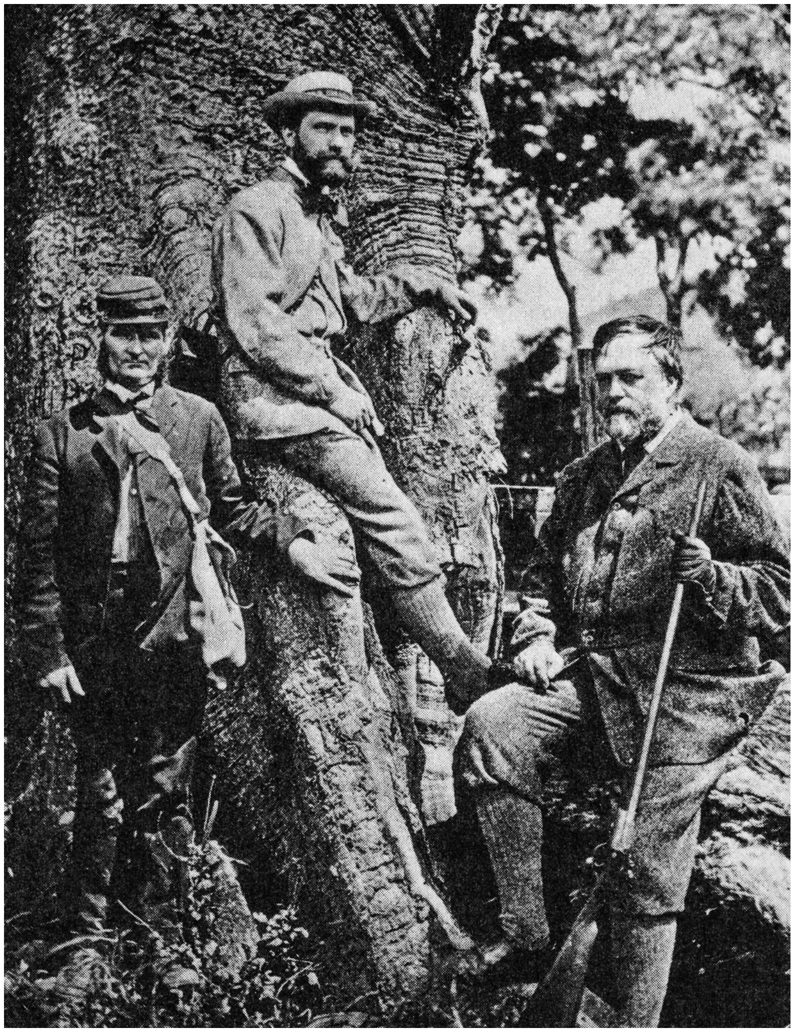


Fig. 16. *Challenger* naturalists in the Virgin Islands: Rudolf von Willemoes-Suhm (center), C. Wyville Thomson (right), and crew member. Natural History Museum, London. Schlee 1973:109.

> *Early this week I got a fascinating thing to work up, namely a 3-inch crab with 1-inch eyes. It is new and, what is even more important, its transparency makes it easy to delineate its interesting anatomy. I have been hard at work on it; the artist has made two large, beautiful plates, and the work is far enough along so that it can be sent to England from Teneriffe. Thomson wants to send it to Huxley, so that he can deliver it to the Royal Society for its Transactions…it is a real delight to work under such conditions with such fine material.*

On 30 June, 114 miles west of Fayal Island in the Azores, the dredge from 1000 fathoms (6000 feet) delivered, among other specimens, "A schizopod crustacean of large size and great beauty of form and brilliancy of coloring" which Willemoes-Suhm judged as "congeneric with the species taken at Station LXIX, at a depth of 2200 fathoms" (Thomson 1878, II:20–21). He established the genus *Gnathophausia* for these two species.

The *Challenger* memoirs by Thomson and by Moseley can be compared with Darwin's *Journal* from his *Beagle* voyage (1831–1836), four decades earlier, though the *Challenger* Expedition had three or four naturalists searching and Darwin mostly had only himself. Thomson took two volumes to discuss all that he had learned during their several crossings of the Atlantic Ocean (Deacon 1971:333–365, Ward 1974:109–112, Mills 1983:22–24), and he had intended to write comparable volumes on the Pacific, had he lived longer. When writing about the *Challenger*'s stop at St. Paul's Rocks, Thomson and Moseley compared their findings with Darwin's (Rozwadowski 2005:27–29). However, Moseley seems not to have consulted Thomson's memoir when writing his own (1880) even though Thomson's had appeared three years earlier. Thomson and Moseley also saw only two bird species nesting there, for which Darwin in his *Journal* (1839:9) used only common names: booby (a gannet) and noddy tern. Thomson (1878, II:95) also mentioned scientific names: booby *Sula fusca* and noddy tern *Sterna stolida*. Moseley reported (1877:797–798), however, that Howard Sa[u]nders (1835–1907), specialist on gulls and terns, had discovered from *Challenger* specimens that there were actually two species of noddy terns: *Anous stolida* and *A. melanogenys*. In retrospect, Moseley remembered that the noddies nested in two kinds of locations, and he speculated that each species might have chosen one kind of location, different from the other species (1892:58). Since nesting noddies were seen there in February by Darwin, in May by Captain James C. Ross in 1839, and in August by *Challenger* naturalists, Moseley (1892:63) concluded that noddies breed there all year.

Thomson also found no land plants, but he did comment on seaweeds that the noddys used for their nests, for which Moseley gave the scientific name as *Caulerpa clavifera*. Boobies laid eggs on bare rocks, but Thomson found that noddies used conferva, growing at the waters edge, plus feathers to build nests, with cement possibly from their stomachs (Thomson 1878, II:95). Moseley thought the cement

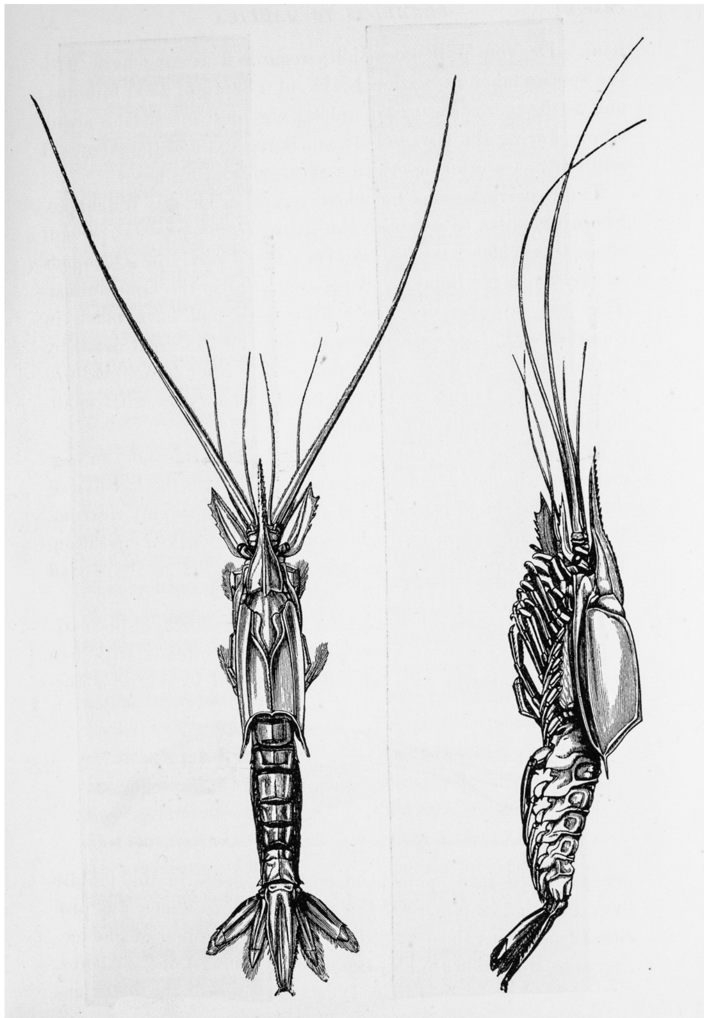


Fig. 17. *Gnathopohausia gigas* Willemoes-Suhm. Thomson 1878:II, facing 21.

used was dung. Darwin mentioned the crab with only the genus name (Darwin 1839:10) but Thomson (1878, II:97) and Moseley (1892:60) could report that *Grapsus strigosus* was also found on several other Atlantic islands, identified by Moseley as Cape Verde Islands. Both Thomson and Moseley reported one insect, *Chelifer*, that Darwin did not see (Moseley also listed a moth *Tortrix* and a small *Dipter*), but Darwin recorded a wood-louse and beetle which neither Thomson nor Moseley could find. A modern ecologist would consider this information from the standpoint of island invasion and extinction, but that perspective originated in the mid-1900s. Darwin generalized that "The smallest rock in the tropical seas, by giving a foundation, for the growth of innumerable kinds of sea-weed and companion animals, supports likewise a large number of fish" (1839:10), whereas Thomson mentioned "one or two red algae" (he was not a botanist either), and the dredge brought up "a handsome *Cidaris*, a species of *Antedon*, some crustaceans of ordinary shallow-water types, and some fine *Gorgonia*" (1878, II:96). He also mentioned numerous fish of the genus *Caranx*, which is related to the Mediterranean tunny, but did not say whether they came from the dredge. Moseley (1892:63–65) named several seaweeds and animals in tidal pools omitted by Darwin and Thomson. Of the 45 marine animal species collected there, 13 were new to science (Edwards 1985:36). Neither Thomson nor Moseley, any more than Darwin, could identify the origin of the rocks, which did not seem volcanic. St. Paul's Rocks are part of the Mid-Atlantic Ridge (Edwards 1985:31), the existence of which the *Challenger* scientists could map in general outline from their soundings (Deacon 1971:355), but they would not have known that it arose from a split in the sea floor.

The *Beagle* had only spent a few hours at Fernando Noronha—some 300 miles to the southwest—where Darwin just had time to study the rocks. The *Challenger* was there for over two days, giving Moseley time to collect plants, and Thomson time to notice that not only boobies and noddies nested on these more substantial islands, but also frigate birds *Tachepetes Aquila*, high up the cliffs (1878, II:107–109). There were also three species of land birds: thrush *Nesocichla eremita,* bunting *Emberiza Braziliensis*, and nearly extinct water-hen *Gallinula nesiotis.* On two smaller neighboring islands, Inaccessible and Nightingale, rockhopper penguins *Eudyptes chrysocome* nested.

Regardless of the similarities to or progress beyond land and ocean-surface observations in Darwin's *Journal of Researches*, the voyage of the *Challenger* was focused primarily on deep-sea exploration, and Thomson's memoir contains fold-out maps indicating dredging locations and temperatures at different levels of the water column at these stations. He also itemized the kinds of data obtained at each station, including 1441 water samples (1878, I:xi–xii). One could seek a correlation between water temperature and animals brought up by a dredge at particular locations. Occasionally, Thomson pointed out what we call ecological information based on dredgings and temperatures: *Fungia symmetrica* was the only

Fig. 18. Rockhopper penguins *Eudyptes chrysocome* which nest on Inaccessible and Nightingale Islands, sheltered by tussock grass. Thomson 1878, II:171.

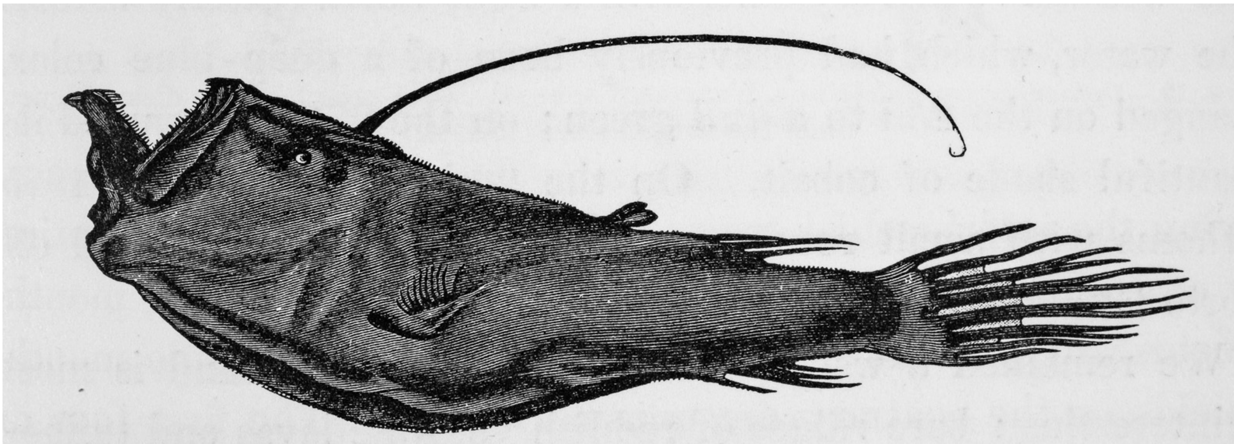


Fig. 19. *Ceratias uranoscopus* in Lophioid family, 90 mm long, with first dorsal fin as long filament used either as a lure for prey or a sensory organ used to detect prey. Thomson 1878, II:67–68.

coral found deeper than 1600 fathoms; it occurred on all kinds of substrate, and it lived at temperature ranges of 1°–20°C; specimens from great depths are much larger and more fragile than related species from shallow waters (Thomson 1878, II:133–134).

