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Working at Water's Edge: Life Sciences at American Marine Laboratories, 1880-1930

Abstract

This dissertation traces the rise of marine-based life science in America between 1880 and 1930, and examines the malleable spaces and technologies that facilitated multifaceted approaches to marine investigation. I begin by establishing baseline spatial and technological requirements for scientific work at the shoreline during this period. In subsequent chapters, I analyze four episodes of highly disciplinary work performed in these spaces: taxonomy, embryology, physiology, and animal behavior. While historians have pointed to a balkanization of scientific disciplines during this period, including reliance on specialized technologies and spaces, this dissertation seeks to highlight the continuities of space and technique in marine science and sheds light on the impact of these commonalities on the development of a cohesive marine science over the remainder of the twentieth century.

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WORKING AT WATER'S EDGE: LIFE SCIENCES AT AMERICAN MARINE
STATIONS, 1880-1930

Samantha K. Muka

A DISSERTATION

In

History and Sociology of Science

Presented to the Faculties of the University of Pennsylvania

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Degree of Doctor of Philosophy

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Supervisor of Dissertation

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ABSTRACT

WORKING AT WATER'S EDGE: LIFE SCIENCES AT AMERICAN MARINE STATIONS, 1880-1930

Samantha Kay Muka

M. Susan Lindee

This dissertation examines the rise of America marine stations between 1880 and 1930, and examines the malleable spaces and technologies that facilitated multifaceted approaches in these *liquid laboratories*. I begin by establishing baseline spatial and technological requirements for scientific work at the shoreline during this period. In subsequent chapters, I analyze four episodes of highly disciplinary work performed in these spaces: taxonomic illustration, embryology and morphology, neurophysiology, and animal behavior. While historians have pointed to a *balkanization* of scientific disciplines during this period, including reliance on specialized technologies and spaces, this dissertation seeks to highlight the *continuities* of space and technique in marine science and sheds light on the impact of these commonalities on the development of a cohesive marine science over the remainder of the twentieth century.

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Introduction

“But what are the special attractions of marine life, that naturalists should so eagerly seek the seashore?” is a question sometimes asked. To this we may reply, that the ocean is the home of the lowest as well as the oldest forms of life, and it is in such forms that the mysteries of life can presumably be most nearly approached. Then there are abundance and variety, and certain important groups that do not occur in fresh water. To the luxuriance of the fauna and flora of the shore, is added that vagrant, pelagic life which is collected by ocean-currents, tides, and winds, and laid at one’s feet as freely as if all nature pleaded for investigation. Moreover, the study of marine life has long been inadequately provided for, its advantages not having been generally recognized until within the last fifteen or twenty years. The comparative newness of the field, its infinite richness, and its importance in determining the origin, history, and relationships of living forms, account for the intense interest recently awaked in marine laboratories.¹

In April 1889, *Science* magazine trumpeted the opening of the Marine Biological Laboratory (MBL) as an important step in the study of marine life. A short article detailing the opening ceremonies of the station outlined the potential of the MBL: it could eventually be the “ideal biological station” by combining consistent workspace with the ability to send men out to far-flung locations for special studies. In effect, it combined the best characteristics of permanent stations with those of itinerant research from boats and temporary stations. The MBL was not the first permanent marine station in the United States, but the opening ceremonies trumpeted the turn towards the use and study of the marine environment in American biology.

Beginning in the 1860s, governments, universities, and private natural history groups interested in surveying and studying marine resources established permanent marine stations throughout the world. Russia, France, Japan, England, Canada, Germany,

¹ *Science* 13: 324 (April 19, 1889) 303.

Italy, The Netherlands, Sweden, and America all established permanent station locations by the end of the nineteenth century. Built by a local scientific society in 1867, the marine laboratory of Arcachon on the Bay of Arcachon may be the oldest laboratory of this kind, but it was definitely not the last. Russia's privately funded Sevastopol Station, founded in 1871, was quickly followed by the Stazione Zoologica Anton Dohrn (1872) in Naples, Italy and the Station Biologique de Roscoff (1872) in Brittany, France. Others swiftly followed and new stations opened in Sweden (Kristiniberg, 1877), Japan (Misaki, 1887), Scotland (Gatty, 1896), England (Plymouth, 1888), America (Penikese Island, 1877 and USBF Woods Hole, 1888), Canada (New Brunswick, 1899) and the Netherlands (Helder, 1890) throughout the 1880s and 1890s. By the turn of the twentieth century most of these countries had established multiple stations.²

Universities, natural history associations, and the United States government all established permanent marine stations along each American coastline and into the Caribbean. Tufts University's Mount Desert Laboratory marked the Northernmost station on the East coast; permanent stations pushed south and east as New York University and Harvard founded a station in Bermuda, the New York Zoological Society settled into British Guiana, and Johns Hopkins established a station in Jamaica. On the Gulf Coast, the University of Texas maintained a station in Galveston, Texas. On the West Coast, laboratories stretched from the University of Minnesota's location in the Juan de Fuca Strait to the San Diego Marine Biological Association in San Diego,

² William Carmichael McIntosh, *The Gatty Marine Laboratory and the steps that led to its foundation in the University of St. Andrews* (Dundee: John Leng & Co. 1896); Jane M. Oppenheimer, "Some Historical Backgrounds for the Establishment of the Stazione Zoologica at Naples" in *Oceanography: The Past Mary Sears and Daniel Merrimen* (eds) (New York: Springer, 1980), 179-187.; V.N. Greze "Centennial of the Institute of the Southern Seas at Sevastopol" *Internationale Revue der Gesamten Hydrobiologie* 56:5 (1971): 811-818.; Charles Atwood Kofoid *The Biological Stations of Europe* (Washington, D.C.: Government Printing Office, 1910)

California. *Science*, the journal for the *American Association for the Advancement of Science*, ran articles announcing the establishment over 25 marine laboratories between 1880 and 1930.³ The United States experienced a swift growth in the number of marine stations between 1880 and 1910. This growth is linked to two separate catalysts: fisheries concerns and the growth of American biology.

In the 1870s, American biologists and fisheries experts became aware of the rapidly decreasing fish stocks in eastern fisheries. Spencer Fullerton Baird, the assistant secretary of the Smithsonian, was asked to investigate the claims by fishermen in both Massachusetts and Rhode Island that the use of certain types of nets was decreasing the fish stocks in these areas. Baird stated that

...the supply, which formally greatly exceeded the demand, now, to a certain extent at least, and in certain localities, has failed; and the impression has become prevalent that the fish themselves, are diminishing, and that in time some kinds, at least, will be almost or quite exterminated. This assertion is made with reference to several species that formerly constituted an important part of the food supply; and the blame has been alternately laid upon one or another of the causes to which this result is ascribed, the fact of the decrease being generally considered as established.⁴

Baird was given a limited amount of time and resources to investigate these claims; he spoke with local fishermen in both states to gauge stock depletion based on local knowledge and presented these findings to both states. Each state ruled differently (Rhode Island banning certain nets; Massachusetts seeing no evidence to do so), and the outcomes convinced Baird that more systematic investigation was required to make any conclusions. According to Baird, “this remarkable contradiction in the results of the two commissions showed the necessity of a special scientific investigation on this subject, to

³ Ralph W. Dexter “History of American Marine Biology and Marine Biology Institutions Introduction: Origins of American Marine Biology” *American Zoologist* 28:1 (1988): 3-6.

