



Review Article

The neglected contributions of William Beebe to the natural history of the deep-sea

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William Beebe (1877–1962) was a very popular 20th century naturalist and an early proponent of studying all organisms in a habitat. Beebe's deep-sea work began with his *Arcturus* Oceanographic Expedition in 1925 with sampling closely modelled on the *Michael Sars* deep-sea expedition. Dissatisfied with ship-based sampling of stations for a few days at best, he established a field laboratory in Bermuda to do intensive deep-water sampling. From 1929 to 1934, plankton net tows were carried out at the same site, over several months each year, totalling over 1500 net tows in deep waters. Here, the sampling efforts and results are reviewed from both the *Arcturus* Expedition and the Bermuda station. Study of the deep-sea samples yielded 43 scientific articles, published from 1926 to 1952, on a large variety of taxa. Beebe is still a popular figure connected in the public view with deep-sea exploration from his famous Bathysphere dives at the Bermuda site. However, his name rarely, if ever, appears in academic reviews of deep-sea biology or deep-sea expeditions. This study is an attempt to draw attention to Beebe's considerable scientific deep-sea work and provide some speculation as to why his contributions might be neglected.

Keywords: deep-sea, deep-sea fish, history of oceanography.

Introduction to William Beebe

Charles William Beebe, generally known as William Beebe, had a long and unusually full and productive life as attested to in book-length biographies of Beebe (Welker, 1975; Gould, 2004), and the detailed bibliography “William Beebe, an Annotated Bibliography” (Berra, 1977). There is also a plethora of short biographies in popular books (e.g. Cullen, 2006; Ballard and Hively, 2017; Morell, 2019). However, the most authoritative account of Beebe's life is that of Gould (2004) as it is based on original source material, unavailable before the death of Beebe's second wife. The following brief account of Beebe's life, situating his deep-sea studies, is based on Gould's (2004) biography.

Beebe, from a young age, was drawn to natural history. By age 14, he was an avid collector of birds and their eggs, insects, shells, and minerals. Age at 16, his last journal entry for the year 1893 was “To be a Naturalist is better than to be a King”, and by age

17, he had his first article, on a bird, published in “Harper's Young People” (Beebe, 1895). An exceptional student in high school, he was given advance placement at Columbia University, skipping the first year. At Columbia, Henry Osborn who would be a large figure in his life supervised him. Osborn was not only Chair of the Zoology Department but also the president of the American Museum of Natural History as well as the head of the New York Zoological Society. Beebe split his days between lectures and labs at the University and days at the American Museum of Natural History. In autumn 1899, Osborn told Beebe that he had completed all the requirements for his degree in zoology except for a maths class he had been avoiding. Osborn gave Beebe a choice between staying in school for another year to complete his missing class or he could go with Osborn to the new, still under construction, Bronx Zoo of the Zoological Society and apply for a job as an assistant curator of birds. The

choice was quickly made. Beebe would spend his entire working life with the New York Zoological Society (now the Wildlife Conservation Society) and never would earn a college degree.

Beebe's career can be roughly divided into four periods. The *first period* of 1899–1908 consists of his early years as curator of birds. In 1908, with the aid of Osborn, he won a status similar to that of the staff scientists at the American Museum of Natural History with 2 months salary paid to conduct research. Thus, the *second period*, 1908–1916, was the start of long expeditions, primarily to South American jungles in this first period but also a year spent investigating pheasants worldwide. He later produced a monumental multi-volume monograph on pheasants regarded as one of the “vital books of science” (Bay, 1948). By 1916, he secured funding for the establishment of a field station in British Guiana, a facility where intensive study of tropical life could be conducted over long periods of time. The *third period* of 1916–1924 then was primarily tropical fauna studies. During this period, Beebe's position evolved from Curator to Head of the Department of Tropical Research. Work conducted during this period has led to Beebe's being declared the “Father of Neotropical Ecology” (Mendyk, 2014). It also included an expedition to the Galapagos, financed by a wealthy zoo supporter; the expedition produced a best seller “Galapagos: World's End” (Beebe, 1924). During this period, he was awarded the Daniel Giraud Elliott Medal of National Academy of Science, an award for remarkable achievements in zoology. Later recipients of the prestigious award were G. Evelyn Hutchinson, Ernst Mayr, and Henry Bigelow. The *fourth period* of 1925–1939 is that of Beebe's field studies of marine fauna, the focus of this article. It begins with the oceanographic voyage of the *Arcturus* and ended with the approach of World War 2. The *Arcturus* voyage inspired Beebe to establish a field station devoted to deep-sea work. The Nonsuch field station in Bermuda was founded, and intensive deep-sea studies were carried out from 1929 to 1935. It was also the site of the famous Bathysphere dives. These dives, one of which was broadcast on radio live, were celebrated in *Science* (Anon, 1930a) and *Nature* (Anon, 1930b), detailed in his book *Half Mile Down* (Beebe, 1934), reported by Beebe in *Science* (Beebe, 1932c), and in lavish articles in the National Geographic Magazine. The activities of this period, exclusive of the bathysphere dives, are dealt with in detail here in this article. The *fifth and last period*, from 1945 to his death in 1962, was a return to the studies of tropical fauna from, but from another field station, one he installed in Venezuela.

Beebe's deep-sea work is often over-looked

Beebe was immensely popular in his time (Gould, 2004) and still in today's popular books is credited not only for drawing attention to the deep-sea with the Bathysphere dives but is also credited with being a pioneer ecologist because of his systematic sampling of the deep-sea (e.g. Cullen, 2006; Ballard and Hively, 2017; Morell, 2019). In many academic works, however, the considerable results (which will be shown below) from the *Arcturus* Expedition and the Nonsuch sampling are simply not mentioned. For example, in Mills' book *History of Biological Oceanography* (Mills, 1989), one finds no mention, nor in Hedgpeth's article “History of Pacific Oceanography” (Hedgpeth, 1974). Similarly, in their review of the oceanography of the Eastern Tropical Pacific, Fiedler and Lavin (2006) mention only Beebe's popular books with no mention of the research reports from the *Arcturus* Oceanographic Expedition. Likewise, a history of deep-sea

biology (Mills, 1983), a history of deep-sea expeditions (Wüst, 1964), and deep-sea plankton studies (Kimor, 2002) contain no mention of Beebe's work, nor that of his colleagues. Even the general comprehensive book on deep-sea organisms of Marshall (Marshall, 1979) cites but one of Beebe's many articles on deep-sea fish.

Histories of marine ecology give a nod to Beebe but not the deep-sea work. Riedl's (1980) review of the development of marine ecology placed Beebe's work in the stage “before its time” but only in reference to revealing “the splendours of tropical shallow seas”. Likewise, Egerton's (2016) instalment of his “History of Ecological Sciences: Marine Ecology featuring Beebe, Bigelow, Ricketts”, while placing Beebe in admirable company, makes no mention of Beebe's deep-sea work. Ironically perhaps, Beebe while largely if not completely unknown to biological oceanographers is recognized by physical oceanographers for his early observation of El Niño event during *Arcturus* Expedition (Wooster, 1980; Quinn et al., 1987).

What follows

Here, the sampling and results, first from Beebe's *Arcturus* Oceanographic Expedition, and then from the Nonsuch studies, are described in an effort to draw attention to a remarkable body of work. Study of the deep-sea samples yielded 43 scientific articles by Beebe and his colleagues on a large variety of taxa. Beebe's famous Bathysphere dives have been dealt with at length (e.g. Matsen, 2005) and will only be considered here in relation to Beebe's scientific reputation. Finally, possible reasons for the fact that such a considerable body of work is often unremarked are considered.

Inspired by the Michael Sars North Atlantic deep-sea expedition: the *Arcturus* Oceanographic Expedition

According to Gould (2004), Beebe's interest in the deep-sea can be traced to his reading about the *Michael Sars* expedition. She describes Beebe as having nearly memorized Murray and Hjort's (1912) *The Depths of the Ocean*. Indeed, a *Michael Sars* inspiration can be seen clearly in comparing the illustration of the pelagic sampling from *The Depths of the Ocean* (Figure 1, from p. 49) with that of the *Arcturus* from Tee-Van (1926, p. 70) shown in the top panel of Figure 2. Furthermore, in describing the equipment and re-fitting of the vessel, Tee-Van (1926) stated that they were indebted for much information, both before and during the expedition, to published accounts of other expeditions but especially to that of Murray and Hjort's *The Depths of the Ocean*. In 1925, few results were available from deep-sea expeditions other than *Michael Sars* and results from it were still emerging. The results of Danish “Great Atlantic Expedition of the *Dana* of 1921–1922” were as yet largely unpublished in 1925 (see Poulsen, 2016).