After over six months study of deep-sea life, Murray concluded that "*Challenger* observations seem to prove that life is distributed all over the ocean floor" (1895; quoted from Saldanha 2002:237). His collection of plankton at surface, mid-level, and bottom provided insights into diurnal migration of plankton (Deacon 1997:342). The *Challenger Report* also announced an inverse relationship between distance from shore and number of benthic species. Thomson summarized their findings (1878, II:301–302, slightly abridged)

1. *Animal life is present on the bottom of the ocean at all depths.*
2. *Animal life is not nearly so abundant at extreme, as it is at more moderate depths, but… members of all the marine invertebrate classes occur at all depths…*
3. *There is every reason to believe that the fauna of deep water is confined principally to two belts, one at and near the surface, and the other on and near the bottom, leaving an intermediate zone in which the larger animal forms, vertebrate and invertebrate, are nearly or entirely absent.*
4. *Although all the principal marine invertebrate groups are represented in the abyssal fauna, the relative proportion in which they occur is peculiar. Thus, Mollusca in all their classes… are on the whole scarce; while Echinodermata and Porifera greatly predominate.*

5. *Depths beyond 500 fathoms are inhabited throughout the world by a fauna which presents generally the same features throughout. Deep-sea genera have usually a cosmopolitan extension…*
6. *The abyssal fauna is certainly more nearly related than the fauna of shallower water to the fauna of the tertiary and secondary periods…*
7. *The most characteristic abyssal forms, and those which are most nearly related to extinct types, seem to occur in greatest abundance and of largest size in the southern ocean; and the general character of the fauna of the Atlantic and of the Pacific gives the impression that the migration of species has taken place in a northerly direction…corresponding with the movement of the cold under-current.*
8. *The general character of the abyssal fauna resembles most that of the shallower water of high northern and southern latitudes, no doubt because the conditions of temperature, on which the distribution of animals mainly depends are nearly similar.*

Thomson's view in point 3, that animal life was nearly absent in intermediate zones was accepted by Alexander Agassiz but challenged by Carl Chun (see above). Besides the list of eight findings quoted, Baruch Kimor credited the *Challenger* Expedition with first focusing attention on "the world of free-floating animals that inhabit the open sea, later known as plankton" (Kimor 2002:211). However, in contrast to its studies on zooplankton, Taylor (1980:516) claimed that the *Challenger* Expedition:

> *…had not generated much useful ecological information on phytoplankton, the sole products in this area being a taxonomic monograph on the diatoms by Castracane (1886) and some passing observations by John Murray on the genus* Pyrocystis *(the first formal descriptions) and the photosynthetic nature of coccolithophorids.*

From the standpoint of marine ecology, the physical and chemical properties of seawater and bottom sediments were also relevant (Mills 1975:18–20). After the *Challenger* returned home with 13,000 kinds of plants and animals, 4417 of which were new species, Thomson and Murray faced the task of unpacking, sorting, and distributing classes or phyla of animals to experts in Europe and America to describe and then to publish their findings. Thomson invited Alexander Agassiz to come help, and Agassiz gladly accepted, to distract him from family tragedy (Dobbs 2005:160–166). Murray and Agassiz formed a strong bond during those weeks. Fifty large volumes appeared, 1885–1895, a monument to the expedition and to Murray (Scaps 2005:44–53), although "Murray seems to have outstripped his times, and certainly the statistical resources of his time" (Mills 1983:30).

Eric Mills has provided a specific example of how distribution of animals to be described worked. Alfred Norman (1831–1918) was a clergyman–naturalist who went on the voyages of *Lightning* and *Porcupine*, and accepted animal specimens from their collections to describe (Mills 1980*b*). His published results were very credible, and he was therefore placed on a committee to allocate *Challenger* specimens.

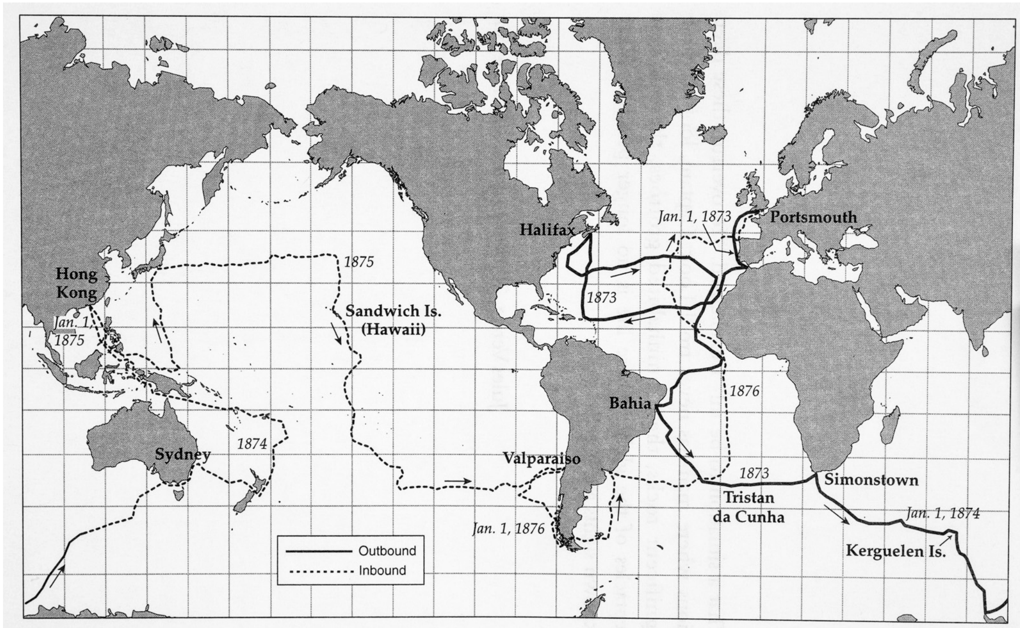


Fig. 20. Map of *Challenger* route around the world. Corfield 2003:x.

He was friends with another clergyman–naturalist who studied amphipod crustaceans, Thomas Stebbing (1835–1926), who volunteered to describe them, either with Norman or alone (Mills 1972:243, 1976*a*, *b*, 2004). Norman was still working on the collections from his own collecting expeditions, and so he allocated the amphipods to Stebbing, who published *Report on the Amphipoda Collected by* H.M.S. Challenger *during the Years 1873*–76, volume 29 of the *Challenger* reports (1888, i–xxiv + 1737 pages + plates) (Mills 1976*b*:70). That volume was part of the reason the Linnean Society of London awarded him its Gold Medal in 1908.

Murray published "On the Structure and Origin of Coral Reefs and Islands" (1880*a*, *b*, 1889) which challenged Darwin's theory (1842) that coral reefs and islands formed on sinking volcanoes (Egerton 2010b:419–423). He had not studied coral reefs and islands any more than Darwin had (Sponsel 2009:303), but he was quite interested in sea floor geology. He judged the accumulation of plankton skeletons on shallow elevations or volcanoes was sufficient for coral substrate (Dobbs 2005:164–165). Alexander Agassiz found Murray's hypothesis more plausible than Darwin's (Dobbs 2005:165–166). Darwin read Murray's article and sent a rebuttal letter to Alexander Agassiz, in response to Agassiz's observations which he had sent to Darwin (5 May 1881, quoted in Dobbs 2005:181–183), but Darwin did not publish his rebuttal. Yet, James Dana (1813–1895) had accepted Darwin's theory (Stanton 1971), and he defended Darwin's and his own ideas in "Origin of Coral Reefs and Islands" (1885). Alexander Agassiz was not at all satisfied with Dana's rebuttal of Murray's hypothesis (Dobbs 2005:187–188). While Agassiz kept his doubts to himself, George J. D. Campbell, eighth duke of Argyll, championed Murray's paper and accused the Darwinians of subjecting it to a "Conspiracy of Silence" (1887). Argyll was not an authority on corals; he opposed Darwin's theory of evolution and merely seized Murray's paper as a convenient club to batter the Darwinian edifice (Stoddart 1988, Van Riper 2004, Dobbs 2005:191–198). Thomas Huxley and others leaped to Darwin's defense. It was impossible to determine whether Darwin or his opponents was right without drilling to the foundation of a coral reef, which only happened decisively in 1950, which showed that Darwin was mostly right (Yonge 1980:443–445, Dobbs 2005:254–256, Sponsel 2009:318–452).

Thomson's decision to allow specialists anywhere in Europe or in American to describe *Challenger* specimens within their expertise not only insured high-quality work, it also helped build an international community of oceanographers (Deacon 1997:367–369). On the other hand, British investigators founded a Challenger Society in 1903 because the British government felt it had already done its bit for oceanography in funding the *Challenger* Expedition; later marine biologists had trouble funding their work (Deacon 1990). Murray was the only *Challenger* scientist who survived and became a member. (Buchanan also survived but did not join.)

In Brisbane, capitol of Queensland, a Great Barrier Reef Committee formed in 1922 to investigate the origin, growth, and natural resources of their adjacent coastal landmark (Yonge 1930:12–13). The Committee began by studying the geology and geography, but by 1926 it decided to encourage coral reef biology. It raised funds in Australia and in Britain to support a year-long expedition of British biologists, which the Royal Society of London also sponsored. Maurice Yonge (1899–1986) joined the British army in 1917 and served about a year (Morton 1992, Allen 2004). In 1919 he entered the University of Edinburgh, from which he graduated in 1922, and stayed on for a Ph.D. in zoology in 1924, after which he received a Carnegie scholarship to study at Cambridge and also spent time at the Stazione Zoologica in Naples. In 1927 he helped organize the Great Barrier Reef Expedition of 18 scientists, which he led in spring 1928; they reached Brisbane on 9 July. Brisbane is at the southern end of the Reef, and the Expedition was to have its headquarters at Low Isles, about two-thirds of the way north to Cape York, which they reached on 16 July. They remained at the Reef until August 1929. The scientific findings would appear in four volumes later, but in 1930 Yonge published *A Year on the Great Barrier Reef: The Story of Corals and of the Greatest of Their Creation*. It contains numerous photographs, diagrams, and maps, was well written and opened opportunities to advance his career. (He became Professor of Zoology at Bristol at age 34, and in 1944 he became Regius Professor of Zoology at the University of Glasgow, and Fellow of the Royal Society in 1946).

German oceanographic activity was stimulated by both the unification of Germany in 1871 (Roll 1990:4), and the *Challenger* Expedition, being conducted by a rival nation. The focus of its *Gazelle* expedition around the world, 1874–1876, was on physical sciences. Science is an enterprise that includes both rivalry and cooperation, and when Germany's *Gazelle* met England's *Challenger* in Montevideo, February 1876, "their captains agreed to arrange their homeward courses in such a way that the best possible coverage of the Atlantic Ocean could be achieved" (Roll 1990:7). Martin Ehrlich and Ramiro Sánchez (1990:488) provided a map of these two cruises in Argentine waters. The voyage of the *Gazelle* was one of a series that Germans launched (Roll 1990:5).

Another example was a Romanian oceanographic survey led by Moldavian native Grigore Antiqa (1867–1944), who had studied at Jena under Haeckel (Ph.D., 1891) and then at Naples under Dorhn (Serpoinau and Malciu 2002:271–272, Bologa 2004:213–214). In May–September 1893, he borrowed a Romanian Navy cruiser, *Elisabeta*, to conduct an oceanographic survey of the Black Sea (Marinescu 1990). Russian expeditions had also surveyed the Black Sea in 1880–1881 and in 1890–1891.