⁴ Spencer F. Baird *Report of the Condition of the Sea Fisheries of the South Coast of New England in 1871 and 1872* (Washington, D.C.: Government Printing Office, 1873), vii.

be prosecuted in the way of direct experimentation on the fishes themselves, their feeding and their breeding grounds.”⁵

The resources for expanding his investigations came on Feb. 9, 1871 when a joint resolution founded the United States Fish Commission. This resolution made Baird the Commissioner of Fishes and formally gave him the resources needed to explore fisheries issues. Baird performed research on fisheries in the Northeast from a house in Woods Hole, Massachusetts; he procured government funding to build a permanent marine station there in 1885.⁶ While Baird envisioned a wide network of USFC marine stations throughout the United States, after his death in 1887, only two more government-run marine stations were founded: Beaufort, North Carolina and Key West, Florida. However, the USFC and newly realized concerns about diminishing stocks energized marine research in the United States by training fisheries personnel and providing monetary support for further investigations.

The United States Fisheries Commission (renamed the US Bureau of Fisheries in 1902) employed thousands of fisheries investigators throughout the United States. The Commission had three divisions: The Division of Inquiry (sometimes referred to as the Division of Scientific Inquiry), the Division of Fisheries, and the Division of Fish-Culture. Each division employed a large amount of young men who gained experience working on boats, local and craft knowledge about catching, transporting, and culturing fishes, and laboratory techniques required to work with a wide range of marine organisms. The Division of Scientific Inquiry was based out of Woods Hole; each

⁵ Ibid.,viii.

⁶ Dean Allard, *Spencer Fullerton Baird and the U.S. Fish Commission* (New York: Arno Press, 1978); Dean C. Allard, "Spencer Baird and support for American marine science, 1871-1887." *Earth Sciences History* 19.1 (2000): 44-57.

summer, the laboratory invited students and professors from Northeastern universities to utilize laboratory space for their research in the hopes that any work on the coast would result in useful data on the marine environment in that region.⁷ The men working for the USFC eventually migrated from low level work to other duties. These early trainees became professional biologists, aquarists, or high level fisheries researchers. This first generation of fisheries trained men, including Charles Townsend (Director New York Aquarium), David Starr Jordan (President of Stanford and founder of the Hopkins Marine Station), and Caswell Grave (Director of the Beaufort Laboratory and Professor at Johns Hopkins), energized research on the marine environment and spread interest in fisheries research to their students and peers.

In addition to providing training the space that expanded marine science, the USBF also galvanized research by funding other marine stations and surveys throughout the United States. The fisheries budget was not inexhaustible and much of it was geared towards fish culture and stocking endeavors; to extend the study of the marine environment on a shoestring, the USBF fostered relationships with marine stations around the United States. For instance, the USBF did not have the budget to operate an independent marine station on the West Coast. Instead, they partially funded surveys and expeditions in collaboration with Stanford's Hopkins Marine Station (run by Jordan, a former Fisheries employee) and the San Diego Marine Biological Association Laboratory.⁸ They collaborated with the New York Zoological Society to help fund

⁷ Samantha Muka, "The Broad Mission of the Division of Scientific Inquiry" *The Bigger Picture: Exploring Archives and Smithsonian History* (Jan. 26, 2012) <http://siarchives.si.edu/blog/broad-mission-division-inquiry>; Henry O'Malley to Director of the Princeton Biological Laboratory, May 11, 1929 Folder "Woods Hole 1919-1931" Box 20 RU 22 Records of the US Fish and Wildlife Service National Archives: Bethesda, MD.

⁸ William Emerson Ritter to George M. Bowers Nov 7, 1902. Box 1 Folder Correspondence 1902 William Emerson Ritter Papers 1893-1944 Scripps Oceanographic Institution: La Jolla, CA.

William Beebe's *Arcturus* voyage; the USBF provided important equipment and two investigators (Mary Poland Fish and her husband, Charles J. Fish) in exchange for information about fish stocks in the Sargasso Sea.⁹ This injection of trained men and federal funding spurred a large range of research into the marine environment and helped to jumpstart the founding of marine stations at the turn of the twentieth century.

In addition to fisheries concerns, the growth of marine stations can also be linked to the growth of American experimental biology during this period. Laboratory based experimental biology, centered primarily in the German university system, migrated into American universities during this period. During this period, it was common for American biologists to travel to German institutions to take graduate degrees in science. Post-Darwin, German biologists moved to the seashore to examine and experiment upon invertebrates in an attempt to understand the evolution of organisms. As these men returned to the United States to teach, and European scholars immigrated to the United States, the laboratory-based biology practiced in Europe followed.¹⁰ Two epicenters of this new biology emerged: The Johns Hopkins University and Harvard University. Both of these universities became, not just epicenters of experimental biology, but petri dishes for the burgeoning interest in marine research.

At Hopkins, W.K. Brooks, who studied with several European-trained biologists at Harvard, focused his particular combination of morphology and physiology training on researching at marine laboratories. While at Harvard, Brooks trained with Alexander Agassiz while working at Penikese Island in Rhode Island. During his tenure at Hopkins,

⁹ Henry O'Malley to William Beebe Nov. 13, 1924. Folder "Woods Hole Plankton Studies 1925" Box 5 RU 22 Records of the Fish and Wildlife Service National Archives: Bethesda, MD.

¹⁰ Garland Allen, *Life Science in the Twentieth Century* (Cambridge, UK: Cambridge University Press, 1978); Jane Maienschein, "Shifting assumptions in American Biology: Embryology, 1890-1910," *Journal of the History of Biology* 14:1 (Spring, 1981): 89-113. Philip Pauly, *Controlling Life: Jacques Loeb & the Engineering Ideal in Biology* (Oxford: Oxford University Press, 1987).

he took students to the Chesapeake Bay, Woods Hole, Beaufort, North Carolina, and the Tortugas Laboratory to conduct research. Brooks trained E.G. Conklin, E.B. Wilson, and T.H. Morgan in the new experimental methods and highlighted the importance of marine research in this endeavor. In turn, these investigators became professors at universities throughout the United States and spread the new experimental method, and strengthened the link between this methodology and marine research.¹¹

E.L. Mark, who studied in Leipzig and experienced the German biological link with the seashore of the Marine Zoological Laboratory of the Austrian government at Trieste, trained a large group of professional biologists at Harvard from 1877 to 1921. Many of these experimental biologists shared Mark's interest in working with marine organisms.