The *Arcturus*, re-named for star of the mariners, was given to the New York Zoological society for the expedition by a wealthy patron, expressly for the expedition. The re-fitting and financial support for the expedition came from other patrons of the Zoological Society. The ship was modified to increase its range and suitability for deep-sea oceanographic work. The modifications included increasing coal storage and refrigerator space, adding a wet and dry lab, and installing custom-made trawling and dredging winches holding 8 km of steel cable (Tee-Van, 1926).

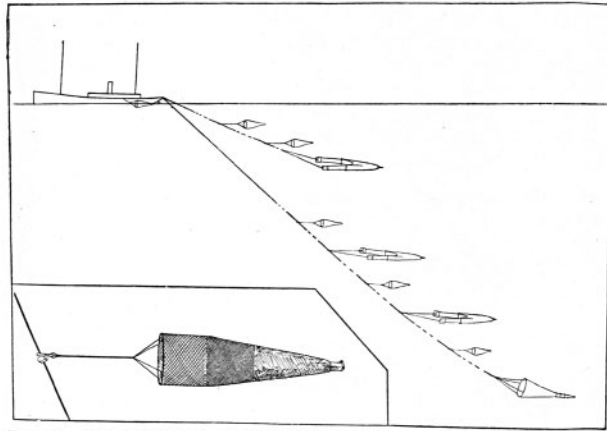


FIG. 32.—THE “MICHAEL SARS” TOWING TEN NETS AND PELAGIC TRAWLS. (Surface net not shown.)

Figure 1. *Michael Sars* pelagic sampling from Murray and Hjort (1912).

The objectives of the expedition were simply stated as “investigating the Sargasso Sea and the Humboldt Current” (Beebe, 1925a). The Sargasso Sea at the time was an area of great interest as it had been recently identified as the breeding site of the eel, previously a major mystery (Poulsen, 2016), and in popular legend, the Sargasso Sea was a sea of ghost ships (e.g. Levick, 1925). The second goal of investigating the fauna of the Humboldt Current was quite possibly simply an excuse to return to the Galapagos.

The *Arcturus* left New York on 11 February 1925 and returned to New York on 30 July 1925. The cruise track is shown in Figure 3. The first sampling of 22 Sargasso Sea stations began February 23 and ended on March 13. The *Arcturus* passed through the Panama Canal and on March 27 began the sampling of 38 stations along a cruise track from Panama to the Galapagos, then the Cocos Islands, and back through the Panama Canal to the Atlantic in late June. They failed to find the Humboldt Current, and Beebe’s observations, reported in *Science* (Beebe, 1926a), have been taken as one of the first observations of an El Niño event (Wooster, 1980; Quinn et al., 1987). On the return leg, 20 more stations were sampled between the Atlantic coast of San Salvador and the homeport of New York. The station locations and summary of ship operations are given in Beebe (1926b). A total of 251 samples were acquired from deep water (≥ 300 m depth) during the cruise, pooling all net, trawl, and dredge sampling.

The expedition was closely followed in the press, as no previous oceanographic expedition had been before, nor quite possibly has ever since been so closely followed in the popular press. For example, *The New York Times* published 35 articles on the expedition from 6 February 1925 to 30 August 1925, thus averaging over one article per week on the *Arcturus* Expedition. Many of the articles were simply transcripts of Beebe’s periodically radioed reports of expedition activities. The coverage in *The New York Times* though also included multi-page articles with illustrations as well as several front-page articles (e.g. Anon, 1925). Beebe’s popular book on the expedition, *The Arcturus Adventure* (Beebe, 1926c), appeared in May 1926 and was glowingly reviewed in *The New York Times* (Duffus, 1926).

Sample material gathered during the expedition was dispatched to renowned experts scattered around the globe. The scientific results took some time to appear, as is usually the case. The ten publications resulting from the *Arcturus* Oceanographic Expedition are given in Table 1. The scientific output of the *Arcturus* Expedition obviously was not of the same magnitude as large-scale expeditions such as the *Michael Sars* in 1910 and the *Dana* 1921–1922 or the expedition shortly after the *Arcturus*, the 1929 Cruise VII of the *Carnegie* (also under-appreciated, see Dolan, 2011). However, the scientific results of the *Arcturus*, while perhaps not considerable compared to other expeditions, were not negligible either. Admittedly, none of the *Arcturus* reports can be called “highly cited”, but some are relatively well-cited (see Table 1) and continue to be cited in recent years such as Bigelow (1928, 1931), Robson (1948), and Treadwell (1928).

The Nonsuch studies

Beebe experienced frustration on the *Arcturus* with the very limited number of samples that can be gathered at a given station from a ship in open waters. His previous experience in sampling tropical terrestrial systems from field stations had involved intensive sampling of small areas over long periods of time. One of his best-known works is “Studies of a tropical jungle: one quarter of a square mile of jungle” (Gould, 2004), the result of investigations over several seasons (Beebe, 1925b). Beebe stated this his idea to establish a shore laboratory from which daily deep-sea sampling could be carried occurred to him on the return leg of the *Arcturus* Expedition, sampling at Station 100 near Bermuda (Beebe, 1931), the genesis then of the Nonsuch laboratory in Bermuda, established 4 years later.

Through his considerable social connections (see Kroll, 1970), he obtained the use of a former hospital and quarantine facility on Nonsuch Island in Bermuda and the use, at cost, of a 28-m tugboat, the *Gladisfen*. Deep water, 1000 fathoms (or 1828 m), was only 8 km offshore. The winches and sounding machine from the *Arcturus* were brought from New York and mounted on the *Gladisfen*, and sampling began in 13 March 1929 and, in that first sampling season, lasted until 22 October 1929. The sampling was always performed at the same site and involved towing nets across a transect of about 13 km. Thus, the basic strategy was to use long horizontal net tows. The net-tow catches were roughly sorted on board, especially to isolate living organisms, and transported back to the Nonsuch laboratory for immediate intensive sorting and examination. Figure 4 shows the sampling site and method schematically, the *Gladisfen*, and the Nonsuch laboratory.

Usually used at all depths were 1 m diameter *Sars* nets, mesh size of 366 μm , without any closing apparatus, and a glass jar protected with padding, for the cod end. The first net set, the deepest net (see scheme in Figure 4a), fished for the longest time period, and the last, surface layer net, fished the shortest time along the transect. Beebe gave a summary of a “typical” deep-sea net tow at 1463 m (Beebe, 1936a), summarized in Table 2. In the example he gave, the catch included about 150 fish of 11 species for just one of the 6 deep-water nets towed that day. Figure 5 shows the number of plankton net tows carried by month from the 1929 sampling campaign to the 1935 sampling campaign. A total of over 1500 net tows were made at the Nonsuch sampling site.

Although Beebe never cited Haeckel, he followed his dictum concerning the importance of sampling the same site over a period of years (Haeckel, 1891). The amount of deep-sea material collected over relatively long periods of time at different depths at