Like Germany, Italy's unification (1861) and the *Challenger* example both inspired its two circumnavigation voyages, of *Caracciolo*, 1881–1884, and of *Vettor Pisani*, 1882–1885, and the prominence of Dohrn's Stazione Zoologica also exerted an influence (Groeben 1990). Before *Caracciolo* departed, Naval officer Marchese Lucifero asked Dohrn for advice on collecting plants and animals, and Dohrn advised him to collect everything he could and preserve specimens in alcohol. Dohrn sent the navy materials and instruments for collecting, though they arrived after *Caracciolo* had departed. Nevertheless, the voyage produced a substantial report (De Amezaga 1885–1886). More advanced planning occurred before *Vettor Pisani* departed. Its second officer in command, Lieutenant Gaetano Chierchia (1850–1922) was trained at Stazione Zoologica during several months in collecting and preserving specimens and collecting information on geographic and environmental locations, much as Meriwether Lewis had been trained at Washington and Philadelphia before the Lewis and Clark Expedition, 1804–1806 (Egerton 2009:440–442). Chierchia carried recommended equipment (illustrated in Groeben 1990:226–230), and his high-quality specimens and reports reflect his training (cited in Groeben 1990:234).

Less ambitious were two voyages by marine zoologist Enrico Hillyer Giglioli (1845–1909), born in London to an English mother (Croce 1990). In 1865 he went on a voyage of an Italian navy vessel, *Magenta*, which sailed to Japan to conclude a trade treaty. He was an assistant to Filippo De Filippi, Director of the Zoological Museum in Turin. However, when De Filippi died in Hong Kong, Giglioli became head of the scientific mission, and upon his return he was appointed associate professor at the University of Turin and wrote a report of over 1000 pages on the zoology of the voyage, published in 1876. In 1881, he undertook marine studies on the Italian naval ship, *Washington*, from which he asserted the existence of an abyssal fauna (but after such a fauna had been discovered on the *Challenger* Expedition in the Atlantic and Pacific).

The Austro-Hungarian deep-sea exploration in the Red Sea in 1895 and 1897 was made practicable by the existence of the Suez Canal. It was a collaborative endeavor, using the sailing steamer *Pola*, by Austrian Academy of Sciences, Vienna Deep-Sea Symposium, University of Vienna, and Natural History Museum of Vienna. Germany had never launched an expedition to the Red Sea, but it had had a number of zoologists and botanists study its fauna and flora (Aleem 1990), and their publications would have been known to the *Pola* naturalist. A major *Pola* finding was that (Uiblein 1997:235):

> *…organisms of shallow-water origin or those closely related to shallow-water dwellers have invaded deeper levels and that the primary cold-water adapted deep-sea fauna typical of the major oceans of the world is almost completely absent.*

In Belgium, naval officer Adrien de Gerlache (de Gomery 1866–1934), as captain of *Belgica*, led an Antarctic expedition in 1897 that included Romanian native, French-educated, biologist Emil Recovita (1868–1947), who collected widely but studied most cetaceans and seals (Serpoinau and Malciu 2002:272–273, Bologa 2004:213, Charlier 2004:372–373 + plate 6, 2013:108).

Claude Maurin (1997) briefly surveyed fishery studies along the Atlantic coasts of Iberia and northern Africa, 1874 to beyond the 1920s, with an extensive bibliography. He included exploratory voyages by Albert I, Carlos, Buen, Murray, and Hjort.

Alexander Agassiz had managed Harvard's Museum of Comparative Zoology before his father died and succeeded him as head (Agassiz 1913:32–44, Dobbs 2000:19–23, 2005:64–70). In 1875, he completed his private marine laboratory on Narragansett Bay, for marine research (Benson 1988:65–66, Dobbs 2005:158, 188). He also led seven oceanic expeditions, 1877–1905, throughout much of the Atlantic and Pacific Oceans, with Mayer/Mayor accompanying him on several of them, beginning in 1896 (Agassiz 1913:2 folding maps, Zinn 1980, Mills 1983:33–35, Stephens and Calder 2006:7–18). In December 1884, Agassiz sailed to Hawaii to study coral reefs, in order to evaluate the competing theories on origin by Darwin and Murray and continued this research for the rest of his life (Dobbs 2005:184–185, 211–240 and see below). On two voyages he tested Carl Chun's claim that plankton occur at all depths of the ocean; Agassiz searched for an intermediate fauna, between surface and bottom, but never found it, due partly to inadequate equipment and partly to sampling waters that lacked intermediate organisms (Mills 1980*a*, 1983:39–44, Spence 2002:290–291). Accurate oceanic plankton sampling remained a difficult challenge well into the 1900s (Herman and Platt 1980). Plankton specialist Kofoid sailed with him in 1904–1905 for six months to the South Seas (Kofoid 1911, Shor 1974:461).

Fig. 21. Alexander Agassiz watching the emptying of the trawl on the *Albatross*. Agassiz 1913: facing 254.

Agassiz was also very interested in formation of coral reefs; he rejected Darwin's theory and went to great lengths to refute it (Dobbs 2005:165–265). His own descriptive findings appeared in two lengthy *Memoirs of the Museum of Comparative Zoology* (1913*a*, *b*). Although Mayer/Mayor was not listed as a coauthor, he had helped collect the corals and illustrated them. Agassiz also published a brief interpretive paper (1903*c*). He wanted to write a semi-popular account on coral reefs but never did. Had he done so, it might have met an unfriendly reception, for in 1908 Wayland Vaughn, America's leading authority on corals (Thompson 1958), told Mayer/Mayor that "Alex's paper on the coral reefs…[was] not worth the powder required to blow it to H—-!" (Stephens and Calder 2006:62). Vaughn's comment obviously referred to "On the Formation of Barrier Reefs and of Different Types of Atolls" (1903*c*), to which Mayer/Mayor had not contributed. In 1920, after Mayor had studied coral reefs in Fiji and Samoa, he also concluded that Murray and Agassiz's interpretation was wrong (Stephen and Calder 2006:134).

Plankton studies

Eric Mills suggested there were three brief periods of creativity in early plankton studies (1897–1908, 1922–1937, 1938–1946) "succeeded by periods of relatively dull but useful consolidation when the new ideas were elaborated and buttressed" (1982:3). Subsequently, he asked, "Why did biological oceanography remain virtually atheoretical for nearly the first century of its development?" (Mills 1983:5). Still later (Mills 1995:29), he stated that biological oceanography did not exist before the 1950s, which means that his question about a theoretical marine ecology concerns the time frame of this discussion (1870s–1920s).

Even though it occurred before part 51's time frame, it is important to note F. J. R. Taylor's discovery (1980:514), which English botanist Joseph Hooker (1817–1911), whom we met in part 42 (Egerton 2012*a*:125–138), explained in the report on his four-year *Erebus* and *Terror* Expedition of 1839–1843 (1844:505), the importance of phytoplankton in the economy of the seas (without using that term, not yet coined):

> *The universal existence of such an invisible vegetation as that of the Antarctic Ocean, is a truly wonderful fact…I now class the Diatomaceae with plants, probably maintaining in the South Polar Ocean that balance between the animal and vegetable kingdoms, which prevails on the surface of our globe...*

Hooker's conclusion deserved widespread attention, which it did not receive, buried in an expedition report on southern explorations. A fellow English botanist, Robert Brown (1773–1858), extended Hooker's insights into Arctic seas (1868).

Returning to our specified time frame, Kiel is in Schleswig-Holstein; Prussia annexed Schleswig after its wars against Denmark (1848, 1864), and annexed Holstein after its war with Austria (1866). Karl Möbius (1825–1908), discussed in part 49, developed his concept of biocönose at Kiel from his studies of oyster beds (Querner 1974, Reise 1990, Egerton 2014*a*:60–62). Although he had been charged to study the British oyster fishery in order to find lessons applicable to the German oyster fishery, Britain's oyster fishery was also struggling with decline (Parsons 2002). Möbius' research did not save Germany's oysters, which eventually died out because of overfishing (Neudecker 1990). After he left Kiel in 1887 to become director of a natural history museum in Berlin, Victor Hensen (1825–1924), who had studied medicine and physiology, became the senior zoologist at Kiel University (Porep 1970, Rothschuh 1972). Hensen was discussed in part 47 as the subject of Haeckel's hasty attack on his quantitative plankton findings (Lussenhop 1974, Haeckel 1991:572, Egerton 2013:236). Haeckel's publication was otherwise a useful synthesis of marine plankton knowledge at the time. Hensen had studied physiology and medicine, partly at Kiel, and afterwards (1859) became an instructor there in anatomy. In 1863 he became interested in marine life, and in 1864 he was appointed associate professor of physiology and director of a physiology laboratory. He served in the Prussian Landtag for four months in 1867–1868, long enough to establish a government Kommission zur wissenschaftlichen Untersuchung der deutschen Meer in Kiel, which he later dominated (Schlee 1973:230–233, Ward 1974:191–194, Mills 1989:10–18, Kölmel 1990, Wegner 1990). The Commission's goal was to learn why commercial fisheries in the Baltic Sea were declining.

A series of coastal stations to monitor the fishery and environment were built between Denmark and Russia, and a naval vessel enabled Hensen to conduct research voyages, beginning in 1871. There had already been two Prussian North Polar Expeditions by ship during late 1860s and a deep sea expedition in 1874–1876, but none focused on biology (Roll 1990:4–9). However, the Norwegian Voringen Expedition, 1876–1878, focused upon migration patterns of fishes, especially cod (Schwach 2007:51–53). Hensen decided to study the metabolic cycle of the sea as a way to determine its productivity, and his expeditions collected physical, chemical, and biological samples and data. Hensen designed a net to collect vertical samples for quantitative data. His "Über die Bestimmung des Planktons oder des im Meere treibenden Materials an Pflanzen und Thieren" (1887) was a quantitative plankton study in which he introduced the term "plankton," coined by a philologist colleague, to indicate floating organisms, living and dead (Hedgpeth 1957:4, Taylor 1980:515, Mills 1989:19). In 1889, Hensen decided to compare the plankton of the North Sea with that of the Atlantic Ocean, and led a 15-week expedition from the Baltic Sea to Greenland, to Bermuda, to the equator and back to Kiel (Schlee 1973:233–236, Mills 1989:22–28). He contributed to and edited a five-volume report on the expedition's findings (1892–1912). An unexpected discovery was that plankton were much more abundant in cold northern than in warm tropical waters—the reverse of the situation on land.

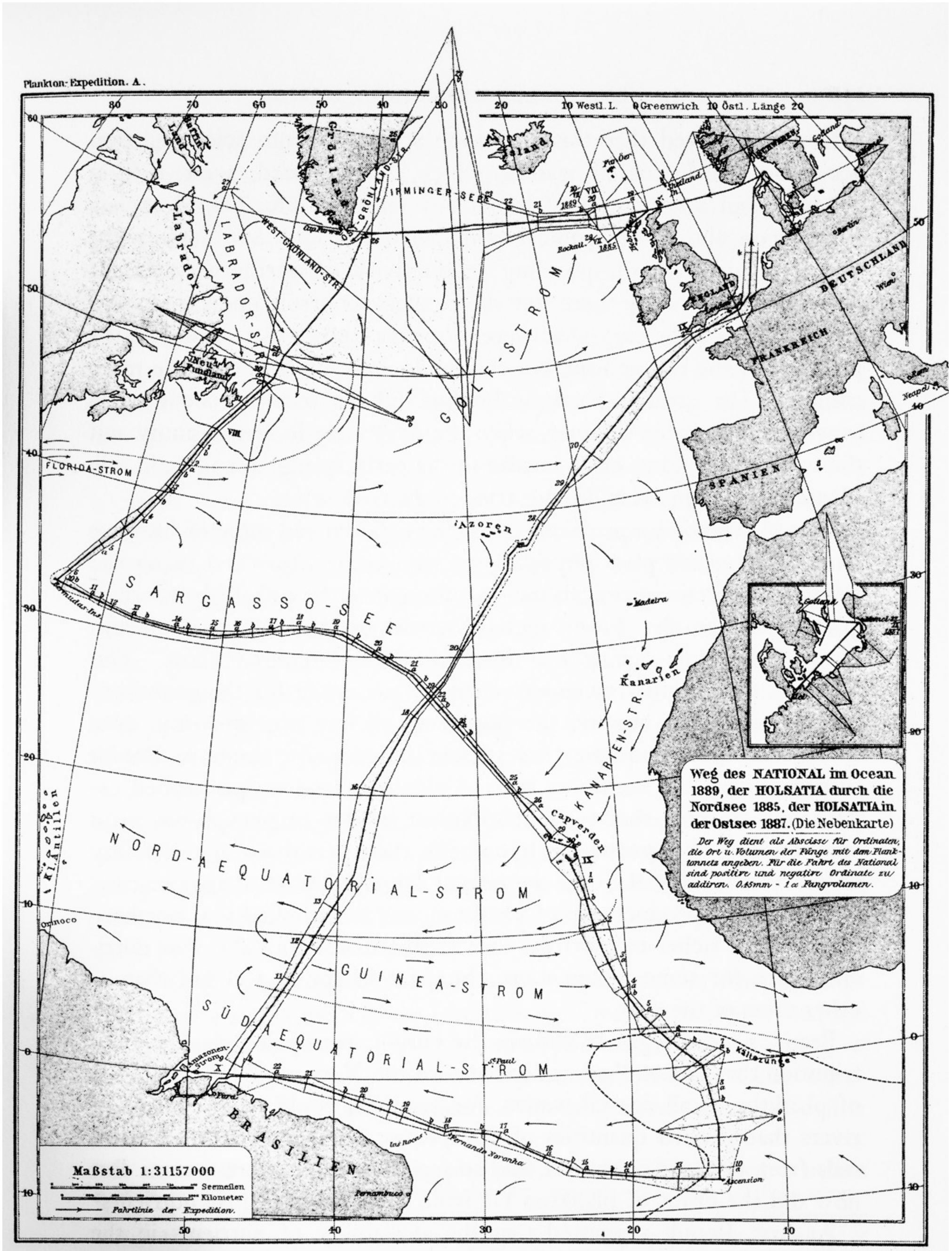


Fig. 22. Path of Hensen's Plankton Expedition (1889) into the Atlantic Ocean, with width of lines on each side of path line indicating relative abundance of plankton. Hensen 1892. From Schlee 1973: 235.