¹¹ Jane Maienschein *Transforming Traditions in American Biology, 1880-1915*. (Baltimore: Johns Hopkins University Press, 1991); Edward Grant Conklin *William Keith Brooks, 1808-1908* (Washington, D.C.: National Academy of Sciences, 1913); Keith Benson *William Keith Brooks (1848-1908): A Case Study in Morphology and the Development of American Biology* (PhD Dissertation: Oregon State University, 1979).



Group of Dr. Mark's students taken in 1907.



- | | | | |
|--------------------|---------------------|-------------------|----------------------|
| 1. W. L. W. Field | 13. F. T. Lewis | 25. L. J. Cole | 37. F. E. Watson |
| 2. C. W. Hahn | 14. H. E. Walter | 26. W. L. Tower | 38. H. B. Ward |
| 3. F. N. Balch | 15. F. W. Carpenter | 27. T. Barbour | 39. T. G. Lee |
| 4. H. S. Davis | 16. P. E. Sargent | 28. W. B. Cannon | 40. J. Reighard |
| 5. M. Copeland | 17. R. H. Johnson | 29. M. A. Bigelow | 41. H. Osborn |
| 6. J. T. Nichols | 18. R. M. Yerkes | 30. H. P. Johnson | 42. E. L. Mark |
| 7. R. S. Breed | 19. H. MacCurdy | 31. C. R. Eastman | 43. M. Reitz |
| 8. S. R. Williams | 20. T. Kincaid | 32. R. P. Bigelow | 44. H. H. Field |
| 9. F. L. Walker | 21. I. A. Field | 33. R. T. Jackson | 45. G. H. Parker |
| 10. G. G. MacCurdy | 22. H. M. Kelly | 34. H. V. Neal | 46. W. McM Woodworth |
| 11. W. M. Barrows | 23. A. G. Mayer | 35. T. W. Vaughan | 47. C. H. Eigenmann |
| 12. S. O. Mast | 24. J. H. Gerould | 36. W. E. Castle | |

Key to Group Picture

Figure 2 A photo of some of E.L. Mark's many students. In Charles Davenport "Edward Laurens Marks" *Bios* (May, 1939): 76-77.

Many of his students would go on to become major figures in marine research throughout the twentieth century. Alfred Goldsborough Mayer was the first director of the Carnegie Institution of Washington's Tortugas laboratory and William Emerson Ritter was the first director of the San Diego Marine Biological Association's laboratory at San Diego (later renamed Scripps). In addition to directors of marine stations, many of his students chaired biology departments and sent many of their students to these institutions.¹² Both Harvard and Johns Hopkins strengthened the link between

¹² Charles B. Davenport "Edward Laurens Mark" *Bios* 10:2 (May,1939): 69-83.

experimental biological investigation and marine stations. As Harvard and Johns Hopkins trained biologists took positions in science departments throughout the United States, more and more universities sent researchers to marine stations, spreading marine science from the East Coast to the Midwest and Western United States through the movement of these individuals. In effect, the marine station provided an “institutional identity” for American biology during this period.¹³

While historians have placed these institutions at the center of the early twentieth century biological narrative, relatively little attention has been paid to examining the entire network of marine stations and the wide range of biological investigation these spaces facilitated. The majority of historical literature examines the founding of the Marine Biological Laboratory in Woods Hole, Massachusetts and its linkage with the Stazione Zoologica Anton Dohrn in Naples, Italy. These spaces greatly resembled each other in structure: both ran on a table system that garnered its running budget by renting space to researchers. Experimental research, and the laboratory environment, was the center of the station. While these two stations have a strong resemblance to each other, they are not particularly indicative of the entire network of either American stations or their function in the biological community. To understand the importance of these spaces, the focus should be widened to include as sites as possible.

Marine stations formed a large, integrated network of malleable spaces that facilitated both broad biological research and became the institutional basis for the nascent field of marine biology at the turn of the twentieth century. Researchers and

¹³Keith R. Benson “Summer Camp, Seaside Station, and Marine Laboratory: Marine biology and its institutional identity” *Historical Studies in the Physical and Biological Sciences* Vol. 32 no. 1 (2001): 11-18.

information flowed easily throughout the network because each station was placed in a carefully chosen location and was outfitted with basic technologies that could be modified to serve both observational and experimental research. In addition, these spaces were linked through a network of publications that facilitated information exchange and the growth of a baseline of knowledge about the ocean environment. Because of the malleability of these spaces and the flow of information throughout the network, I call these stations *liquid laboratories*.

Liquid laboratories served as an institutional base for American biology by allowing easy and consistent access to fresh and living organisms for observation and experimentation. These researchers were not necessarily interested in studying the marine environment, but instead utilized marine organisms to examine a host of biological questions. The “engineering ideal” in biology pushed researchers to find organisms that had enough natural plasticity to survive and thrive during experimental procedures.¹⁴ This ideal favored specimens that could go on “living, synthesizing proteins, moving, reproducing, and so on despite catastrophic interference in their constitution, environment, or form” in the laboratory.¹⁵ Many marine organisms satisfied this form of plasticity.

In addition to the importance to the wider biological community, these stations also served as the crucible of American marine science. Keith Benson has pointed out that marine biology as a professional group did not exist during this period and therefore it would be anachronistic to say that marine stations was part of this profession’s

¹⁴ Pauly, Philip J. *Controlling Life: Jacques Loeb & the Engineering Ideal in Biology* Oxford University Press: New York (1987).

¹⁵ Hannah Landecker, *Culturing Life: How cells became technology* (Boston: Harvard University Press, 2007), 10.

“institutional identity.” While it is true that the term ‘marine biology’ and the profession of ‘marine biologist’ were not in use during this period, the stations facilitated the growth of knowledge about the marine environment and jumpstarted research that would blossom into a full-fledged profession post-WWII. Biological surveying of the area surrounding was the largest ongoing project at marine stations; each year, stations amassed data on the local flora and fauna available in that area. In addition to surveys, specimen collection and observation of organisms in their natural environment was an important step in many experiments. These observations contributed to knowledge of the marine environment and the construction of major questions about that environment that would form the basis of marine biological investigations throughout the twentieth century.¹⁶

This dissertation attempts to develop a “big-picture” of these liquid laboratories at the turn of the twentieth century in order ascertain how these spaces became integral to both the larger American biology and burgeoning marine biological communities. In particular, I would like to know what were the basic components of these stations, what made these spaces so useful to biologists, and how were so many different disciplines able to utilize a single space for increasingly specialized research? Robert Kohler has called for historians to gather “basic empirical evidence” of laboratories throughout history in order to ascertain how these spaces function in the scientific process.¹⁷ In order to develop this “big picture” of marine stations, I have examined archival and printed information from a wide range of marine stations including teaching, fisheries, and

¹⁶ For information on the growth of marine biology and the definition of “marine biology” see Erik Ellis. “What is marine biology?: Defining a science in the United States in the mid 20th century.” *History and philosophy of the life sciences* 29, no. 4 (2006): 469-493.