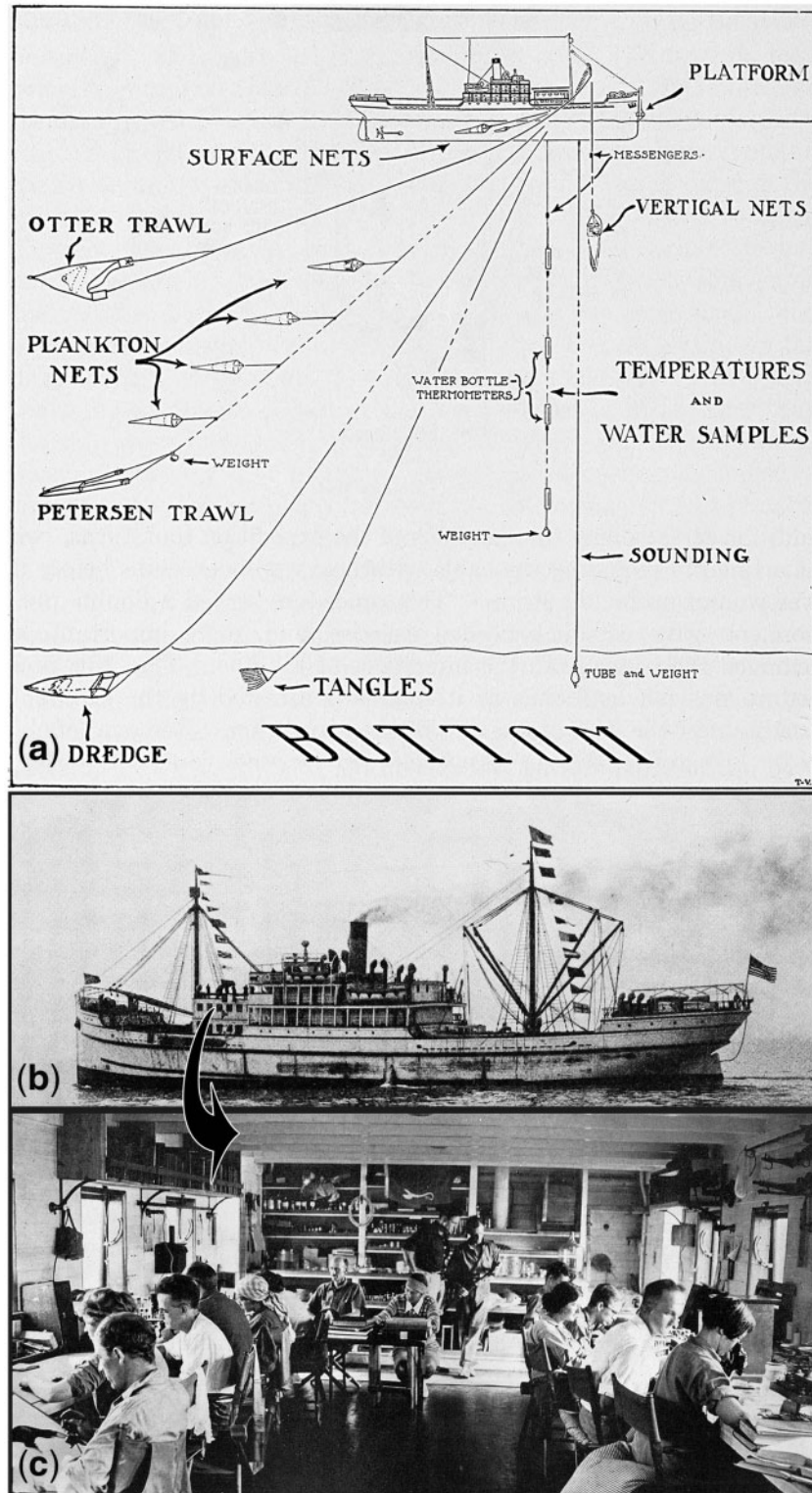


Figure 2. The *Arcturus* Oceanographic Expedition from Tee-Van (1926): (a) the sampling equipment, (b) the vessel, a sturdy 82-m coal-burning steam-ship built 6 years earlier as trawler to work the Alaskan coast, re-fitted and re-named for the expedition. (c) The dry lab, location on the ship shown by the arrow, on the deck above the wet lab. Beebe is seated the desk in the rear, facing the camera.

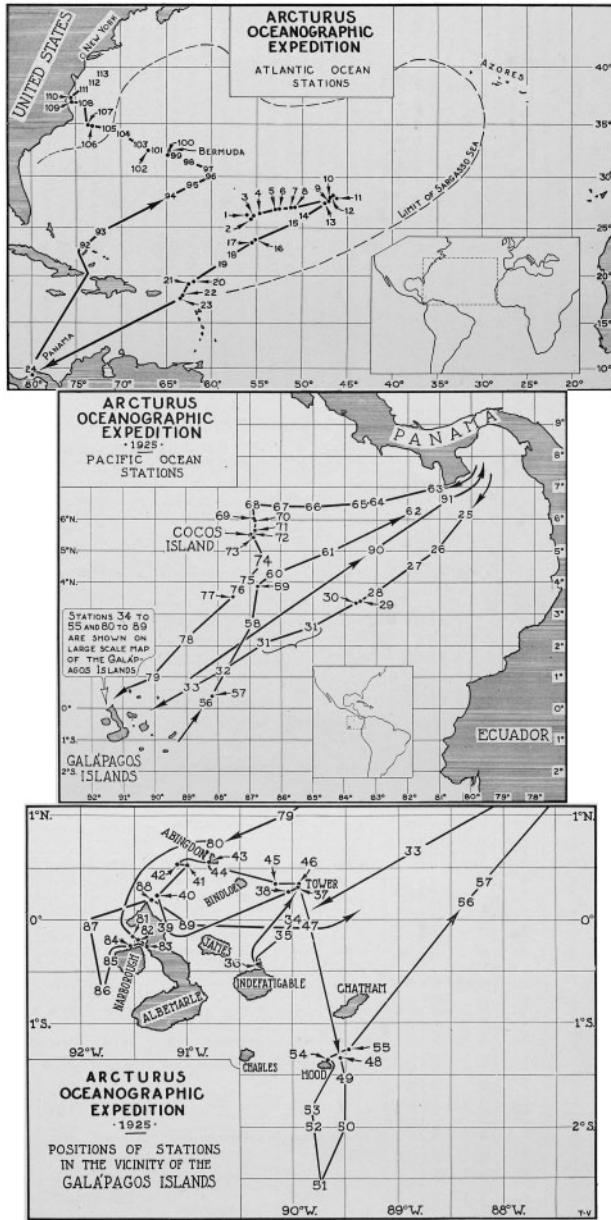


Figure 3. Cruise track and Station Maps of the *Arcturus* Oceanographic Expedition from Beebe (1926b).

the same location was unprecedented at that time and, to my knowledge, has never been repeated. Regular deep-sea sampling has, in recent years, been conducted at other sites such as the Bermuda Atlantic Time-Series Station and off Los Angeles at the San Pedro Ocean Time-Series Station but at only monthly, not daily, intervals and typically focused on microbial populations (e.g. Vergin *et al.*, 2013; Kim *et al.*, 2014). Thus, the data gathered by Beebe are difficult to compare with any contemporary sampling, hindering possible assessment of long-term changes in the deep-sea ecosystem off Bermuda.

The unique intensive sampling performed allowed Beebe and his colleagues to work out details of the development and ecology of individual forms and their inter-relationships. An example is the working out the life history of a deep-sea fish, characterized by morphologically odd developmental stages, and sexual

Table 1. *Arcturus* Oceanographic Expedition publications

Taxa	Reference	# Cites
Siphonophores	Bigelow (1931)	14
Medusa	Bigelow (1928)	10
Echinoderms	Fisher (1928)	6
Polychaetes	Treadwell (1928)	21
Cephalopods	Robson (1948)	12
Fish	Beebe (1926a)	44
Fish	Beebe (1926d)	0
Fish	Trotter (1926)	26
Fish	Gregory (1928)	12
Fish	Nigrelli (1947)	7

dimorphism: *Idiacanthus fasciola*. Below is a very brief summary of Beebe’s short report in *Science* (Beebe, 1933a) and his detailed report of 94 pages (Beebe, 1933b) in *Zoologica*.

The odd stalk-eyed deep-sea fish shown in the top panel of Figure 6 was previously thought to be the species *Stylophthalmus paradoxa* Brauer 1902. It was iconic of the odd morphologies of deep-sea forms, for example decorating the cover of Chun’s book on the *Valdivia* German deep-sea expedition (Chun, 1903). The middle panel of Figure 6 shows the intermediate forms Beebe found allowing him to identify putative *S. paradoxa* as actually the larval form of *I. fasciola*. His brief report in *Science* stated that the stalk-eyed forms were mostly found in samples from above 200 m depth while post-larval forms were found in samples from about 750 to 1500 m depth (Beebe, 1933a). In his detailed report (Beebe, 1933b), he also showed that forms thought to be larvae of *I. fasciola* (the small forms in the bottom panel of Figure 6), were non-feeding adult males with enlarged livers and degenerate digestive tracts. The remarkable sexual dimorphism discovered by Beebe is among the most extreme known among fish (Fairbairn, 2013).

Trophic relationships were also studied with the Nonsuch samples. For example, the large amount of data gathered on the depth distribution of a variety of taxa in the deep layers allowed the diagnosis of where predators from surface layers, for example tuna, fed, and based on the gut contents of the tuna prey, what prey the tuna were both directly and indirectly consuming. Beebe (1936b) analysed the gut contents of 58 black-finned tuna to reconstruct, in part, tuna food webs as the gut contents of the prey ingested by the tuna were identified. Thus, not only was the tuna prey revealed, but also the food of the tuna prey were revealed. Figure 7 shows the gut contents of a tuna specimen and the partially re-constituted food web of the individual.