Hensen's plankton studies represented a conceptual advance—a beginning of quantification of food chains—but his concept was sidetracked by Haeckel's controversy over the accuracy of Hensen's sampling technique and his assumption that plankton were distributed uniformly within a given area (Porep 1972, Schlee 1973:229–237, Lussenhop 1974, McIntosh 1985:53–54, Mills 1989:29–31, Kimor 2002:210–211). Haeckel also thought it unlikely that northern waters were more productive than tropical waters (Haeckel 1890). Haeckel believed that food from rivers was adequate to support fish in the North Sea, whereas Hensen did not and suggested they depended upon a plankton food chain (Mills 1989:41). Hensen henceforth devoted much time and effort into demonstrating the reliability of his methods and conclusions (Mills 1989:29–35). He did establish the close connection between plankton abundance and fish abundance (Lenz 2004).

Karl Brandt (1854–1931) studied zoology at Berlin, received his Ph.D. at Halle, and went to the University of Kiel in 1887 to replace Möbius (Mills 1982:3–5, 1989:43–59). Brandt participated in Hensen's Atlantic Plankton Expedition and got involved with Hensen's quest to understand oceanic plankton as a foundation for fisheries management. Brandt had a very sensible idea, coming largely from Hensen, that did not turn out to be correct, though it was well worth exploring. He understood the revolution that had occurred in plant physiology during the 1800s, especially Liebig's law of the minimum and new findings on the nitrogen cycle, and its impact on agriculture (Schlee 1973:236–237, Egerton 2012). He hypothesized that the same processes work in the ocean as on land. He explained this at a fairly early stage in his research in a public address he gave at the University of Kiel, which was published with footnotes, and then translated, without footnotes, into French (1899) and English (1901). Plants are producers, animals are herbivorous and carnivorous consumers, and bacteria decompose dead matter. There were plenty of phytoplankton and zooplankton in the sea, and also some bacteria, but were there enough bacteria to perform nitrogen recycling? This turned out to be the crucial question. He hypothesized that denitrifying bacteria involved in the nitrogen cycle were active all year in warm waters, but active only in warm weather in northern climates, which left more nitrates for phytoplankton in the northern waters than in tropical waters (Mills 1989:51).

Much research proceeded at Kiel and elsewhere into the abundance and actions of marine bacteria, with somewhat contradictory results. The organization of the International Council for the Exploration of the Sea (see below) facilitated such research. By the early 1900s, the preponderance of evidence began to show that marine bacteria were not abundant enough as nitrifiers and could not play the role that Brandt postulated (Mills 1989:68–73). World War I, 1914–1918, intervened before the marine nitrogen cycle was fully understood, and in a late monograph, "Stickstoffverbindungen im Meere," Brandt saw "no reason to reject my hypothesis that denitrifying bacteria break down the excess of nitrogen compounds,

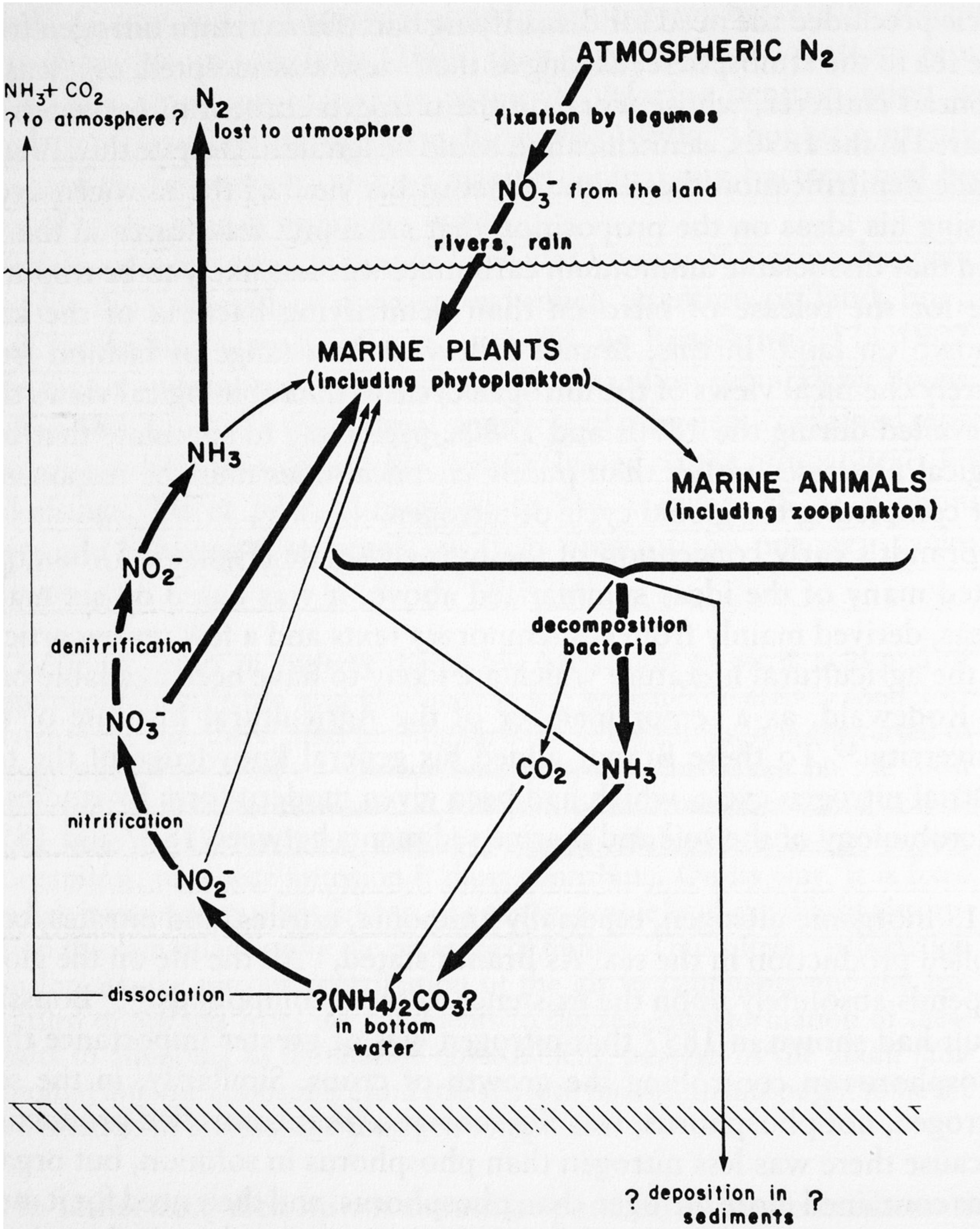


Fig. 23. Karl Brandt's concept, around 1900, of nitrogen cycle at sea, expressed in a modern diagram. Mills 1989:64.

and that it is they that maintain the existing equilibrium in nature" (Brandt 1927:204–205, translated in Mills 1989:94). Various critics found technical details on which they differed from Brandt, but besides those, there was a different and important mechanism at work not appreciated by Brandt—vertical circulation distributed nutrients, including nitrates (Mills 1989:108). Finally, Brandt (1929) "abandoned denitrification as a controlling factor, capitulating to two decades of criticism" that physical circulation was an important factor in productivity (Mills 1990:23). Hensen and Brandt were right about the need to understand the dynamics of plankton as a foundation for managing fisheries, but it was a complex story for which an analogy with land plant physiology was inadequate.

Another zoologist on Hensen's 1889 expedition was Friedrich Dahl (1856–1929), who concentrated mainly upon copepods, but also studied insects, marine vertebrates, and some land animals (Damkaer and Mrozek-Dahl 1980:467–469). He studied distributions of five species of *Copila*, observing the influence of the waters of the Amazon in the Atlantic. Working up the collections after the expedition was a huge responsibility, and he eventually married Maria Johanna Grosset (1872–1972), who was involved in sorting and illustrating the collections. Each of them published studies on the expedition's copepods.

Hans Lohmann's work at Kiel (1903) on quantitative plankton dynamics built upon Hensen's contributions (Mills 1982:5–6, 1989:133–138). Lohmann (1863–1934) was from Hanover, studied at Göttingen in 1885, then transferred to Kiel in 1886 and earned a Ph.D. there (1889). He collected plankton at Messina, Italy, April 1896–February 1897 and at Syracuse, 1900–1901. He discovered and named nanoplankton, by using filter paper rather than a net, and he concluded nanoplankton provided food for many zooplankton. He decided that previous plankton studies were not fully valid since they had not included nanoplankton, and in April 1905–August 1906 he collected at the mouth of Kiel Fjord and then published a "study [which] is still one of the most complete ever done on planktonic organisms" (Mills 1989:134), documenting the abundance and annual production of organisms ranging from bacteria to macroplankton. The Kiel tradition of marine research was strong enough to survive two world wars (Krauss 1990, Rumohr 1990).

Norwegian zoologist G. O. Sars, co-leader of the *Vøringen* Expedition, discussed above, studied especially the biology of cod and herring (Broch 1954, Schwach 2007), for which Hooker's report (1844) would have been quite relevant background knowledge, but there is no indication that either leader knew about either it or Brown's Arctic report. Since Sars was a zoologist studying in the Arctic, it is understandable that he was unfamiliar with botanical literature concerning the Antarctic. He seemed also unaware of the existence of an aquatic microflora at all, for he discussed (1879:200–201) a "havslim" (ocean-slime) consumed by the "åte" (organisms that nourished fish), which included zooplankton, eggs, and larvae of marine animals (Schwach 2007:51–52). He at least knew that the åte included copepods *Calanus finmarchus*.

Later in Norway, Haaken Gran (1870–1955) studied phycology at Det Kongelige Fredericks Universitet (now University of Oslo); he graduated in 1894 and earned a doctorate in 1902 (Portretter 2001). In 1897, he began working with Hjort, and he also traveled to Delft to study marine bacteria with Dutch microbiologist Martinus Beijerinck, and while there he described three new species of denitrifying bacteria, which he suspected washed into coastal waters from land (Mills 1989:69, 72). Gran conducted his doctoral research in 1900–1901 during early voyages of *Michael Sars* under Hjort, and he wrote a dissertation on "Das Plankton des Norwegischen Nordmeeres" (1902). In 1901, Gran suspected that coastal blooms of phytoplankton were stimulated by nutrients flowing from land (Mills 1989:149). Eric Mills (1989:152) commented on Gran's "remarkable intuitive understanding of the conditions under which phytoplankton lived," which was superior to his contemporaries:

> *All his publications, beginning with his doctoral thesis of 1902, reveal a sophisticated appreciation of the dynamic interaction between cells and their environment that is strikingly absent in the publications of the Kiel school.*

Gran published the first synthesis on phytoplankton in English as a chapter in Murray and Hjort's *The Depths of the Ocean* (1912), which described his own researches; it had a broad influence. Gran doubted that nitrification occurred in open seas, and his conclusion held sway until 1981 (Mills 1989:73). He did not accompany Hjort to Canada to participate in the Canadian Fisheries Expedition, 1914–1915, but published a discussion of the expedition's plankton (1919). T(heodore) C(hristian Frey (b. 1869), director of the University of Washington's Friday Harbor Laboratories, invited Gran twice (1928, 1930) to teach summer courses there on diatoms, to encourage such research on the Pacific coast (Benson 1990).