¹⁷ Kohler, Robert E. “Lab History: Reflections” *Isis* 99:4 (December 2008): 762.

research oriented spaces. I have analyzed data from the archives of six stations and the recently digitized journals and annual reports of over 15 stations. In addition, I have mined major academic journals of the period for publications that resulted from work in these spaces. By taking the widest view possible, I hope to build a big-picture of the structure and function of the liquid laboratory during this period.

The Paradox of Place and Space

The study of marine stations has often focused on the laboratory space to the detriment of examining the full experience of researching in a marine environment. Much of the historiography has focused on the experiences of experimental biologists such as Jacques Loeb. Loeb did both embryological and animal behavior research at the Marine Biological Laboratory (MBL) in Woods Hole at the turn of the twentieth century. By the time he started researching at the MBL, he was already relatively established in his career. Loeb did not collect his own research subjects, but instead requested specific organisms from the collectors at the station. He worked on the most consistently available organisms, such as echinoderm eggs, for studies of artificial parthogenesis and embryology, effectively decoupling his research from the larger environment. Loeb's work at marine laboratories during this period is well known, but it is not representative of all research done at these stations. In extrapolating from Loeb's work to represent that of all researchers' at all marine stations, historians of science claim that these spaces are more laboratory than field and that they approach or actually embody "placelessness."¹⁸

¹⁸Jane Maienschein, *Transforming Traditions in American Biology, 1880-1915*. (New York: Johns Hopkins University Press, 1991).; Seymour S. Cohen, "Some Struggles of Jacques Loeb, Albert Mathews, and Ernest Just at the Marine Biological Laboratory" *Biological Bulletin* 168 (June 1985): 127-136.

Thomas Gieryn theorizes that one way that scientific knowledge goes from “place-saturated contingent claims” to “placeless transcendent truths” is through the development of truth spots.¹⁹ Truth spots can be constructed and achieved through a variety of means, from claiming nativity (Walden) to welcoming witnesses (Indore Institute of Plant Industry) or exchanging a sense of place for space (Lewis Thomas Laboratory). Place, according to Gieryn, contains unique histories and nicknames, architectural particulars and idiosyncrasies, whereas space is a featureless geometric volume that is indistinguishable from other spaces where scientific discovery may occur. The Indore Institute of Plant Industry became a truth spot by acting as a mimetic model, inviting witnesses (the public) to view the work, and as a holistic place that included a large number of workers including scientists and farmers so that research could be performed and enacted that same time. Place was important for the truth claims made at Indore. In the Lewis Thomas Laboratory, the creation of a truth spot was achieved through the erasure of place markers. By utilizing standardized equipment and model organisms that are available throughout the world during any season, modern genetics and biology laboratories make the jump from place to space by erasing contingencies of place in order to make universal claims.

Robert Kohler’s work on the lab-field border in biology states that early twentieth century biologists sought to infuse laboratory science with field experience in a bid to radically alter the traditional laboratory experience. In essence, they sought to infuse space with place by creating a permeable boundary between the lab and field. But, according to Kohler, this program failed at marine stations. While students often

¹⁹ Thomas Gieryn. “Three truth spots” *Journal of the History of Behavioral Sciences* 38:2 (Spring 2002): 113.

collected materials for courses in these locations, it was a low status job in which upper level researcher, (such as Loeb) did not partake (Kohler does point out that William Morton Wheeler and Thomas Harrison Montgomery did collect but they were exceptions to the rule). Without the need or desire to collect, senior researchers worked primarily at the bench, prompting Kohler to state that

Marine stations, despite their seaside location, were essentially extensions of campus labs, bound tightly by the web of teaching and supply to laboratory culture. In marine labs it was not the natural surroundings but cultural habits and customs that shaped practices most powerfully. Morphologists' desire for fresh material was a harbinger of the ideal of a new natural history, but it was just a small step across the laboratory threshold. Microscopic morphology was a laboratory practice where it was performed, and its cultural geography is visible in the siting and spatial customs of marine labs.²⁰

There are two problems with Kohler's allocation of marine stations into modern "placeless" laboratories merely relocated at the seaside: the author utilizes a sample size of only one marine station (Marine Biological Laboratory) and one biological discipline (Experimental Morphology).

The MBL is the most studied of the marine stations in the United States and is consistently utilized in history of science literature as a synecdoche for the entire network. It was founded in 1888 by a board of trustees to serve as a laboratory space for teaching and research. Located in Woods Hole in the same area as the United States Bureau of Fisheries marine station, the MBL was a private institution maintained by the table system (made popular by the Naples Zoological Station) and the fees charged for taking classes. While a variety of researchers could visit the MBL, it quickly grew to prominence as the place to study invertebrate zoology and experimental morphology and

²⁰ Robert E. Kohler. *Landscapes and Labscapes: Exploring the Lab-Field Border in Biology* (Chicago: University of Chicago Press, 2002), 44.

physiology (specifically experimental embryology). This reputation was largely due to many of the prominent figures that worked at the MBL, including Jacques Loeb and Frank Lillie. One of the most popular classes offered each summer was the invertebrate zoology course which concentrated on teaching physiology, morphology, and embryology with local invertebrates and was taught by a rotating cast of researchers.²¹

Many marine stations contained some elements of the MBL, but none contained all of them. The structure of the MBL resembles that of the Naples Zoological Station: it was run by a board of researchers and charged fees for the use of facilities. This model was popular in many of Europe's earliest marine stations but it was not as common in the United States. The Marine Biological Association of San Diego Station (renamed the Scripps Institution of Biological Research in 1912) and The Carnegie Institution of Washington's station in the Dry Tortugas were run by private boards, but they did not operate on the table system; instead, they offered space to any researchers that could afford to visit. The United States Bureau of Fisheries laboratories, which hosted a wide range of researchers, were run by the government and of course, university laboratories were overseen by those institutions. The MBL balanced private research with teaching. University laboratories had summer courses available (mostly to graduate students) but other private laboratories and the USBF stations did not offer courses. Finally, unlike the MBL which has become known for its focus on experimental morphology and physiology, other marine laboratories maintained an open-door policy that welcomed researchers from a wide array of disciplinary groups, ranging from botany to ornithology. Kohler's assertion that marine stations were basically laboratories located at the seashore,

²¹ W.D. Russell-Hunter. "An Evolutionary Century at Woods Hole: Instruction in Invertebrate Zoology" *Biological Bulletin* 168 (June, 1985): 88-98.

and hence that “the natural surroundings” were less important than laboratory culture, does not represent the entire marine network. The focus on a single station, and particularly the work of a single researcher, that emphasized experiment over observation obscures the vast number of disciplines and groups working at these stations and the importance of the whole station, and not just the laboratory environment, to their work. In fact, marine stations operated within a paradoxical tension: they strove to be both extremely localized (places) and also universal (spaces).