The 33 publications resulting from the analysis of Nonsuch samples are given in Table 3. While a large variety of taxa were studied, most of the publications were on deep-sea fish and authored by Beebe. Many of Beebe’s studies of fish included ecological information such as gut contents, observations of parasites, seasonal occurrences, frequencies of occurrences, as well as occurrences in the gut tract of other species, thus identifying the fish’s “enemies”.

Deep-sea fish descriptions

Beebe described over 80 species of fish (Berra, 1977). According to the WoRMS database, at present, the descriptions of 37 accepted species are credited to Beebe and colleagues (WoRMS 2020). Of the 37 accepted species described by Beebe and

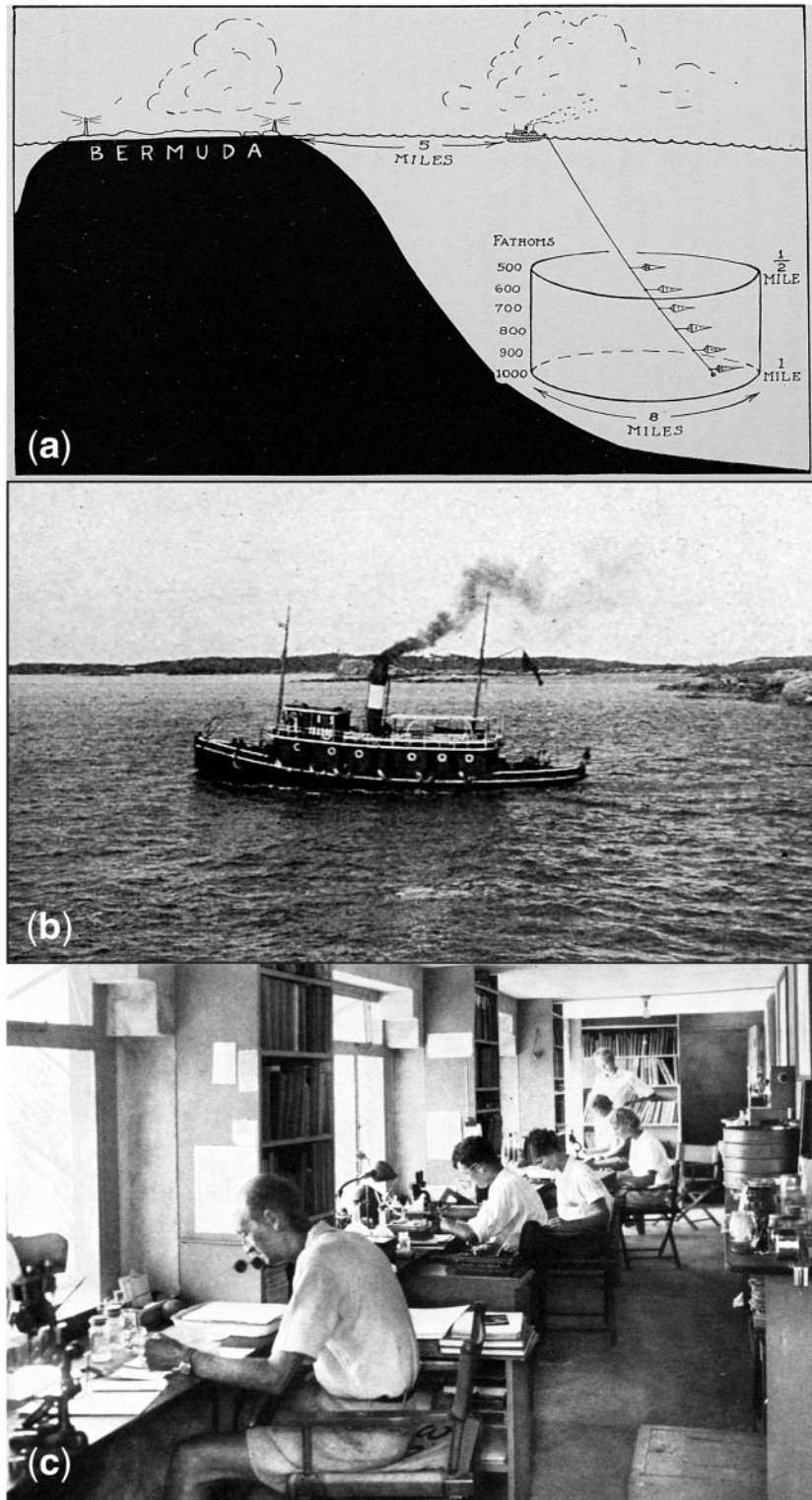


Figure 4. The Nonsuch sampling, vessel, and laboratory: (a) the sampling scheme, (b) the *Gladisfen*, a 28-m tugboat. (c) The laboratory on Nonsuch Island. From Beebe (1931). Beebe is seated at the first desk, far left.

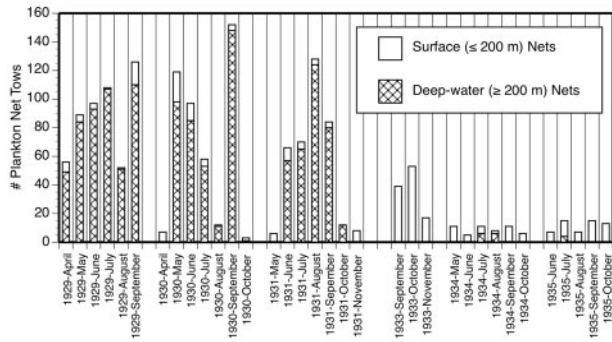


Figure 5. The number plankton net tows performed by month from 1929 to 1935, separated into surface layer and deep-water sampling. No net sampling was done in the 1932 season dedicated to Bathysphere dives.

Table 2. Typical deep-water Nonsuch net tow catch

Invertebrates

- (1) Copepods, a dozen or more species, mostly calanoids, with also *Corycaeus*, *Oithona*, etc.
- (2) Schizopods, chiefly small species of *Euphausia*, with a dozen others belonging to two or three genera.
- (3) Shrimps, one specimen, *aff. Pandalus danae*.
- (4) Ostracods, a few of one or two species.
- (5) Amphipods, few and small, a dozen individuals of four or five species.
- (6) Sagitta, apparently two or three species.
- (7) Polychaetes, one *Tomopteris septentrionale*.
- (8) Siphonophores, *Diphyys truncata*.
- (9) Sponges, fair number of spicules of various kinds.
- (10) Radiolaria, large numbers of portions of a hexagonal framework and a few small, conical specimens mostly incomplete; numbers of perforated spherical species and *Astrophaeroidea*.
- (11) Diatoms: one each *Asteromphalus heptactis*, *Melosira moniliformis*, *Coscinodiscus*.
- (12) Tintinninoidea, one *Tintinnopsis cylindrica* and one *Parafavella* near *P. acuta*.
- (13) Foraminifera, few, of two or three species.

Fish

- (1) Fish larvae: three specimens
 - one of a deep-sea species, with very large lower jaw and black spots on sides.
- (2) Fish, adolescent, and adult:
 - *Bregmaceros maclellandii*, 45 mm (1 specimen)
 - *Cyclothone microdon* (117 specimens)
 - *Cyclothone pallida* (1 specimen)
 - *Cyclothone signata* (14 specimens)
 - *Lampadena chavesi* (1 specimen)
 - *Lampanyctus warmingi*, 11–21 mm (6 specimens)
 - *Lestidium intermedium*, 87 mm (1 specimen)
 - *Myctophum benoiti*, 11–12 mm (3 specimens)
 - *Myctophum laternatum*, 12 mm (13 specimens)
 - *Omosudis lowi*, 11–38 mm (2 specimens)
 - *Stomias ferox*, 80 mm (1 specimen)

From [Beebe \(1936a\)](#), the example from a tow at 800 fathoms (1463 m) depth on 5 July 1930. The net was the usual 1 m diameter Sars net, mesh size 366 μm, towed for 4 h [time from [Beebe \(1931\)](#)] on a transect of 12.9 km distance yielding a putative volume sampled of 12 875 m³. The tintinnid listed as *Parafavella*, a genus of boreal sea tintinnids, was likely *Parundella acuta* as found by [Wailles](#) later in the Nonsuch samples ([Wailles, 1936](#)).