Kofoid had become interested in plankton while director of the Illinois River Station, 1895–1900, and after moving to the Zoology Department, University of California, Berkeley, he transferred that interest from freshwater to saltwater. However, he took unfinished work from Illinois with him to California and published two large volumes on quantitative studies of Illinois plankton, 1903–1908. As mentioned above, he was planktologist on Agassiz's Pacific voyage in 1904–1905. He invented two pieces of equipment for collecting plankton at particular depths (Goldschmidt 1951:24–25). In 1908–1909 he prepared to go to the Stazione Zoologica in Naples for research, and the U.S. Bureau of Education invited him to report on work there and elsewhere in Europe; hence his book discussed above.

Professor August Pütter, Bonn University, published papers in 1907–1912 arguing that oceanic plankton were insufficiently abundant to nourish all the animals they supposedly fed (Herdman 1923:314–320). He concluded that some marine animals must depend additionally upon dissolved organic matter in sea water. Kishinouye's studies on sardines in Japanese waters seemed to support Pütter's claims. Other marine ecologists challenged Pütter's conclusions, and this controversy, like the earlier one between Hensen and Haeckel, led to greater concern for precise measuring of plankton quantities.

In Japan, planktology arose, beginning in 1900, at three universities where fisheries were studied: Imperial Fisheries Institute (= Tokyo University of Fisheries), Tokyo Imperial University (= University of Tokyo), and Agriculture School of Tohoku Imperial University (= Hokkaido University) (Omori 1997). Professor Kintaro Okamura (1867–1936), phycologist, translated plankton writings into Japanese in 1900, founding Japanese studies. Seiji Kokubo published the first Japanese textbook on marine planktology in 1923.

Fisheries: European

During the 1870s the industrial revolution began to increase the catch capacity of fisheries, and fishermen needed to increase their catch to pay for the new technology (O"Leary 1996:160–179). That increased catch capacity originated in Europe slightly earlier than in America. As the fisheries off west European coasts declined in the late 1800s, biologists wanted a better understanding of the situation.

Although Eric Mills entitled his 1989 book *Biological Oceanography: an Early History, 1870–1960*, he argued later (1995) that the term "biological oceanography" only became appropriate when physical, chemical, and geological oceanography actually became the context for marine ecology during the 1950s. Even so, a major step in that direction was the founding of the International Council for the Exploration of the Sea in 1902 (Deacon 1971:390–391, Schlee 1973:206–216, 223–225, Cushing 1988:203–212, Mills 1989:75–91, Smith 1994:113–124, Rozwadowski 2002, 2004, Smed 2004*a*, *b*, Schwach 2013). At the 1892 meeting of the Scandinavian Naturalists in Copenhagen, Swedish chemist–oceanographer Otto Pettersson (1848–1941) lectured on the hydrographic characteristics of the North and Baltic Seas and recommended a further joint investigation among scientists in Denmark, Norway, and Sweden (Mills 1989:81–83, Smed 2004*a*:140, Svansson 2004:20). Representatives of these countries agreed, as did scientists from Britain and Germany. Their cooperative survey occurred successfully in summers of 1893 and 1894, which inspired Petterson to propose at the International Geographical Congress, London in 1895, a permanent organization. The Congress passed a resolution of approval.

Sars received his first grant from the Norwegian government to begin research on cod in 1864, and he confirmed what fishermen knew but scientists did not, that cod eggs float in seawater, and by 1873 he had found a correlation between herring migration and seawater temperature (Solhaug and Saetersdal 1972:401–403). He continued research on cod until 1893, when Johan Hjort took over.

Norwegian marine biologist Johann Hjort (1869–1948) was son of a professor of ophthalmology at the national university in Oslo, and he began studying medicine there, but switched to zoology and studied that at the University of Munich and the Stazione Zoologica in Naples (Maurice 1948, Russell 1948, Hardy 1950, Merriman 1972, Ward 1974:185–191, Schwach and Hubbard 2009:26–27, Schwach 2014:3–4). He became lecturer in zoology, curator of the museum, and research fellow to study sea fisheries at the Oslo university. He had participated in the 1893–1894 survey (Merriman 1972, Schwach 2014), visited Britain and reported to Pettersson that Murray was interested in such an organization if Fridtjof Nansen (1861–1930) of Norway would also participate (Smed 2004*a*:141). Nansen had been educated as a zoologist, but subsequently his career veered into physical oceanography (Multhauf 1978). In summer 1897 Murray met with Hjort and Nansen and suggested that Norway host an organizational meeting in Kristiania (now, Oslo). Organizational meetings were then held in Stockholm (1899) and Kristiania (1901), and the organization was formally organized in Copenhagen in 1902, with headquarters in Copenhagen and a Central Laboratory in Kristiania run by Nansen, to insure uniformity of methods used to investigate physical and biological properties of the sea. The expansion in 1901 of Sweden's Hydrografiska Kommissionen to Svenska Hydrografisk-Biologiska Kommissionen is a national example of response to this new international concern (Söderqvist 1986:59–60).

Three ICES committees were established to research fish migrations, over-fishing, and Baltic fisheries. Although Swedish chemist Otto Pettersson (1848–1941) was "the prime mover of the whole project" (Schlee 1973:174–180, Mills 1989:81–82, Rozwadowski 2002:9, Svansson 2004), the first president of ICES was Walther Herwig (1834–1912), who had been active in furthering German research in fisheries, and had headed the German delegation to the organizational meetings (Smed 1990). Herwig was a skilled administrator and negotiator, and his appointment was also a strategy to keep Germany involved in ICES (V. Schwach, *personal comment*). Each ICES member country established a national committee as part of its membership.

Russian research was influenced by these developments among its western neighbors. In 1897, a philanthropic-research committee organized the Murman Scientific-Fishery Expedition (1898–1908) to study along the Barents Sea's Murman Coast, led initially by zoologist Nikolai Knipovich (Knipowitch, 1862–1939), who had graduated from St. Petersburg University. Research began with a small schooner purchased in Norway, but in 1899 a research ship, the *Andrei Pervoznanny*, was specially built (Plakhotnik 1973, Lajus 2002, 2004:128). In 1902 Knipovich had a disagreement with the philanthropic-research committee, resigned, and was replaced with Leonid Breitfuss. Both men published important findings

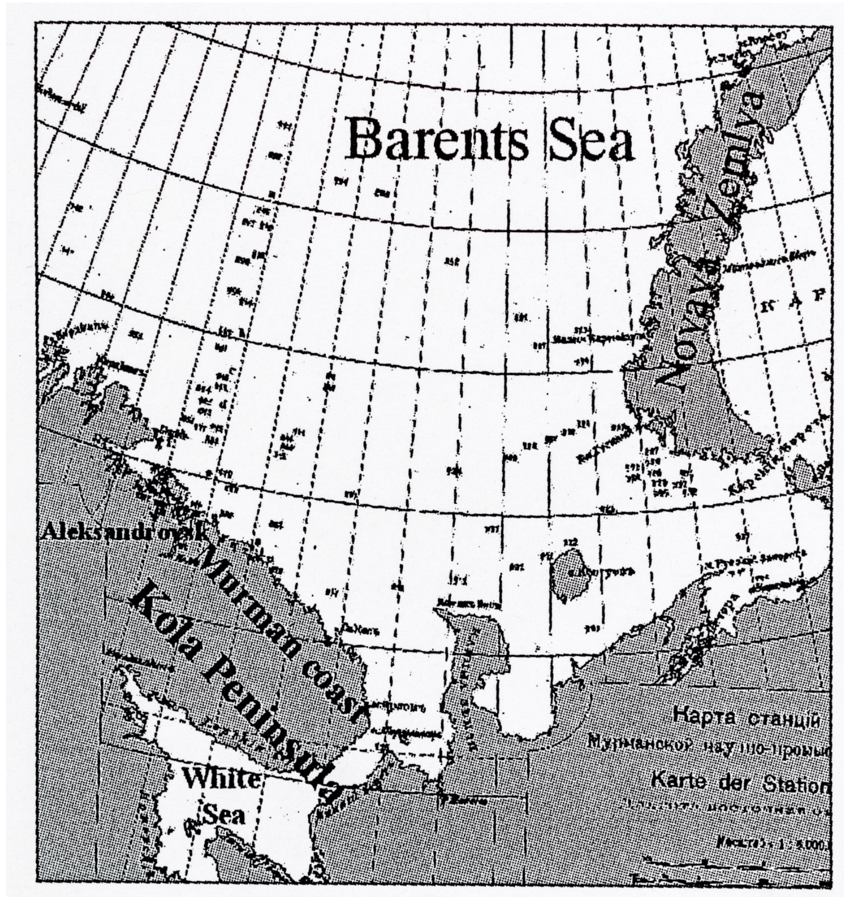


Fig. 24. (a) Nikolai Mikhailovich Knipovich. (b) Murman Coast of Barents Sea. Lajus 2004:128, 129.

from that expedition, and Knipovich subsequently led a series of expeditions to study the oceanography of other Russian waters.

Oceanography and fishery biology began in Norway in 1860. In 1897 Hjort discovered the commercial potential of a deep-sea prawn *Pandalus borealis*. He became the first head of the Norwegian Institute of Marine Research, at Bergen, 1900–1916. He had the use of a research vessel, *Michael Sars*, built in 1900 to study the biology of Norway's fisheries and waters and beyond. (Solhaug and Saetersdal [1972:403] thought "This 132-foot steamship was probably the first specially constructed ocean-going fishery research vessel," but we saw, above, that the U.S. Fish and Fishery Commission built its *Albatross* in 1883.) In 1906, after reorganization, he was appointed leader for the science department of the Board and became Director at the Fiskeridirektoratet (Directorate of Fisheries). He became Norway's foremost leader in marine science in his effort to integrate science with economic modernization in the fishing industry (Schwach and Hubbard 2009:26–27).

Involvement in ICES work undoubtedly facilitated Hjort and Murray's collaboration in research on the *Michael Sars* in summer 1910 (Mills 1983:58–60). Murray developed a phosphate mine on Christmas Island, Indian Ocean, around 1900, which provided funds to support some of his personal researches, including this voyage (Burstyn 1974:590, 1975) The writing of *The Depths of the Ocean* (Murray and Hjort 1912) with over 800 pages, with contributions from others, was too long to be a textbook, but it was the first handbook of oceanography, using the northeast Atlantic as an example of oceans. It serves as a "dividing line between 'earlier' and 'later' biological oceanography" (Mills 1983:5). That book was followed by Hjort's monumental monograph, "*Fluctuations in the Great Fisheries of Northern Europe*" (1914), which explained his theory of determining the success of first-year classes of fish as predictors of future commercial success of that fishery (Schlee 1973:222–229). Hjort's insight was a significant breakthrough, but it also led Norwegian fishery biologists to discount the impact of overfishing on fishery stocks (Schwach 2012:4, 2013:104).

Hjort's monograph led to an invitation by the Biological Board of Canada to lead a Canadian Fisheries Expedition, 1914–1915, which he accepted (Hachey 1965:290–292, Mills 2009:111–136, Schwach and Hubbard 2009:29). The expedition was a success (Hubbard 2006:68):

> *The expedition gave Canadian biologists their first clues to offshore spawning areas; it also introduced them to ecological life histories (...the movements of fish from feeding to spawning grounds and other migratory points), and enabled them to work out the influences of currents, temperatures, depths, and food concentrations.*

Hjort also benefited, for he found that his model of herring population dynamics held in Canadian as well as Norwegian waters (Schwach and Hubbard 2009:32). Canadian fisheries biologists were strongly influenced by Hjort's perspectives on fishery biology goals and techniques, and he helped them tap into networks of foreign fishery biologists (Schwach and Hubbard 2009:32–41).

Because of a disagreement with the Norwegian government about wartime neutrality and the export of fish, in 1917 Hjort resigned and went abroad to study (Schwach (2002:40). Upon his return, he became Professor of Marine Biology, University of Oslo, 1921–1939. He simultaneously served the International Council for the Exploration of the Seas as vice-president, 1921–1938, and as president, 1938–1948. "…for half a century Hjort was one of ICES' leading characters both scientifically and organizationally" (Schwach 2002:39).