Specific location was extremely important to the identity of a marine station. Administrators sought locations that contained unique specimens and allowed researchers access to an underexplored stretch of coastline. Before stations were founded, surveys of the area had to show that there was both an abundance of a wide range of species. This assured researchers that there would be interesting and also consistently available specimens. In addition, the location had to offer a glimpse of a new portion of the ocean environment. The growing interest in understanding the marine environment meant that investigators wanted to collect data from as many stable locations as possible in order to develop a fuller understanding of the ocean. However, these stations also strove to be highly universal and to make their laboratory spaces as interchangeable as possible to facilitate the transfer of people, tools, and techniques throughout the network. They did this by providing malleable technologies and spaces that were the same regardless of location. This tension between the universal and local was meant to facilitate the widest range of research and the largest amount of data on the ocean environment possible.

Malleable technologies

Liquid laboratories provided basic spaces that could be manipulated by researchers interested in a wide range of disciplinary questions. All marine stations contained similar equipment, consisting of basic glassware, aquarium hookups for running water, collecting equipment, and baseline chemicals for preserving specimens and performing basic chemical experiments. Within the network, there was no specific station to visit if you were interested in performing experimentation with specialized equipment: marine scientists did not agglomerate based on technological availability. Manipulation of these resources required what sociologists of science have identified as “tinkering” and “gadget-scientists.”²² If their work required specialized technology, researchers either brought it with them- an expensive and onerous process- or they worked within local contingencies and converted available technologies into useful tools by “using what is at hand, making-do, using things for new purposes, patching things together, and so on.”²³ Working within these contingencies meant converting found objects and available spaces into the equipment that would serve the required purposes.

The marine station was able to serve as an institutional basis for both the American biological community and the growing marine science community because the basic technologies contained therein allowed diverse investigators to take advantage of the fresh and live marine organisms. When visiting the marine station, researchers encountered highly malleable technologies that allowed them to manipulate both the laboratory space and organisms for very specific studies. Of particular value was basic

²² For information on tinkering, see Karen Knorr-Cetina. *The Manufacture of Knowledge: An Essay on the Constructivist and Contextual Nature of Science*. (Oxford: Pergamon Press, 1981); For information on gadget-scientists at marine laboratories, see Frank Nutch “Gadgets, Gizmos, and Instruments: Science for the Tinkering” *Science, Technology, and Human Values* 21:2 (Spring 1996): 214-228.

²³ Clarke, Adele E. and Joan H. Fujimura (eds) *The Right Tools for the Job: At work in Twentieth-Century Life Sciences* Princeton, NJ: Princeton University Press (1992),11.

glassware. Marine stations provided basic glassware with which researchers could easily construct either balanced or circulating aquaria to meet their research needs.

The process of keeping aquatic forms alive for observation in basic glassware is extremely old, but the modern forms of aquaria, both balanced and circulating, were developed in the middle of the nineteenth century. The balanced aquarium, in which the interaction between flora and fauna creates a “balanced” environment oxygenated enough to sustain life without consistent water changes, was developed by Nathaniel Bagshaw Ward in 1841. Called the ‘aquavivarium’, the balanced aquarium took off in the mid 1850s when it was popularized by Philip Gosse. Gosse, a popularizer of natural history and especially the natural history of the English coastline, wrote several books detailing his naturalist collecting at the English shore and the use of the aquarium to observe and display his collections within his home. The marine collecting craze raced through England and the link between marine collecting and the balanced aquarium was born.²⁴

The circulating aquarium was equally important to marine stations. The origin of the circulating aquarium is harder to pin down than that of its balanced counterpart. Marine organisms require a constant supply of oxygen. In nature, water is oxygenated by diffusion at the surface, through the release of oxygen as a plant bi-product (such as is the case in the balanced aquarium) or by aeration and movement of the water over rocks. If the aquarium contained a small amount of life, it was possible that the surface of the water could be consistently aerated through diffusion, but if one desired to keep several organisms in a laboratory aquarium, an alternate system of aeration was required. To restore oxygen saturation to deoxygenated water,

²⁴ David Allen “Tastes and Crazes” in *Cultures of Natural History* N. Jardine, J.A. Secord, and E.A. Spary (eds). Cambridge: Cambridge University Press (1996), 394-407.

various plans for aeration were employed by aquarium-keepers. Ingenious pumps were attached to the tanks, by means of which streams of air were forced through the water. Some persons employed syringes filled them with water and squirted the water into the tank with such force as to carry a quantity of air among the inhabitants of the aquarium. Others were content with taking up some of the water and letting it fall back with a splash, so as to produce the same result.²⁵

Manually aerating or pumping compressed air into the tank were effective but inefficient. Hand aeration is labor intensive and requires constant attention to the tank; using compressed air can often over-aerate the water, causing injury or death to the inhabitants. In addition, this form of aeration still required that the tank be consistently emptied and cleaned and that the water be refreshed due to a buildup of impurities from natural waste.

To solve the problem of water aeration, interested parties developed an aquarium that maintained a constant flow of oxygenated water into the aquarium by removing or recycling deoxygenated water. The simplest system required hooking up the aquarium to a source of constantly running water. Tubing brought fresh water into the tank and removed used water; the water level and temperature remained constant by the input/output system and the water remained clean due to constant replacement. However, this system required a constant supply of running water which smaller laboratories and personal homes might lack. On September 24, 1895 G.P. A. Gunther was granted a patent for his “Fish-Tank or Aquarium” with a built in filter that recycled water by cleaning and oxygenating it. This system alleviated the need for a constant flow of water. Gunther felt

²⁵ Rev. J.G. Woods *The Salt and Fresh Water Aquarium* (London: George Routledge and Sons, 1880), 7.

his tank could best serve those keeping home aquaria or for keeping fish that required a constant flow of water in their native habitats (such as trout or salmon).²⁶

You could purchase a filter tank from pet stores, but researchers at marine stations often tinkered with found materials to modify simple glassware into filtered systems similar to Gunther's.²⁷ Louis Murbach, working on the neurophysiology of medusa at Woods Hole, published his method for building "an automatic aerating device for aquaria" in *The American Naturalist* in 1907. Murbach modified a tank with "a glass filter pump, two wide-mouth bottles, about 8 X 15 cm., and 6 X 12 cm., a cork stopper to fit the larger bottle, a stand with balance beam, glass and rubber tubing."²⁸ Utilizing basic glassware components, researchers could construct either a balanced or circulating aquarium upon their arrival at marine stations. The malleability of basic technologies and spaces meant that marine stations could house a range of researchers with diverse scientific goals.