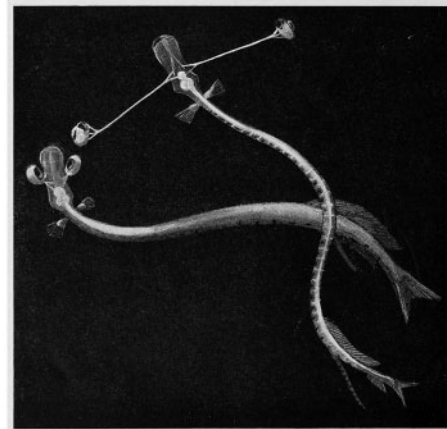


Fig. 51. Stalk-eyed larva and post-larva. (From a painting by [Elsa Bostelmann](#)).

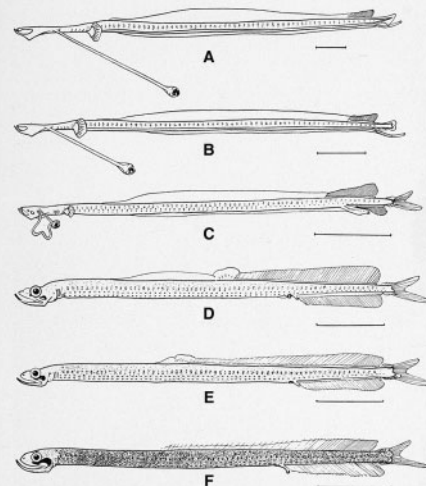


Fig. 50. Growth stages of male: A and B, sexually indeterminate larvae, 16 mm and 25 mm, respectively; C, male post-larva, 40 mm; D, male adolescent, 35 mm; E, male transitional adolescent, 35 mm; F, male adult, 38 mm. The relative size of the specimens is indicated by the straight lines. For ease in comparison the larvae of [Fig. 49 \(A and B\)](#) are reproduced in this figure also.



Figure 6. Life-history stages and sexual dimorphism in *I. fasciola*. Top panel shows the stalk-eyed larvae previously thought to be another species. Middle panel shows developmental stages of the male. Bottom panel shows the relatively small transparent males and dark females. All figures from [Beebe \(1933b\)](#).



FIG. 3.

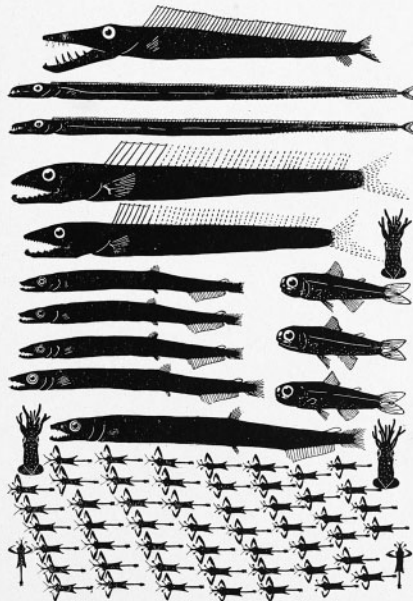


FIG. 4.

FOOD OF THE BERMUDA AND WEST INDIAN TUNAS OF THE GENERA PARATHUNNUS AND NEOTHUNNUS.

TUNA NO. 24,513					
3 <i>Diaplas rafinesquei</i>	5 <i>Paralepis</i> sp.	2 <i>Benthodesmus atlantica</i>	3 Geryllids, (2 species)	60 <i>Squilla</i> yr.	3 Squids
1 Shrimp	1 <i>Cycolothus</i> sp.	2 Shrimp	1 Fish		
3 Hyperids	1 Larval Fish	1 Squid	1 Squid		
1 Gammarid	1 Squid				

Figure 7. Gut contents of Black-Finned Tuna from Bermuda (upper panel) and a re-constituted food web from prey items recognizable in the guts of the tuna's prey (lower panel), from Beebe (1936b).

colleagues, 16 are deep-sea forms (Table 4). In addition to these 16 species, 2 other deep-sea species, presently accepted as valid, were described by Harry (1952) from Nonsuch samples and named after Beebe's colleagues: *Cetomimus teevani* and *Cetomimus craneae* for John Tee-Van and Jocelyn Crane. Thus, 18 species of deep-sea fish were first described from Beebe's deep-water samples.

Why are Beebe's contributions of the natural history of the deep-sea ignored?

According to Occam's Razor, for any given question, the simplest explanation is the most likely to be true. The simplest explanation for the neglect of Beebe's contributions is that the contributions are of no consequence and so need not to be acknowledged. However, judging scientific contributions as inconsequential or considerable is obviously subjective. There are no clear means to estimate the present value of past studies other than the obvious landmark works such as Darwin's *On the Origin of the Species* (Darwin, 1859). The quantity and originality of Beebe's contributions have been described here so the position taken is not *should* Beebe's contributions to our knowledge of deep-sea be recognized, but rather *why are they not?*

While there are possibly many reasons, below will be considered three major, but not mutually exclusive, reasons why Beebe's contributions, consciously or unconsciously, may have been slighted. The first is that the quasi-totality of his deep-sea scientific work appeared in one journal possibly lacking a reputation of rigour, *Zoologica*. The second is that Beebe's scientific reputation suffered from his having described four deep-sea fish species from visual observations during the Bathysphere dives. The third is that Beebe was an early victim of the "Sagan Effect" wherein media-driven fame negatively effects scientific reputation.

The journal *Zoologica* was created as an outlet for the scientific work conducted by those working for the New York Zoological Society or its facilities or collections. According to Matsen (2005, p. 157), *Zoologica* was "not considered to be in the top ranks of taxonomy because of inconsistencies in their peer review", unfortunately citing no sources for the statement. Thus, there is no evidence other than one undocumented opinion.

The possibility that Beebe's scientific reputation was damaged by his description of four deep-sea fishes based solely on visual observations (none of the species are currently recognized) appears in biographies of Beebe (Welker, 1975; Gould, 2004; Matsen, 2005) without, however, any documentary evidence beyond noting the sharp criticism of Beebe's Bathyscaphe-based descriptions in a review of Beebe's book *Half Mile Down* by the ichthyologist Carl Hubbs in *Copeia* (1935). Notably, Hubbs later cited Beebe's articles on surface and deep-sea fish in *Zoologica* as authoritative (Hubbs and Kampa, 1946, Hubbs et al., 1953) suggesting that he did not doubt all of Beebe's work nor that *Zoologica* article was untrustworthy. Other reviews of *Half Mile Down* appeared in *Nature* (Anon, 1935a), the *Quarterly Review of Biology* (Anon, 1935b), the *Geographical Journal* (CMY, 1936), and two by the Ichthyologist John Nichols, one in *Natural History* and the other in the *Saturday Review of Literature* (Nichols, 1934a, b). None of the reviews other than Hubbs contains overt criticism of the description of fish from visual observations only.

The last major possibility to consider is that Beebe was an early victim of the "Sagan Effect". This phenomenon posits that scientists who receive lots of media attention have their scientific work de-valued by the scientific community. It is based on the view that the astronomer Carl Sagan was denied election to the Academy of Science (USA) despite ample qualification because of his status as a media figure (Gwynne, 1997). Another well-known scientist, the palaeontologist, Stephen Jay Gould, is also thought to have had his scientific reputation suffer from the "Sagan Effect" (Shermer, 2002) as he was also a "Celebrity Scientist"

Table 3. Publications from Nonsuch sampling

Taxa	Reference	# cites	Taxa	Reference	# cites
Tintinnids	Wailes (1936)	1	Fish	Beebe (1929b)	4
Copepods	Wilson (1936)	5	Fish	Beebe (1933c)	6
Euphausiids	Tattersall (1936)	2	Fish	Beebe (1933a)	0
Siphonophores	Totton (1936)	8	Fish	Beebe (1933c)	6
Medusa	Bigelow (1938)	22	Fish	Beebe (1933d)	6
Shrimp	Chace (1940)	62	Fish	Beebe (1933e)	1
Polychaetes	Berleley (1936)	0	Fish	Beebe (1933f)	9
Polychaetes	Treadwell (1941)	23	Fish	Beebe (1933g)	2
Amphipods	Shoemaker (1945)	44	Fish	Beebe (1935a)	11
Ribbon Worms	Coe (1945)	4	Fish	Beebe (1935b)	4
Cephalopods	Pickford (1950)	5	Fish	Beebe and Crane (1936)	12
Fish	Beebe (1932a)	22	Fish	Beebe (1937)	25
Fish	Beebe (1932b)	0	Fish	Beebe and Crane (1937a)	2
Fish	Beebe (1933b)	0	Fish	Beebe and Crane (1937b)	9
Fish	Beebe and Vander Pyl (1944)	35	Fish	Beebe and Crane (1939)	27
Fish	Beebe and Tee-Van (1932)	3	Fish	Harry (1951)	13
Fish	Beebe (1929a)	2	Fish	Harry (1952)	6