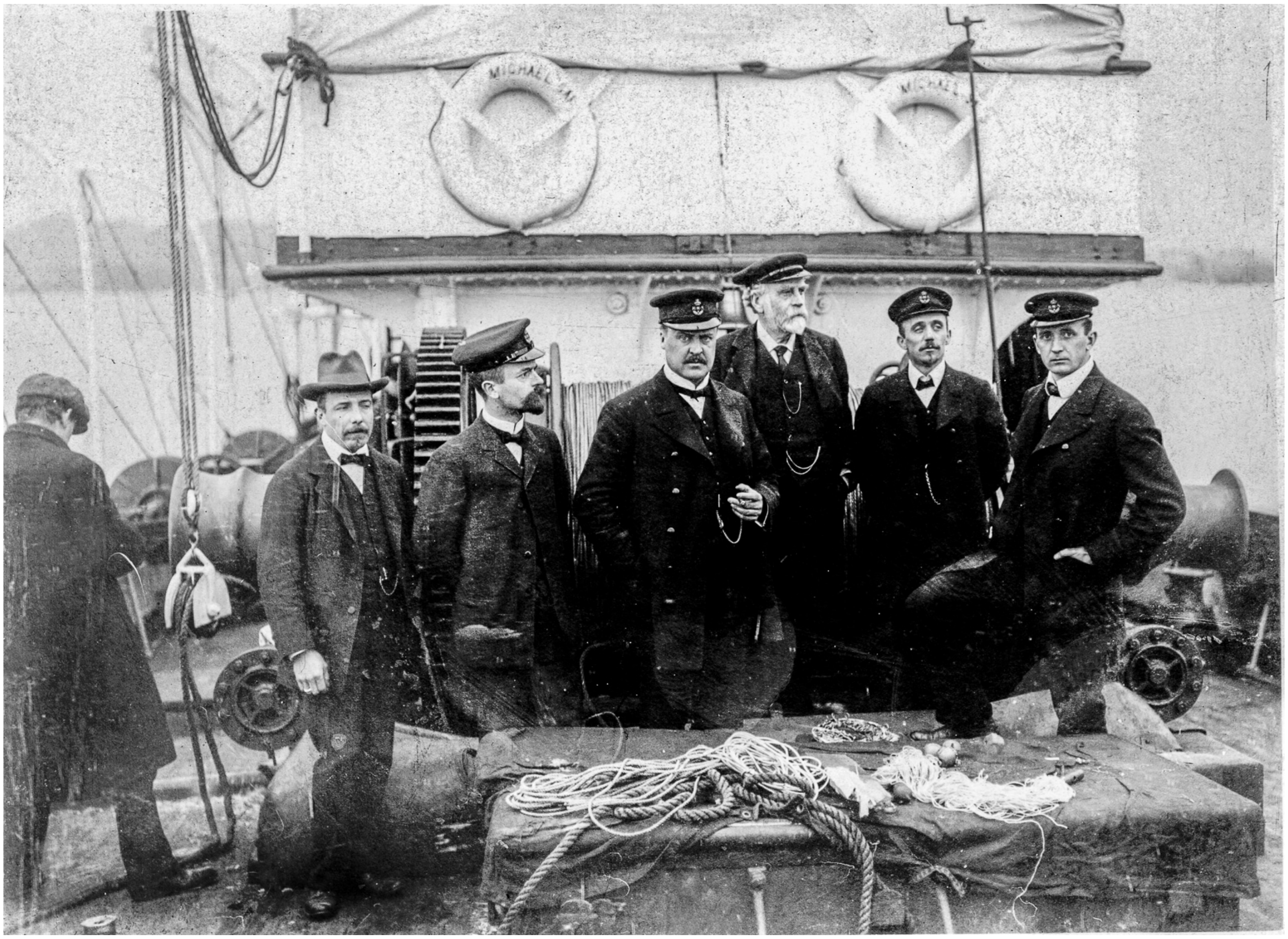


Fig. 25. Marine biologists on *Michael Sars*, 1910: Einar Koefoed, Haaken H. Gran, Johan Hjort, John Murray, and Bjørn Helland-Hansen (man in back, unknown). Courtesy of Institute of Marine Research, Bergen, Norway. From V. Schwach.

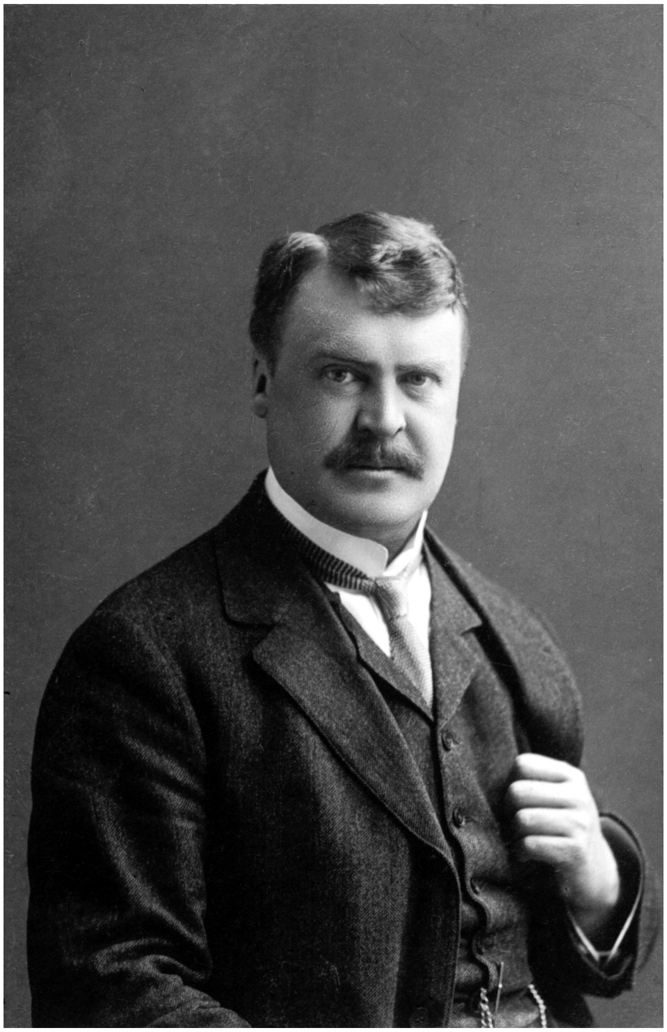


Fig. 26. (a) Johan Hjort, about 1915. Courtesy of Harold Hjort, Oslo. From V. Schwach. (b) Alister Hardy. Web page.

Danish Johannes Schmidt (1877–1933) began his career as a botanist, but in 1902, while in the Department of Botany, University of Copenhagen, he became biologist of the Danish Commission for Investigation of the Sea (Regan 1933, Spjeldnaes 1975). By 1904 he was publishing on the post-larval stages of a few species of Atlantic fish, and in 1906 he published his first "Contributions to the life-history of the eel (*Anguilla vulgaris,* Flem)." Immature eels in the Mediterranean Sea had been mistakenly named as a separate species. Eels are catadromous—breeding at sea, with young later migrating into continental rivers. Where eels bred was unknown, but Schmidt collected larval and post-larval developmental stages in different locations. He pinpointed the smallest specimens to the Sargasso Sea, and he discovered that it takes European eels three years to swim from their birthplace to Europe (Schmidt 1912, 1922, Morcos et al. 2004:200, Prosek 2010:6–8). American eels breed west of the European species (with some territorial overlap) and then take a year to reach American rivers. Adults die in the Sargasso Sea after breeding, and the young are guided in their migrations to continental rivers entirely by inherited instinct. Schmidt's research was widely appreciated, and he received many medals, an honorary doctorate, and honorary memberships in learned societies (Regan 1933:151).

The success of ICES inspired thoughts of doing for the Mediterranean what ICES was doing for the North Atlantic. The Genoese physician–ichthyologist Decio Vinciguerra (1856–1934) made such a proposal at the Ninth International Geographical Union in 1908, which endorsed it. Perhaps that venue was suggested by his partner in pushing the project, Kiel professor of geography and oceanography Otto Krummel (1854–1912), who had participated in Hensen's plankton expedition (1889) and published an account of it. An organizing committee for this new scientific society met at Albert's new Oceanographic Museum on 30 March 1910 and planned a first meeting of the Commission Internationale pour l'Exploration Scientifique de la Méditerranée (CIESM) in February 1914. A third meeting was postponed because of World War I and finally occurred in Paris in June 1919. At that meeting were representatives of Egypt, France, Greece, Italy, Monaco, Spain, Tunisia, and Turkey. Cyprus joined later in 1919, and since Black Sea countries were welcomed, subsequent joiners were Romania (1925), Serbia (1927), Palestine (1929), Lebanon and Syria (1930), and Morocco (1933). France, Italy, and Spain provided research vessels.

Fishing in European marine waters declined sharply during World War I, and the significantly increased fish populations discovered after the war indicated prewar overfishing (Gulland 1974:42, Larkin 1978:58, Finley 2011:17–18). However, instead of exercising restraint based upon this lesson, commercial fishermen were eager to make up for lost time and soon brought fish stocks down to prewar levels: "In 1914, the average landing from a trawler in the North Sea was 1,575 pounds. When fishing resumed in 1919, the average daily landing was 3,392 pounds. But within five years the boom had turned to bust" (Clover 2006:103).

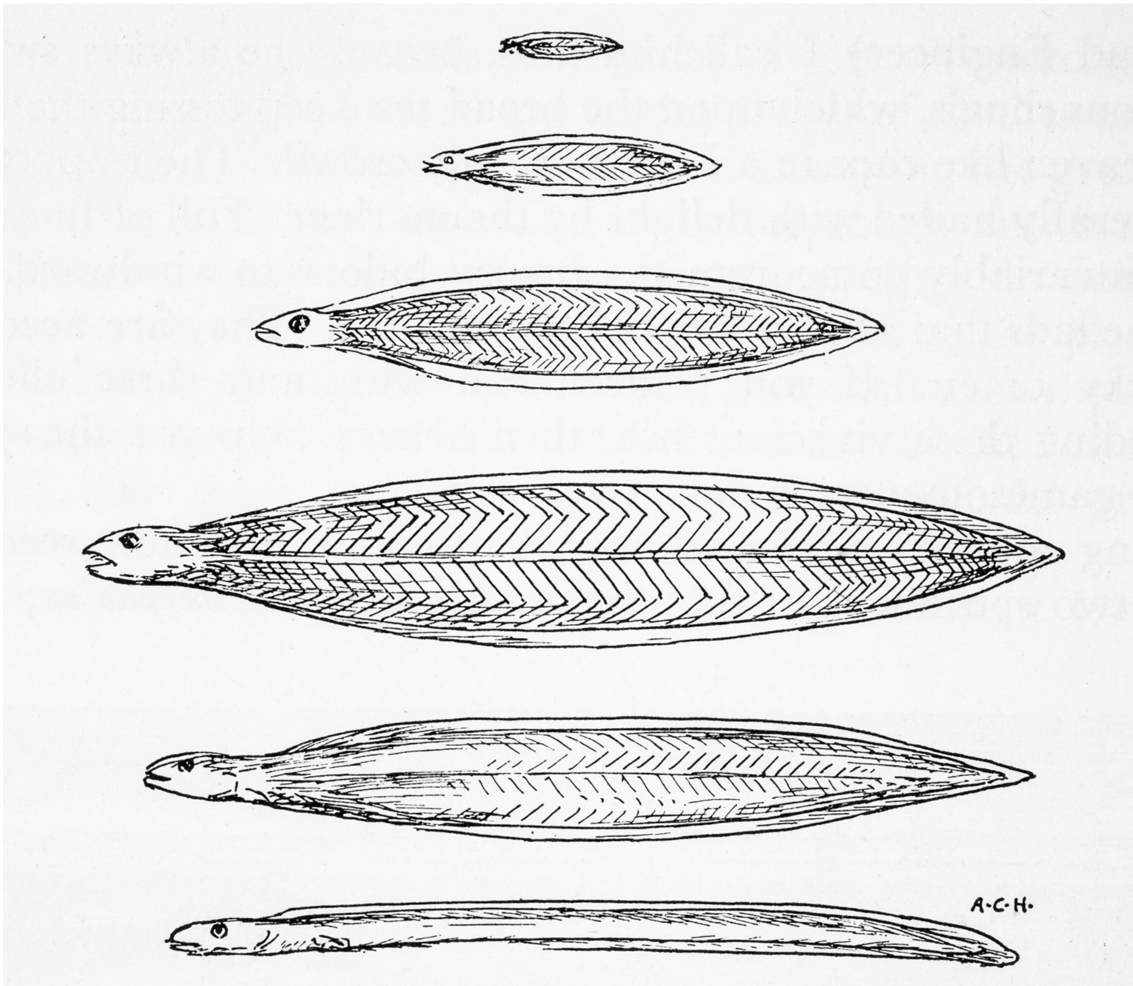


Fig. 27. Eel development from an early stage in the Atlantic to adulthood in European streams. Hardy 1967:102. Originally from Hardy, *The Open Sea*, part 2, 1959:91.