Aquariums enabled a wide range of research at marine stations. Changes in the basic structure allowed investigators from a wide range of disciplines to utilize these readily available systems for highly specialized research. Dimensional shifts changed a roomy tank into a specialized holding pen for specific specimens. For easier illustration and observation, glass partitions were inserted into larger aquaria to shrink spaces. Their light weight made them highly portable. Investigators easily changed locations while maintaining a living organism in a semi-permanent environment to examine multiple variables on a single system. The aquarium's simplicity became a building block for

²⁶ G.P.A. Gunther 1895. Fish Tank or Aquarium. US patent number 546,883. Filed Feb. 11, 1895 and issued Sept. 24, 1895.

²⁷ For information on hobbyist and home aquarium equipment see Katherine C. Grier *Pets in America: A History* (New York: Harvest Books, 2007), Chapter 6 "Buying for your Friend"

²⁸ Louis Murbach, "An Automatic Aerating Device for Aquaria" *The American Naturalist* 41:482 (Feb. 1907): 62-63.

more complex systems. Investigators found it easy to add pumps, screens, and lighting technologies onto the basic glass structure. These systems could be assembled from found objects and, after the need for the system had passed, easily disassembled to provide basic building blocks for the next researcher, regardless of their disciplinary interests.

These simplistic systems helped researchers overcome the “milieu threshold” that separated investigators from their aquatic subjects.²⁹ Researchers could not access aquatic subjects in their natural milieu- manned submersibles with visualization capabilities were in their infancy and the earliest diving costumes were cumbersome and significantly limited the diver’s range of motion. In order to work with live organisms, they constructed an artificial environment in which to keep their subjects; during this construction they gained valuable feedback about the conditions the organisms needed to survive both in captivity and by extension, their natural environments. This feedback loop contributed to the rise of ecological thinking in the biological sciences and lead to the use of these spaces as mimetic model systems.³⁰

Researchers developed an understanding of the marine environment, and the natural milieu of their subjects, through their attempts to keep subjects alive in captivity. The ability to maintain living marine organisms in captivity required what James Atz, the

²⁹ Christina Wessely. (Trans. Silke Feltz) “Wässrige Milieus. Ökologische perspektiven in Meeresbiologie und Aquarienkunde um 1900.” *Berlin Wissenschaftsgeschichte* 36 (2013): 133.

³⁰ For information on the role of the aquarium on ecological thinking, see Lynn Nyhart *Modern Nature: The Rise of the Biological Perspective in Germany* (The University of Chicago Press: Chicago, 2009); For information on mimetic models and modeling in oceanographic science, see Naomi Oreskes, “From Scaling to Simulation: Changing meanings and ambitions of models in geology.” in *Science without Laws: Model Systems, Cases, and Exemplary Narratives* Angela N.H. Creager, Elizabeth Lunbeck and M. Norton Wise (eds) Duke University Press: Duke, N.C. (2007), 93-124. Christine Keiner, “Modeling Neptune’s Garden: The Chesapeake Bay Hydraulic Model, 1965-1984.” *The Machine in Neptune’s Garden: Historical Perspectives on Technology and the Marine Environment* Rozwadowski, Helen M. and David K. van Keuren (eds) Science History Publications: Sagamore Beach, MA (2004), 273-314.

former director of the New York Aquarium, referred to as ‘a wet thumb.’ According to Atz, the ability to keep aquatic organisms alive in captivity for extended periods required craft knowledge that “the vast majority of experimentalists and their technicians simply do not possess.”³¹ Admittedly, most researchers lacked the ability to keep a large variety of organisms in captivity, but they did cultivate a ‘wet thumb’ when working with their specific research subjects. Investigators combined extensive field research with laboratory experimentation to ascertain the exact variables that needed to be present in their experimental systems. Successfully maintaining animals in captivity not only developed their ‘wet thumb,’ but also advanced researchers’ understanding of the life cycle and natural history of their organisms in their native milieu.

Information Sharing: Publication

Marine stations shared information on their particular place, and the work that was being performed there, by distributing research in specialized journals. Anton Dohrn, the founder of the Naples Zoological Station, considered publication integral to the mission of his institution. Dohrn established three separate publishing venues for workers at the station: *The Fauna and Flora of the Gulf of Naples and Bordering Sea Regions*, *Messages etc.*, and the *Zoological Annual Report*. The first two publications focused specifically upon work at the NZS, but Dohrn stated that the content would “not stand by itself without being embedded in connections as it is often the case amongst publications of academies and other research groups. Instead, the content of our publications will always be connected to zoological, botanical, hydrographic and geological relationships...” Finished, illustrated monographs would be published intermittently as

³¹ James W. Atz, “Some Principles and Practices of Water Management for Marine Aquariums” in *Sea Water Systems for Experimental Aquariums* John R. Clark and Roberta L. Clark (eds) Research Report 63 (Washington D.C.: Bureau of Sports Fisheries and Wildlife, 1964), 3.

Fauna and Flora, notes, smaller articles, and station business were published in *Messages*, and the *Zoological Annual Report* would serve as a reference source for researchers to keep up-to-date on the entire field.³² Following in Dohrn's footsteps, American stations recognized the importance of publishing and distributing their results throughout the network.

W.K. Brooks believed that there were "too few scientific journals to facilitate publication and exchange of scientific information." To alleviate this problem, Brooks published the findings of the students and researchers at Hopkins' marine stations in a series of journals published through the University.³³ The USBF reserved the right to publish materials from its researchers in their *Bulletin* first. Other stations followed suit, publishing research anywhere on the spectrum of polished manuscripts to field notes and year end reports.³⁴ Most of these publications served a dual purpose of keeping investors, governing boards, and University presidents apprised of research in these spaces and as a way to circulate information throughout the network.

Libraries were important spaces in marine stations; even the remotest laboratories with rustic living conditions (such as the Carnegie Laboratory in the Dry Tortugas) kept a library for research and marine laboratory journals. These publications made up much of the library resources at these locations.³⁵ By reading these sources, a researcher could

³² Anton Dohrn, "Vorwort" *Mitteilungen aus der Zoologischen Station zu Neapel* (Translated by Silke Feltz) (Leipzig: Wilhelm Engelmann, 1879), iii.

³³ Benson. *William Keith Brooks (1848-1908): a case study of morphology and the development of American Biology* (PhD dissertation Oregon State University-1979)

³⁴ W.D. Russell-Hunter, "From Woods Hole to the World: *The Biological Bulletin*" *Biological Bulletin* 168 (June, 1985): 200-202.