Table 4. Deep-sea fish species descriptions attributed to Beebe

Original name	Accepted name	Expedition	Sampling depth	Reference
<i>Diabolidium arcturi</i> (Beebe, 1926)	<i>Linophryne arcturi</i> (Beebe, 1926)	Arcturus 1925	915	Beebe (1926d)
<i>Linophryne brevibarbata</i> (Beebe, 1932)	<i>Linophryne brevibarbata</i> (Beebe, 1932)	Bermuda 1929	1647	Beebe (1932a)
<i>Saccopharynx harrisoni</i> (Beebe, 1932)	<i>Saccopharynx harrisoni</i> (Beebe, 1932)	Bermuda 1931	1647	Beebe (1932a)
<i>Dolopichthys gladisfenae</i> (Beebe, 1932)	<i>Spiniphryne gladisfenae</i> (Beebe, 1932)	Bermuda 1930	1281	Beebe (1932a)
<i>Chaenophryne draco</i> (Beebe, 1932)	<i>Chaenophryne draco</i> (Beebe, 1932)	Bermuda 1931	1098	Beebe (1932a)
<i>Eustomias schiffi</i> (Beebe, 1932)	<i>Eustomias schiffi</i> (Beebe, 1932)	Bermuda 1930	1098	Beebe (1932a)
<i>Photichthys nonsuchae</i> (Beebe, 1932)	<i>Woodsia nonsuchae</i> (Beebe, 1932)	Bermuda 1929	1098	Beebe (1932a)
<i>Leptostomias bermudensis</i> (Beebe, 1932)	<i>Leptostomias bermudensis</i> (Beebe, 1932)	Bermuda 1931	915	Beebe (1932a)
<i>Dolichopteryx binocularis</i> (Beebe, 1932)	<i>Dolichopteroides binocularis</i> (Beebe, 1932)	Bermuda 1931	732	Beebe (1932a)
<i>Eustomias satterleei</i> (Beebe, 1933)	<i>Eustomias satterleei</i> (Beebe, 1933)	Bermuda 1929	1830	Beebe (1932a)
<i>Bathophilus altipinnis</i> (Beebe, 1933)	<i>Bathophilus altipinnis</i> (Beebe, 1933)	Bermuda 1929	1464	Beebe (1933c)
<i>Photostylus pycnopterus</i> (Beebe, 1933)	<i>Photostylus pycnopterus</i> (Beebe, 1933)	Bermuda 1929	1464	Beebe (1933c)
<i>Psammobatus spinosissimus</i> (Beebe and Tee-Van 1941)	<i>Bathyraxia spinosissima</i> (Beebe and Tee-Van 1941)	Arcturus 1925	1400	Beebe and Tee-Van (1941)
<i>Gigantactis perlatus</i> (Beebe and Crane, 1947)	<i>Gigantactis perlatus</i> (Beebe and Crane, 1947)	Zaca 1938	915	Beebe and Crane (1947)
<i>Himantolophus azurlucens</i> (Beebe and Crane, 1947)	<i>Himantolophus azurlucens</i> (Beebe and Crane, 1947)	Zaca 1938	915	Beebe and Crane (1947)
<i>Linophryne quinqueramosa</i> (Beebe and Crane, 1947)	<i>Linophryne quinqueramosa</i> (Beebe and Crane, 1947)	Zaca 1938	915	Beebe and Crane (1947)

(Fahy, 2015). The phenomenon may appear odd to us today. In recent years, with outreach efforts often mandated, any stigma associated with media attention is thought to be negligible with media attention actually linked to increases in citation rates (Russo, 2010).

As time goes on, any or all the effects considered above should diminish. Knowledge of the relative prestige of *Zoologica*, the unorthodox naming of 4 out of the over 80 fish species, and the amount of media coverage given Beebe, should all decline with time but perhaps not at the same rate. Do any measures of prestige show a temporal change indicating an abrupt shift at some point in time, for example in the late 1930s following the Bathysphere dives? Two metrics were examined simply because data were relatively accessible: the number of marine species named for Beebe from the WoRMS website (WoRMS Editorial Board (2020), searching for marine and freshwater species

containing the term ‘beebe’ and citations per year to Beebe publications using the Web of Science (www.webofknowledge.com, consulted 20 January 2020). Cumulative numbers of species named for Beebe with time and total citations to Beebe articles with time are shown in Figure 8.

Surprisingly, the point in time corresponding to changes in both temporal trends is in the mid-1960s is following Beebe’s death (in 1962) and the changes in the two measures show opposite trends. Following Beebe’s death, there is an abrupt halt to naming species for Beebe that begins again only in recent years, since 2013. With regard to citations to Beebe articles, there appears to be an increase in citation rates following his death. The opposing temporal trends are very difficult to explain. The paired negative inflections of species naming declining and increase in citation rate increasing may simply reflect a shift in academic activity away from taxonomy and towards an increasing

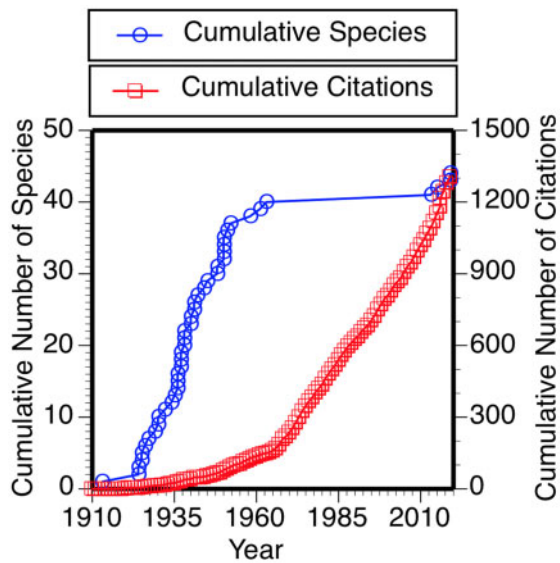


Figure 8. Cumulative number of species named for William Beebe and cumulative number of citations to Beebe's work with time.

importance of publishing. Regardless though, both metrics show no sign of a shift corresponding with the Bathysphere dives, a source of a great deal of media attention as well as the contentious fish descriptions. In conclusion, there lacks clear evidence of any particularly strong reason behind the apparent slighting of Beebe's deep-sea work by the scientific community.

Finally, there are two additional facts that may have contributed to a lack of recognition for Beebe's work by oceanographers. The first, following Anthony Adler (2019), is an adherence in the history of the marine sciences to what he terms the "great ship narrative" in which developments are linked to large-scale expeditions to the detriment of work done in laboratories and field stations (Adler, 2019). Nonsuch was the first, and remains the only, field laboratory devoted to deep-sea research. The second is the fact that, unlike most well-known scientific figures of the 20th century, Beebe did not train any students, nor did his close collaborators in his deep-sea work, John Tee-Van and Jocelyn Crane, as they all were employed by the New York Zoological Society. Following the Nonsuch laboratory days, John Tee-Van moved into administrative posts of the New York Zoological Society, eventually assuming the directorship (Gould, 2004) and Jocelyn Crane became a very well-known expert, not on deep-sea life, but on hermit crabs (Yost, 1959). One could say then that Beebe had no "academic children" for his deep-sea work, a factor perhaps contributing to a lack of recognition for his deep-sea work.

Conclusion

Here is shown that the contributions of William Beebe to our knowledge of the natural history of the deep-sea are considerable, ranging from the descriptions of many new forms to observations on developmental stages and basic ecologies of many species. The reason(s) behind the fact that his contributions appear to be largely neglected remains unclear. However, hopefully this attempt to shed light on Beebe's contributions will lead to their recognition.