ICES ran smoothly until World War I disrupted international cooperation, 1914–1918. The September 1914 meeting had to be canceled, and since some countries ceased paying their dues, there were insufficient funds to continue very many ICES activities (Smed 2013:185–186). A reorganizational meeting was held in London in March 1920, but Germany and Russia were not invited (Smed 2013:204–205). Germans overcame their isolation in 1928 when the Gesellschaft für Erdkunde zu Berlin celebrated its centennial by sponsoring an International Conference on Oceanography to which it invited foreign participants, and in 1929 Germans were invited to both the Oceanographic Congress meeting in Seville and the Fourth Pacific Science Congress meeting in Batavia-Bandoeng (Lenz 2002:118–119). Ultimately, ICES survived two world wars and still flourishes (Cushing 1988:213–233, 259–276, Rozwadowski 2002:85–122).

Fisheries: American

ICES publications were read beyond European boundaries, and fisheries biology also progressed beyond those boundaries (Idyll and Kasahara 1969, Castro 1997). Fisheries biology is mostly a practical science, that previously only occasionally interacted with marine ecology (Parsons 1980:541–542). (It will be discussed more extensively in part 55 of this history, on population ecology.) Dean Allard's doctoral dissertation, *Spencer Fullerton Baird and the U.S. Fish Commission* (1967, published 1978) provides an introduction to U.S. fishery biology and the U.S. Fish Commission, 1871–1887. Two histories discuss the Fisheries Research Board of Canada (Hachey 1965 [no illustrations], Johnstone 1977 [well illustrated]). In 1870, fish culturists met in New York City and founded The American Fish Culturists' Association, but by 1884, members realized that their collective interests were broader than raising fish, and it changed its name to American Fisheries Society (Thompson 1970:1–6). AFS' centennial history (Benson 1970) contains topical articles by 23 members, some on freshwater fisheries and others on saltwater fisheries. Three saltwater chapters are discussed here: on sardines, halibut, and tuna. There are also histories of ichthyology in Canada (Dymond 1964) and in the United States since 1850 (Hubbs 1964).

The fishery for North Atlantic halibut *Hippoglossus hippoglossus* had collapsed during the mid-1800s (Cushing 1988:33–36), and there was a concern that this be avoided in the fishery for Pacific halibut *H. stenolepis* (Bell 1970, Cushing 1988:125–129). Halibut are right-eye flounder that can reach 500 pounds and 9 feet long and eat various animals and are eaten by sea lions, orca, and sharks. A positive factor for this fishery was that Canada and the United States were both involved, and after accusing each other of irresponsible practices, they established treaty limits on the catch (Cushing 1988:208–210, Hubbard 2006:185). Minnesotan William F. Thompson (1888–1965) earned his B.A. and Ph.D. from Stanford University (1911, 1930), having worked for David Starr Jordan and studied under Charles Henry Gilbert

(Dunn 2002:5). He joined the California Fish and Game Commission, 1913, but the British Columbia Commissioner of Fisheries hired him to study its halibut fishery, 1914–1917 (Dunn 2002:6–12). He developed a system of data collecting that provided more information than previous systems; he found the logs of commercial fishermen reliable, and that their fishing boats had to travel farther each year to catch the same amount as before, that fishermen's catch per unit of effort declined, and that the fish caught became progressively smaller, all signs of overfishing (Cushing 1988:125–129).

The California sardine *Sardinops sagax caerulea* is probably the same species as the Peruvian pilchard, in which case the name for both would be Pacific pilchard. It is in the herring family Clupidae. It eats plankton and originally there were schools of up to ten million that swam along coasts from southern Alaska to Baja California (or south to Peru, depending on systematic status). California began collecting catch statistics in 1916 at Monterey and southern California, with a fairly steady increased catch extending to 1942. In 1917 Thompson returned to the California Fish and Game Commission and "was instrumental in creating one of the finest state fisheries agencies in the nation" (Dunn 2002:15). During World War I the sardine fishery became the largest in the United States, with 72,580 tons caught just off California's coast. In 1919 Thompson was put in charge of studying this fishery (Mangeldorf 1986:37). The fishery on the American Pacific Coast for sardines would eventually collapse, due to overfishing, though not until 1952 (Ahlstrom and Radovich 1970:185). Irregular water temperature cycles were likely also a factor, since sardines flourish in warm water but not in cold water. In 1966, a year after Thompson died, fishery biologist Garth Murphy (born, 1922; Ph.D., 1965), at Scripps Institution, published a lengthy analysis, "Population Biology of the Pacific Sardine (*Sardinops caerulea*)," in which he pointed out that the decline in sardines had been accompanied by a rise in anchovy populations, and that a moratorium on sardine fishing would not cause a revival of sardines unless also accompanied by harvesting enough anchovies to free resources for sardines (1966:77). The Pacific sardine population did recover in the late 1970s, and the harvest in 2010 was 66,817 metric tons, in 2011, 46,324 tons, and in 2012, 99,859 tons.

Tuna had been eaten in Mediterranean countries and Japan since antiquity, but had not become commercially fished in North America until 1903, when a fishery for albacore *Thunnus alalunga* began in California, and a cannery was built in San Diego in 1911 (Schaefer 1970:237, Ellis 2008:215–217, Finley 2011:40). Japanese biologist Kamakichi Kishinouye (1867–1929), at the Imperial University of Tokyo, was first to study the tuna fishery, beginning in 1911, and Japanese immigrants to Hawaii introduced tuna fishing there (Kishinouye 1923; Vaughan 1930, Finley 2011:39). By 1914, the California catch reached 9000 tons, but a poor catch in 1916 caused a switch to skipjack *Katsuwonus pelamis* and yellowfin *Thunnus albacares* (Schaefer 1970:237). The fishery for all three species increased rapidly thereafter, and the fishing area increased beyond California to Baja California, and during the 1930s

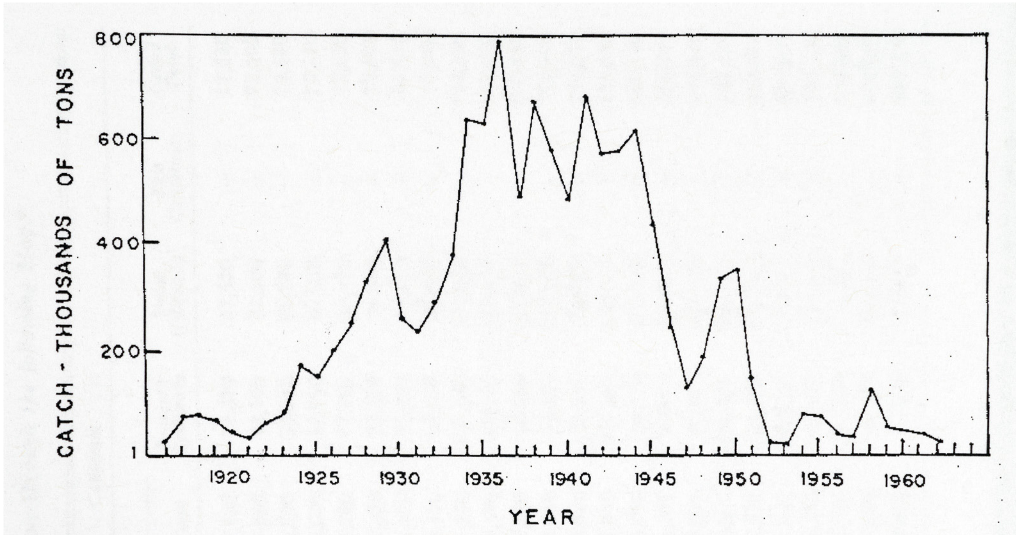


Fig. 28. U.S. Pacific sardine catch, 1915–1962. Murphy 1966:2.

into waters of Oregon, Washington, and British Columbia. Skipjack and yellowfin are the most widely distributed species, in all oceans, and the only two species still caught in high numbers (Brower 2014:77).

Fisheries: Japanese

Japan had had a closed society, only interacting with the Dutch until the 1850s. As a nation of Pacific islands, its fisheries were an important resource. Fisheries education began at Japanese universities in the 1880s, though various programs came and went (Matsuda 2002:405–407). American Dr. John C. Cutter first taught fisheries science at Sapporo Agricultural School in Tokyo, 1880–1888. However, he had an M.D. degree and published a textbook, *Comprehensive Anatomy, Physiology, and Hygiene* (edition 2, 1884). He was neither ecologist nor ichthyologist. Yet Japanese students seemed to learn what they needed to know. One, Kazutaka Ito, founded the Hokkaido Salmon Hatchery in 1888. Japanese fishery students were also sent abroad to study in various countries. A Department of Fisheries was established at Sapporo in 1906, and it was reorganized into a fisheries college in 1919. During the 1890s, fishery science was also introduced into certain high schools (Matsuda 2002:409). During 1888–1892, fishery biologists surveyed the species-by-species resources around the Japanese islands, and then marine mammals, 1893–1894, and the occurrence of red tide in 1899 (Matsuda 2002:410). A Japanese

Meteorological Observatory was built in 1875, a Fisheries Experiment Station in 1893, and there is a Japanese Society of Scientific Fisheries.

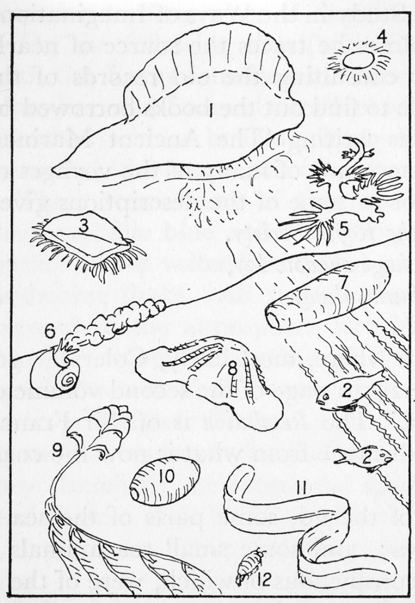
Alister C. Hardy

Alister Hardy (1896–1985) was Yonge's contemporary, and their work proceeded at the same time; he is discussed last because he did not publish his account of his expedition until over four decades after Yonge's book appeared. Hardy was the son of a wealthy architect in Nottingham and grew up near Robin Hood's Sherwood Forest (Hay 2011:3–4). He attended Oxford University for a semester in 1914 before joining the British Army in World War I (Hay 2011:53–59). After the war, he returned to Oxford and studied zoology under Julian Huxley. There were few zoology students at Oxford, but one of them was Sylvia Garstang (one of Walter Garstang's five daughters [Hardy 1950, Hay 2011:72]). Hardy only married Sylvia in December 1927, but long before, her father's specialization had influenced the direction of his own interests. In 1921, after graduating from Oxford, he received a scholarship to the Stazione Zoologica in Naples to study fish parasites (Hay 2011:83–93). However, that opportunity was incompatible with his psychological state—loneliness for his future wife and offer of a job in fisheries research which he wanted—and he only agreed to stay six months of his two-year scholarship and continued the research back in England. He accepted a research position with the British Department of Agriculture and Fisheries to study environmental conditions in the North Sea. Much later, he recalled "[his] years in Lowestoft as one of the happiest times in his life" (Hay 2011:97).

In 1925–1927 he served as chief zoologist on an expedition aboard *Discovery* to the Antarctic, where he collected and studied plankton (Hardy 1967). It was the most elaborate British scientific voyage since the *Challenger* voyage, financed by a tax imposed on British whalers' barrels of whale oil, for the purpose of preventing the Antarctic whale fishery from killing all the whales, as it had done in the Arctic whale fishery in the early 1900s (Hardy 1967:24–37). That expedition coincided with the first season of an Antarctic factory ship with stern slipway (Gulland 1974:13). By summer 1930–31, there were 41 factory ships and 200 whale-hunting ships in the Antarctic. The whaling industry was unwilling to wait for publication of scientific studies before attacking the Antarctic whales. The blue whale fishery that season killed 5703 blue whales and reached its peak in 1931, with 29,410 killed and declined to zero in the 1968–69 season; fin whales killed in 1925–1926 were 4,366, peaked in 1938 with 28,009 killed, and killed 3002 in 1970; sei whales killed in 1925–1926 was 1, peaked in 1965–1966 with 20,380 killed, and killed 5857 in 1970. Concern for international regulation of whaling catch began at the League of Nations in 1931, with rather slow progress being made (Gulland 1974:15–37).