³⁵ The Scripps Institution of Oceanography Library (closed on June 29, 2012 during the writing of this dissertation) contained one of the largest selections of marine station journals and annual reports, including those of the Carnegie Institution of Washington, The Hopkins Marine Station, Mount Desert, Johns Hopkins, University of Washington, Bermuda, the United States Bureau of Fisheries, and full publications from complete runs of many Canadian, English, Japanese, and French marine stations as well. For a full finding aid, see <http://libraries.ucsd.edu/locations/sio/> (accessed 3.11.2014). The combined MBLWHOI

ascertain what organisms were available throughout the network, what scientific questions were being explored in these locations, new techniques for maintaining captive organisms, and new methods for modifying the basic technologies that were found throughout the network. While circulation outside of the marine station community proved low for these publications, each station sought to include as many publications from throughout the network as possible in order to facilitate exchange of information.

An American Story

This dissertation focuses on American stations between 1880 and 1930. But does my focus on American stations make this an American story? The paradoxical tension between space and place in these institutions means that the network of marine laboratories founded by Americans can be considered as both inherently American but also distinctly universal.

American marine stations contained similar technologies to their European counterparts. The reliance on malleable technologies appears to be similar, as does the exchange of individuals with a wide range of research agendas throughout this network. In fact, Americans continued to visit European stations long after the establishment of American laboratories. Naples, Roscoff in France, and Plymouth Laboratory in England were extremely popular with Americans interested expanding their research in new locations with new specimens. Traveling to Naples continued to be an important pilgrimage for American biologists into the middle of the 19th century. Those Americans that traveled to these European locations could be assured that these stations contained

Library catalog also contains nearly every marine station publication. <http://www.mblwhoilibrary.org/> (accessed 3.11.2014) The inventory at the Tortugas station shows copies of USBF Bulletins, as well as journals from the Bermuda station. Folder Tortugas, Lab, Building, Quarters, and Grounds L7/15 Carnegie Institutional of Washington Archives: Washington, D.C.

similar technologies and laboratory structures to those in America. In this sense, the marine station bauplan was similar throughout the world during this period.

However, American marine stations were a particular combination of fisheries, aquarist, and academic concerns during this period. While many Americans did visit European stations, far fewer Europeans visited American stations. Instead, these spaces became social and cultural meeting places for American researchers. They allowed these investigators to connect and exchange information and ideas, directly linking researchers throughout the United States into a principally American system. Life science research was performed at marine stations throughout the world, but life sciences performed at these marine stations resulted in a particular form of knowledge that shed light, not only on general biology, but on the American marine environment. While each individual station functioned as an independent unit, the network connected primarily American researchers and produced a large amount of information about America's water resources. In addition, much of the research was at least partially funded or performed in connection with the US Bureau of Fisheries.

Although the funding and knowledge produced both indicate a national story, more work needs to be done on marine stations worldwide to truly understand the uniqueness of the American network. The intense exploration of the Naples-MBL link did not just eclipse the larger American narrative, but also research on European, Asian, Russian, and other North American stations. Ongoing research into marine networks in France, the Netherlands, and England will eventually allow a more robust comparison with American stations.

This dissertation traces the importance of these liquid laboratories in the development of four strains of American life sciences: taxonomy, embryology and morphology, neurophysiology, and animal behavior. **Chapter 1** examines the basic components of marine stations that allowed them to function as liquid laboratories. I outline the process of choosing a location and the basic technologies that existed in these locations. The chapter examines the foundation of marine stations from both an environmental and a technological perspective, focusing on the fundamental pieces of these establishments and drawing out the similarities that bound these institutions together into a cohesive network. **Chapter 2** explores the importance of the field work experience on the work performed in these spaces. Marine illustrators were an integral part of early marine science; field work was an important aspect of the development of their craft. Experiencing the marine environment, and viewing organisms close to their original habitat, greatly influenced their understandings of their subjects and the final images they produced. **Chapter 3** looks at the use of the marine station as a space for exploration of embryology and morphology at the turn of the twentieth century. While much has been written on the history of embryology at the MBL, most of the research has highlighted experimental work in the laboratory. This chapter examines how embryological research was tethered to the changeable marine environment, forcing researchers to develop intimate knowledge of their organisms, change their research habits, and develop new laboratory techniques in order to successfully take advantage of working with fresh specimens at the seashore. **Chapter 4** traces the rise of the use of jellyfish as model organisms in neurophysiology research at marine laboratories. At the turn of the twentieth century, jellyfish were found to contain a rudimentary nervous system that

resembled those in higher mammals. Researchers at marine laboratories sought to utilize these extremely delicate organisms in neurophysiological studies. Through tinkering with basic glassware, studying and mimicking the natural history of the organism, and finally pinpointing specific species with extreme plasticity in the laboratory environment, neurophysiologists succeeded in utilizing these organisms and placing marine station research at the center of their field during this period. **Chapter 5** highlights the malleability of marine stations, and the technologies contained therein, by revisiting the Loeb-Jennings debate on phototropism. Both Loeb and Jennings utilized marine organisms to defend their position on phototropism but each chose a different experimental set up with different organisms to test their theories. By examining the differences in these experimental set ups- we can see that the laboratory environment was so malleable that researchers interested in the same question chose different organisms and tools in their pursuit of knowledge.

Taken together, these chapters offer a vision of the broad range of the research, and researchers, at American marine stations at the turn of the twentieth century. This dissertation will show how the most basic technologies and spaces facilitated a wide range of highly disciplinary research and explain how these liquid laboratories became the epicenter of a new wave of American biology and the birthplace of American marine biology.

Chapter 1

A network of liquid laboratories: building an institutional identity for American biology and marine science

On April 24, 1908 Alfred Goldsborough Mayer called for a change in the way that scientific marine exploration was being conducted. In a *Science* article, Mayer, considered one of the earliest marine biologists in America, stated that science was no longer being served by the mass collecting of meteorological, tide, and sea depth data or by the millions of preserved specimens that were brought back by previous marine expeditions, such as the *HMS Challenger* and the *USFC Albatross*. Less than a year into the *Albatross*' longest voyage in the Pacific, Mayer stated that marine science had progressed to a point where more work needed to be performed on shore than on ship. The collecting of marine specimens should be combined with biological work at temporary research stations set up in locations on the expedition route. According to Mayer, "The marine expeditions of the future should...aim to establish well-equipped but temporary shore stations at salient points, landing investigators here and there and leaving them with servants, food, lodging, apparatus and naphtha launches to avail themselves of all the varied advantages afforded by a land laboratory."³⁶ Only by combining the collection of specimens and the investigation of these forms in a laboratory could scientists learn anything useful about the nature of these creatures and their interaction with their environment.

Mayer's call came at a time when institutions throughout the United States were establishing both temporary and permanent marine stations. Beginning in 1873 with

³⁶ Alfred Goldsborough Mayer, "A Plan for Increasing the Efficiency of Marine Expeditions" Vol. 27 No. 695 (Apr. 24, 1908): 669-671.