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References

- Adler, A. 2019. *Neptune's Laboratory: Fantasy, Fear, and Science at Sea*. Harvard University Press, Cambridge, MA, USA. 241 pp.
- Anon. 1925. BEEBE AND ARCTURUS HOME WITH MARVELS; Floating Laboratory Brings in Myriad-Lighted Fish and Bejeweled Crabs. SARGASSO LEGEND A MYTH Explorers Found No Wrecked Ships Caught in Weeds—The Humboldt Current Gone. N.Y. Times, July 31, 1925, pp. 1 and 8.
- Anon. 1930a. Explorations of the deep sea. *Scientific Monthly*, 31: 192.
- Anon. 1930b. Deep sea investigations by submarine observation chamber. *Nature*, 126: 220.
- Anon. 1935a. Penetrating ocean depths. *Nature Supplement*, 586–587.
- Anon. 1935b. Half mile down. *Quarterly Review of Biology*, 10: 215.
- Ballard, R., and Hively, W. 2017. *The Eternal Darkness: A Personal History of Deep-Sea Exploration*. NJ Princeton University Press, Princeton, NJ, USA. 388 pp.
- Bay, J. C. 1948. Some vital books in Science: 1848-1947. *Science*, 107: 485–491.
- Beebe, W. 1895. The bird called 'Brown Creeper'. *Harper's Young People*, 16: 79.
- Beebe, W. 1924. *Galapagos, World's End*. G.P. Putnam's Sons, New York. 443 pp.
- Beebe, W. 1925a. Report of the director department of tropical research. New York Zoological Society Twenty-Ninth Annual Report, pp. 87–91.
- Beebe, W. 1925b. Studies of a tropical jungle: one quarter of a square mile of jungle at Kartabo, British Guiana. *Zoologica*, 6: 5–193.
- Beebe, W. 1926a. Note on the Humboldt current and Sargasso Sea. *Science*, 63: 91–92.
- Beebe, W. 1926b. The Arcturus Oceanographic Expedition. *Zoologica*, 8: 1–45.
- Beebe, W. 1926c. *The Arcturus Adventure*. G.P. Putnam's Sons, New York. 439 pp.
- Beebe, W. 1926d. A new ceratoid fish: preliminary description of a new genus and species. *Bulletin of the New York Zoological Society*, 29: 80.
- Beebe, W. 1929a. Deep sea fish of the Hudson Gorge. *Zoologica*, 12: 1–19.
- Beebe, W. 1929b. *Haplophryne hudsonius*: a new species; description and osteology. *Zoologica*, 12: 21–36.
- Beebe, W. 1931a. Bermuda Oceanographic expeditions 1929-1930. Introduction. *Zoologica*, 13: 1–14.
- Beebe, W. 1932a. Nineteen new species and four post-larval deep-sea fish. *Zoologica*, 13: 47–107.
- Beebe, W. 1932b. A new deep-sea fish. *Bulletin New York Zoological Society*, 35: 175–177.
- Beebe, W. 1932c. Exploration of the deep sea. *Science*, 76: 344–344.
- Beebe, W. 1933a. New data on the deep sea fish *Stylophthalmus* and *Idiacanthus*. *Science*, 78: 390–390.
- Beebe, W. 1933b. Deep-sea fishes of the Bermuda Oceanographic expeditions. Family *Idiacanthidae*. *Zoologica*, 16: 149–241.
- Beebe, W. 1933b. Preliminary account of deep sea dives in the bathysphere with special reference to one of 2200 feet. *Proceedings of*

- the National Academy of Sciences of the United States of America, 19: 178–188.
- Beebe, W. 1933c. Deep-sea stomiatod fishes. One new genus and eight new species. *Copeia*, 1933: 160–175.
- Beebe, W. 1933d. Deep-sea isopondylous fishes. Two new genera and four new species. *Zoologica*, 13: 159–167.
- Beebe, W. 1933e. Deep-sea fishes of the Bermuda Oceanographic expeditions. Introduction. *Zoologica*, 16: 5–11.
- Beebe, W. 1933f. Deep-sea fishes of the Bermuda Oceanographic expeditions. Family Alepocephalidae. *Zoologica*, 16: 15–93.
- Beebe, W. 1933g. Deep-sea fishes of the Bermuda Oceanographic expeditions. Family Argentinidae. *Zoologica*, 16: 97–147.
- Beebe, W. 1934. Half Mile Down. Harcourt, Brace and Co., New York. 344 pp.
- Beebe, W. 1935a. Deep-sea fishes of the Bermuda Oceanographic expeditions. Family Derichthyidae. *Zoologica*, 20: 1–23.
- Beebe, W. 1935b. Deep-sea fishes of the Bermuda Oceanographic expeditions. Family Nessorhamphidae. *Zoologica*, 20: 25–51.
- Beebe, W. 1936a. Plankton of the Bermuda oceanographic expedition & introduction. *Zoologica*, 24: 75–80.
- Beebe, W. 1936a. Bermuda Oceanographic expeditions 1929–1930. Individual nets and data, 1932–1935. *Zoologica*, 21: 69–73.
- Beebe, W. 1936b. Food of the Bermuda and West Indian tunas of the genera *Parathunnus* and *Neothunnus*. *Zoologica*, 21: 195–225.
- Beebe, W. 1937. Preliminary list of Bermuda deep-sea fish. *Zoologica*, 22: 197–208.
- Beebe, W., and Crane, J. 1936. Deep-sea fishes of the Bermuda Oceanographic expeditions. Family Serrivomeridae. Part 1. Genus *Serrivomer*. *Zoologica*, 20: 53–102.
- Beebe, W., and Crane, J. 1937a. Deep-sea fishes of the Bermuda Oceanographic expeditions. Family Serrivomeridae. Part II. Genus *Platuronides*. *Zoologica*, 22: 331–348.
- Beebe, W., and Crane, J. 1937b. Deep-sea fishes of the Bermuda Oceanographic expeditions. Family Nemichthyidae. *Zoologica*, 22: 349–383.
- Beebe, W., and Crane, J. 1939. Deep-sea fishes of the Bermuda Oceanographic expeditions. Family Melanostomiidae. *Zoologica* 24:65–238.
- Beebe, W., and Crane, J. 1947. Eastern Pacific expeditions of the New York Zoological Society. XXXVII. Deep-sea ceratoid fishes. *Zoologica*, 31: 151–182.
- Beebe, W., and Tee-Van, J. 1932. New Bermuda fish, including six new species and forty-three species hitherto unrecorded from Bermuda. *Zoologica*, 13: 109–120.
- Beebe, W., and Tee-Van, J. 1941. Eastern Pacific expeditions of the New York Zoological Society. XXV. Fishes from the tropical eastern Pacific. [From Cedros Island, Lower California, south to the Galápagos Islands and northern Peru.] Part 3. Rays, Mantas and Chimeras. *Zoologica*, 26: 245–280.
- Beebe, W., and Vander Pyl, M. 1944. Eastern Pacific expeditions of the New York Zoological Society. XXXIII. Pacific Myctophidae (fishes). *Zoologica*, 29: 59–95.
- Berra, T. M. 1977. William Beebe: An Annotated Bibliography. Archon Books, Hamden, CN, USA. 157 pp.
- Berleley, E. 1936. Plankton of the Bermuda Oceanographic expeditions. 111. Notes on Polychaeta. *Zoologica*, 21: 85–87.
- Bigelow, H. B. 1928. Scyphomedusae from the Arcturus Oceanographic expedition. *Zoologica*, 8: 495–524.
- Bigelow, H. B. 1931. Siphonophorae from the Arcturus Oceanographic expedition. *Zoologica*, 8: 525–592.
- Bigelow, H. B. 1938. Plankton of the Bermuda Oceanographic expeditions. VIII. Medusae taken during the years 1929 and 1930. *Zoologica*, 23: 99–189.
- Chace, F. A. 1940. Plankton of the Bermuda Oceanographic expeditions, IX: the bathypelagic caridean Crustacea. *Zoologica*, 25: 117–209.
- Chun, C. 1903. *Aus Den Tiefen Des Weltmeeres*. Verlag von Gustav Fischer, Jena, Germany. 592 pp.
- CMY. 1936. Half mile down. *Geographical Journal*, 87: 276–278.
- Coe, W. R. 1945. Plankton of the Bermuda Oceanographic expeditions; bathypelagic nemerteans of the Bermuda area and other parts of the North and South Atlantic Oceans, with evidence as to their means of dispersal. *Zoologica*, 30: 145–168.
- Cullen, K. 2006. *Marine Science: The People behind the Science*. Chelea House, New York. 174 pp.
- Darwin, C. 1859. *On the Origin of the Species*. Murray, London. 502 pp.
- Dolan, J. R. 2011. The legacy of the last cruise of the Carnegie: a lesson in the value of dusty old taxonomic monographs. *Journal of Plankton Research*, 33: 1317–1324.
- Duffus, R. I. 1926. “Arcturus”, Whither Away? Mr. Beebe Reports His Latest Adventure in Science. *N.Y. Times*, May 23 p BR1.
- Egerton, F. N. 2016. *History of Ecological Sciences, Part 58A: marine Ecology, mid-1920s to about 1990, Featuring Beebe, Bigelow, Ricketts*. *Bulletin of the Ecological Society of America*, 97: 372–402.
- Fahy, D. 2015. *The New Celebrity Scientists: Out of the Lab and into the Limelight*. Rowman & Littleman, Lanham, MD, USA. 285 pp.
- Fairbairn, D. J. 2013. *Odd Couples: Extraordinary Differences between the Sexes in the Animal Kingdom*. Princeton University Press, Princeton, NJ, USA. 300 pp.
- Fiedler, P. C., and Lavin, M. F. 2006. Introduction: a review of eastern tropical Pacific oceanography. *Progress in Oceanography*, 69: 94–100.
- Fisher, W. K. 1928. Sea stars from the Arcturus Oceanographic expedition. *Zoologica*, 8: 487–493.
- Gould, C. G. 2004. *The Remarkable Life of William Beebe, Explorer and Naturalist*. Island Press, Washington, DC. 447 pp.
- Gregory, W. K. 1928. Studies on the body-forms of fishes. *Zoologica*, 8: 325–421.
- Gwynne, P. 1997. Can you promote science without losing respect? *The Scientist*, 11: 1–3.
- Haeckel, E., 1891. Plankton-Studien. *Jenaische Zeitschrift für Naturwissenschaft*, 25: 232–336. (English translation: Report of the U.S. Commissioner of Fish and Fisheries for 1889 to 1891 (1893). pp. 565–641).
- Harry, R. R. 1951. Deep-sea fishes of the Bermuda Oceanographic expeditions. Family Paralepididae. *Zoologica*, 36: 17–35.
- Harry, R. R. 1952. Deep-sea fishes of the Bermuda Oceanographic expeditions. Families Cetomimidae and Rondelettiidae. *Zoologica*, 37: 55–72.
- Hedgpeth, J. W. 1974. One hundred years of Pacific oceanography. *In* *The Biology of the Oceanic Pacific*, pp 137–155. Ed. by C. B. Miller. Oregon State University Press, Corvallis, OR, USA.
- Hubbs, C. L. 1935. Half mile down. *Copeia*, 1935: 105.
- Hubbs, C. L., and Kampa, E. M. 1946. The early stages (egg, prolarva and juvenile) and the classification of the California flying fish. *Copeia*, 1946: 188–182.
- Hubbs, C. L., Mead, G. W., and Wilimovsky, N. J. 1953. The wide-spread, probably antitropical distribution and the relationship of the bathypelagic iniomous fish *Anotopterus pharao*. *Bulletin of the Scripps Institute of Oceanography*, 6: 173–198.
- Kim, D. Y., Countway, P. D., Jones, A. C., Schnetzer, A., Yamashita, W., Tung, C., and Caron, D. A. 2014. Monthly to interannual variability of microbial eukaryote assemblages at four depths in the eastern North Pacific. *The ISME Journal*, 8: 515–530.
- Kimor, B. 2002. Deep-sea plankton exploration in historical perspective. *In* *Oceanographic History: The Pacific and Beyond*, pp. 210–214. Ed. by K. R. Benson and P. Rehbock. University of Washington Press, Seattle, WA, USA.