Upon returning from the *Discovery* Expedition in 1927, Hardy became the first professor of zoology

Fig. 29. (a) Blue or transparent animals at or near the surface of a tropical sea. (b) Identifications. Hardy 1967: facing 96 and 96.



1. The 'portuguese man-of-war', *Physalia physalis*.
2. The fish *Nomeus gronovii*, which associates with *Physalia*, seen against the long trailing tentacles of the latter.
3. *Velella velella* or 'Jack sail-by-the wind'.
4. *Porpita sp.* (*umbella*?)
5. The pelagic sea-slug *Glaucus atlanticus*.
6. The snail *Ianthina janthina* with its bubble float.
7. The salp *Salpa fusiformis*.
8. The ctenophore *Deiopea*.
9. The siphonophore *Hippopodius hippopus*.
10. The pelagic tunicate *Doliolum*.
11. 'Venus's girdle', the ctenophore *Cestus veneris*.
12. The amphipod *Brachyscelus rapax*.

at a new Hull University (Hay 2011:152–153). Although he had to organize courses, he also worked on the *Discovery Reports*, which took three decades to publish. In 1942 he accepted an invitation to become Regius Professor of Natural History at the University of Aberdeen in Scotland (Hay 2011:176–178). A previous professor of natural history there had opened the first marine research station in Britain in 1879, at Stonehaven, 15 miles south of Aberdeen (Hay 2011:178). There was also a Scottish Fisheries Research Services Marine Laboratory in Aberdeen, on the River Dee. The herring fishery was important to Aberdeen commercial fishermen, as it was also to Hardy. In his inaugural address at Aberdeen he confessed he was only partly interested in the practicalities of fisheries, and that his strongest interest was in ecology, hoping that "this science of Interrelationships of animals and their environment will eventually have a reaction for the benefit of mankind quite apart from any intermediate economic one" (Hay 2011:181). However, he had been at Aberdeen for only four years when his former zoology professor at Oxford, Edwin S. Goodrich (1868–1946) retired, and Hardy replaced him in January 1946 (Hay 2011:185–187). Charles Elton ran his Bureau of Animal Population at Oxford and was pleased with Hardy's administration (Crowcroft 1991:93). David Lack had become head of the Edward Gray Institute of Ornithology at Oxford in August 1945 (Anderson 2013:82–84), but his biographer says nothing about his opinion of Hardy's administration. Despite Hardy and Lack being theists in a sea of skeptics, neither man's biography described any interaction between them.

Hardy was a many-talented marine biologist: besides being a diligent observer, he was a skillful landscape artist, a good illustrator of animals, an inventor of scientific equipment, a photographer, and a capable author. These talents are all evident in his well-illustrated account of *Discovery*'s voyage, written much later (but based upon his journal from the voyage): *Great Waters: A Voyage of Natural History; to Study Whales, Plankton and the Waters of the Southern Ocean* (1967). While biologists were having craftsmen make equipment and they were testing it, Hjort invited them to a cruise on the *Michael Sars*, where he showed off his equipment and techniques (Hardy 1967:52–54). One of the things they compared were techniques for shooting markers into the skins-blubber of whales, which subsequent whalers could return to the investigator for a reward; this process provided evidence of migrations. Hardy's most famous invention was a continuous plankton recorder, on which he began work in 1922; a cloth sieve that collected them and wound them onto a drum, without one layer touching the next (Hardy 1956–1959, I:76–79, Lane 1969:51–52, Ward 1974:225–228).

Great Waters, which drew heavily upon the *Discovery Reports* and upon Hardy's *The Open Sea: Its Natural History* (two volumes, 1956–59), was an introduction to oceanography and marine ecology at a popular level, though it seems unlikely that anyone who had not studied zoology would read the whole book. Just as Murray and Hjort had written an introduction to oceanography using the northeast Atlantic as an example, Hardy did likewise, using the Southern Ocean as his example. However, at 542 pages,

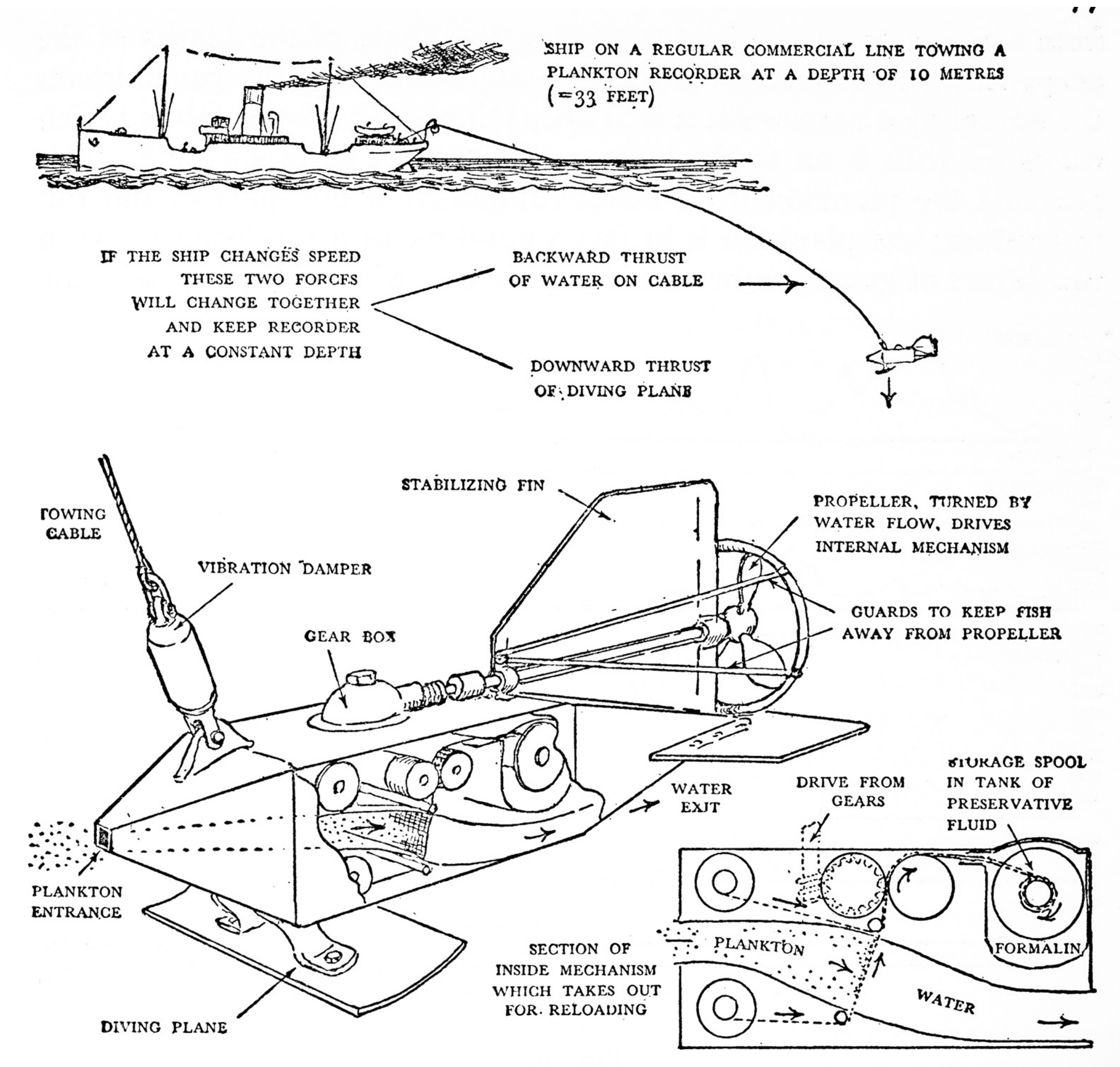


Fig. 30. Drawing of Hardy's continuous plankton recorder. Hardy 1956–1959, I:77.

which included numerous illustrations and maps, *Great Waters* was less encyclopedic than Murray and Hjort's *Depths of the Ocean* (1912). The *Challenger* had ventured below the Antarctic Circle at one point on its voyage, but no modern research voyage had focused mainly on the Southern Ocean before the voyage of *Discovery*. Hardy acknowledged Hensen's discovery that plankton were more abundant in temperate and cold waters, but he discovered that tropical plankton had a greater number of species (1967:92). He particularly studied krill, which were eaten by all four baleen whales in the south (fin, blue, humpback, sei) and by some species of fish, seals and penguins. There were 35 volumes of *Discovery Reports*, 1929–1966 (Hardy 1967:523–534).

Hardy was knighted in 1957 by Queen Elizabeth for his services to British fisheries through his zoological researches. By then, he postulated that sometime in the future, ”vast stretches of the continental shelf will be truly farmed,” and that "weeded" species which aquaculturalists removed would be converted to poultry feed (Hardy 1956–1959, II:299, Hubbard 2013:90–91).

Conclusions

Marine ecology achieved intellectual and organizational maturity during the period 1870–1920s. Marine biological stations arose before 1870 in Belgium and France but proliferated in western Europe and North America during the 1870s and later. Anton Dohrn's Stazione Zoologica (1873) in Naples was a model that inspired others to emulate it, in Europe and America, and eventually, elsewhere. Substantial monies were invested in buildings, ships, and equipment, and the returns in knowledge and publications were immense. Oceanographical voyages began slightly before stations were established, and a kind of climax was achieved when the British government, advised by the Royal Society of London, provided the ship *Challenger* to survey the ocean depths around the world for 3.5 years, 1872–1876. On board were outstanding naturalists who made excellent collections of biological specimens from land and sea, and afterwards John Murray distributed specimens to specialists in Europe and America to describe, supervising publication of 50 large volumes that substantially enlarged scientists' knowledge of marine life and ocean depths. At about the same time, Victor Hensen began plankton researches at the University of Kiel in order to understand fluctuations in fish populations, discovering that plankton were more abundant in cold than in warm waters. He and his successor, Karl Brandt, devoted much time and effort in trying to understand why. Their publications were met with some skepticism that led eventually to an understanding of very complex conditions and plankton responses to environmental factors: light, water circulation, and nutrients. Such studies spread in Europe and America, and European marine scientists organized the ICES in 1902, which facilitated international studies and communication on fishery and marine ecology. Fishery research flourished also in North America, Japan, and elsewhere, encouraged by the American Fisheries Society and other organizations. Alister Hardy was a notable English marine

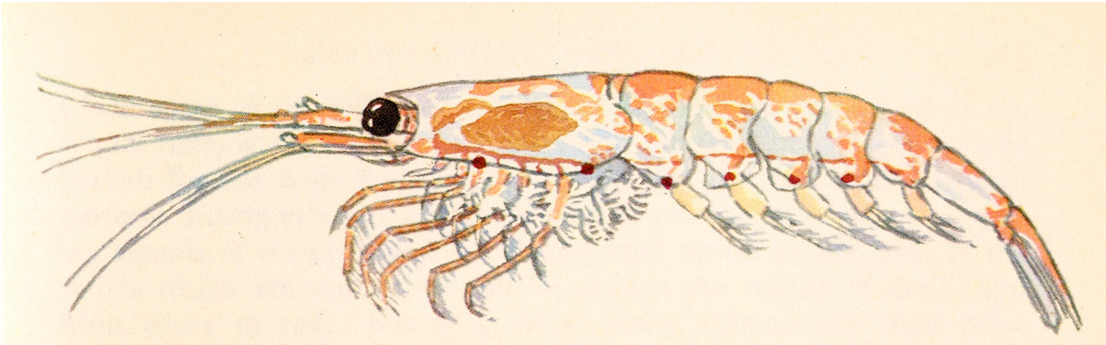


Fig. 31. Krill *Euphausia superba*. It has 10 luminous organs (illustrated, p. 168), which glow in the dark. Hardy 1967:facing 224.

biologist who had broad interests, but specialized to some extent in plankton, the food of fish and whales, advancing knowledge about them during the 1920s and later. An interesting footnote: both Alexander Agassiz and John Murray obtained wealth from investments in mines, which they devoted to funding their research.

Although the formalizing of marine ecology is a more elaborate and complex story than those of plant ecology, animal ecology, and limnology, this did not translate into marine ecology being the most dominant of the four. In terms of ecology textbooks, land ecologies seemed to have had an edge over aquatic ecologies, likely because land organisms were more accessible than aquatic organisms, and because ecologists live primarily on land, not in the water.

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