- Kroll, G. 1970. *America's Ocean Wilderness: A Cultural History of Twentieth-Century Exploration*. University of Kansas, Lawrence, KS, USA. 249 pp.
- Levick, M. B. 1925. Old Myths Defy the Light of Science. *N.Y. Times*, August 30, p SM11.
- Matsen, B. 2005. *Descent: The Heroic Discovery of the Abyss*. Pantheon Books, New York. 286 pp.
- Marshall, N. B. 1979. *Developments in Deep-Sea Biology*. Blandford, Poole, Dorset. 566 pp.
- Mills, E. L. 1983. Problems of deep-sea biology: an historical perspective. *In The Sea V.8*, pp. 1–79. Ed. by G. T. Roxwe. John Wiley & Sons, San Francisco, CA, USA.
- Mills, E. L. 1989. *Biological Oceanography: An Early History*. Cornell University Press, Ithaca, NY, USA. 378 pp.
- Mendyk, R. W. 2014. The herpetological contributions of William Beebe: naturalist, explorer, and father of neotropical ecology. *Herpetological Review*, 45: 76–84.
- Morell, V. 2019. *Becoming a Marine Biologist*. Simon & Schuster, New York. 193 pp.
- Murray, J., and Hjort, J. 1912. *The Depths of the Ocean*. Macmillan and Co., London. 821 pp.
- Nichols, J. T. 1934a. Half mile down. *Natural History*, 35: 88–89.
- Nichols, J. T. 1934b. Life in the Bathysphere. *Saturday Review of Literature*, December 8 1934.
- Nigrelli, R. F. 1947. Spontaneous neoplasms in fishes. Fibro-carcinoma-like growth in the stomach of *Borophryne apogon* Regan, a deep-sea ceratoid fish. *Zoologica*, 31: 183–184.
- Pickford, G. E. 1950. The *Vampyromorpha* (Cephalopoda) of the Bermuda Oceanographic expeditions. *Zoologica*, 35: 87–95.
- Poulsen, B. 2016. *Global Marine Science and Carlsberg: The Golden Connections of Johannes Schmidt (1877-1933)*. Brill, Leiden. 524 pp.
- Quinn, W. H., Neal, V. T., and Antunez De Mayolo, S. E. 1987. El Nino occurrences over the past four and half centuries. *Journal of Geophysical Research*, 92: 14449–14461.
- Riedl, R. 1980. Marine ecology—a century of changes. *Marine Ecology*, 1: 3–46.
- Robson, G. C. 1948. The cephalopoda decapoda of the Arcturus Oceanographic expedition, 1925. *Zoologica*, 33: 115–132.
- Russo, G. 2010. Meet the press. *Nature*, 468: 465–467.
- Shermer, M. B. 2002. This view of science: Stephen Jay Gould as historian of science and scientific historian, popular scientist and scientific popularizer. *Social Studies of Science*, 32: 489–525.
- Shoemaker, C. R. 1945. The Amphipoda of the Bermuda Oceanographic expeditions, 1929–1931. *Zoologica*, 30: 185–266.
- Tattersall, W. M. 1936. Plankton of the Bermuda Oceanographic expeditions. V. Notes on Schizopoda. *Zoologica*, 21: 95–96.
- Tee-Van, J. 1926. The Arcturus: equipment and operation. *Zoologica*, 8: 47–106.
- Totton, A. K. 1936. Plankton of the Bermuda Oceanographic expeditions. VII. Siphonophora taken during the year 1931. *Zoologica*, 21: 231–240.
- Treadwell, A. L. 1928. Polychaetous annelids from the Arcturus Oceanographic expedition. *Zoologica*, 8: 449–485.
- Treadwell, A. L. 1941. Plankton of the Bermuda Oceanographic expeditions, X: polychaetous annelids from Bermuda plankton, with eight shore species, and four from Haiti. *Zoologica*, 26: 25–30.
- Trotter, E. S. 1926. Brotulid fishes from the Arcturus Oceanographic expedition. *Zoologica*, 8: 107–125.
- Vergin, K., Beszteri, B., Monier, A., Thrash, J. C., Temperton, B., Treusch, A. H., Kilper, F., *et al.* 2013. High-resolution SAR11 ecotype dynamics at the Bermuda Atlantic time-series study site by phylogenetic placement of pyrosequences. *ISME Journal*, 7: 1322–1332.
- Welker, R. H. 1975. *Natural Man: The Life of William Beebe*. Indiana University Press, Bloomington, IN, USA. 224 pp.
- Wales, G. H. 1936. Plankton of the Bermuda Oceanographic expeditions. II. Notes on protozoa. *Zoologica*, 21: 81–84.
- Wilson, C. B. 1936. Plankton of the Bermuda Oceanographic expeditions. IV. Notes on Copodea. *Zoologica*, 21: 89–93.
- Wooster, W. S. 1980. Early observations and investigation of El Nino: the event of 1925. *In Oceanography: The Past*, pp. 629–641. Ed. by M. Sears and D. Merriman III. Springer-Verlag, New York.
- WoRMS Editorial Board 2020. *World Register of Marine Species*. VLIZ. <http://www.marinespecies.org> (last accessed 24 February 2020).
- Wüst, G. T. 1964. The major deep-sea expeditions and research vessels 1873-1960, a contribution to the history of oceanography. *Progress in Oceanography*, 2: 1–52.
- Yost, E. 1959. *Women of Modern Science*. Dodd, Mead & Company, New York. 176 pp.

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