Louis Agassiz's Penikese Island laboratory, the United States saw a rapid increase in the number of marine stations. *Science*, the journal for the *American Association for the Advancement of Science*, ran articles announcing over 25 marine laboratories between 1880 and 1930. While not all of these laboratories were permanent, many continue to operate today, including Tufts' Mt. Desert Marine Laboratory, the Marine Biological Laboratory, the United States Bureau of Fisheries laboratories at Woods Hole, MA and Beaufort, N.C., The Marine Biological Station at San Diego, Harvard and New York University's Bermuda Biological Station, Hopkins Marine Laboratory of Stanford, and Cold Spring Harbor Laboratory. Today, all 21 coastal states host at least one marine station.³⁷

A large body of historical literature traces marine stations' ideological and historical growth. The bulk of the work looks at the history of the Marine Biological Laboratory and several others in the Northeast founded at the end of the 19th century, and focuses on the first 15 years of their existence.³⁸ But little historical work analyses these

³⁷ Ralph W. Dexter, "History of American Marine Biology and Marine Biology Institutions Introduction: Origins of American Marine Biology" *American Zoologist* Vol. 28 No. 1 (1988): 3-6.

³⁸ Ronald Rainger, Keith Benson, and Jane Maienschein, eds. *The American Development of Biology* (Philadelphia: The University of Pennsylvania Press, 1988); Jane Maienschein, "Agassiz, Hyatt, Whitman, and the Birth of the Marine Biological Laboratory" (Jun., 1985): 26-34; Jane Maienschein, "History of American Marine Laboratories: Why Do Research at the Seashore?" *American Zoologist* 28:1 (1988) 15-25; Jane Maienschein, *100 Years exploring life, 1888-1988* (Boston: Jones & Bartlett Publishing, 1989); Keith R. Benson, "Review paper: The Naples Stazione Zoologica and its impact on the emergence of American marine biology," *Journal of the history of biology* 21 (1988): 331-341.; Philip Pauly, "Summer resort and scientific discipline," in Rainger et al. *The American Development of Biology*, 121-150; Keith R. Benson, "Why marine stations? The teaching argument," *American zoologist*, 28 (1988): 7-14; Keith Benson, "Laboratories on the New England shore: The 'somewhat different direction' of American marine biology," *New England quarterly*, 56 (1988): 53-78; Ralph Dexter, "The Annisquam Seaside Laboratory of Alpheus Hyatt," *Science monthly*, 74 (1952): 112-116 and "The Summer School of Biology at the Peabody Academy of Science, 1876-1888," *AIBS bulletin*, 7 (1957), 21-23.; Keith Benson. "Laboratories of the New England Shore: The 'Somewhat Different Direction' of American Marine Biology" *The New England Quarterly* (1988) 55; Devlin, C. Leah and P.J. Capelotti, "Proximity to Seacoast: G.W. and the Marine Laboratory at Point Judith Pond, Rhode Island, 1896-1900" *Journal of the History of Biology* (1996):251-265; Dean C. Allard, "The Fish Commission Laboratory and Its Influence on the Founding of the Marine Biological Laboratory" *Journal of the History of Biology* 23:2 (1990)251-270; Paul S. Galtsoff *The Story of the Bureau of Commercial Fisheries Biological Laboratory* Circular 145 (Washington, D.C.: Department

institutions as a coherent group representing a specific type of scientific space. Histories of private laboratories such as the Marine Biological Laboratory are often separated from those of federal fisheries laboratories at Woods Hole and Beaufort and University based institutions such as Stanford's Hopkins Marine Station or the University of Washington's Friday Harbor Laboratories. Keith Benson has called for a reexamination of marine laboratories to include the larger community of Western and Southern United States and to trace the "institutional identity of American biology" through the extensive network of marine laboratories.³⁹

At first glance, this large number of marine laboratories seems to have little in common. Public and private universities, federal institutions and private organizations all founded stations. Some laboratories focused on teaching, while others focused on individual research. Marine laboratories covered a large stretch of American coastline; locations varied greatly. But this image of dissimilarity is misleading.

Early 20th century marine laboratories shared many commonalities, including shared ideas regarding suitable locations for marine work, similar baseline technological requirements, and common practices for maintaining a working station that appealed to scientists from multiple disciplines who wished to explore both basic biological questions and specific marine concerns. Most importantly, they shared a common baseline objective: to provide an environment close enough to the seashore for investigators to have access to an abundance of fresh and marine organisms. These spaces became lodestones for investigators with differing interests, but a common need to work with

of the Interior, 1962); Douglas A Wolfe *A History of the Federal Laboratory at Beaufort, North Carolina 1899-1999* (Washington, D.C.: U.S. National Oceanic and Atmospheric Administration, 2000).

³⁹ Keith R. Benson, "Summer Camp, Seaside Station, and Marine Laboratory: Marine Biology and Its Institutional Identity" *Historical Studies in the Physical and Biological Sciences* 32:1 (2001): 11-18.

living marine organisms, establishing an institutional identity for both mainstream and marine biology in America.

This chapter focuses on the commonalities that linked marine stations into a larger network at the turn of the twentieth century. Researchers established stations in ecologically and geographically significant locations that they felt offered a glimpse into the larger examination of the ocean environment. Each station was highly localized. However, each station also contained basic technologies and spaces that allowed them to function within the wider network. This chapter will explore the tension between the localized and universal aspects of these spaces. By examining these aspects, we can see how these stations became nodes within a larger marine science network. The differences in locations facilitated a large body of knowledge about the marine environment; the similarities of each location facilitated the easy movement of researchers, technologies, and ideas throughout the larger network.

Location

The process of choosing a location for permanent marine stations often stretched over many years and multiple locations. The proposed location for the Carnegie Institute of Washington marine laboratory was debated in print and private correspondence for a year (1902-1903), before the Dry Tortugas was chosen (if not agreed upon) as the optimal location. Johns Hopkins University marine laboratory site was especially peripatetic, operating in the lower Chesapeake Bay area for two seasons (1878-1879), moving to the Beaufort, North Carolina region for seven seasons (1880-1885), and then

intermittently shifting to the Bahamas (first in 1890) and different ports in Jamaica (the first in 1891), all the while maintaining a large presence at the USBF Beaufort station.⁴⁰

Historians of science have questioned the importance of the marine station location, suggesting that they were merely seaside versions of urban laboratories and not necessarily “place-based.”⁴¹ In fact, laboratories were founded in locations that met exacting standards. Throughout the process of deciding on a permanent location, administrators and investigators were searching for locations meeting specific criteria. Identifying a location for a permanent or semi-permanent station was a protracted process of balancing specimen availability with favorable weather patterns, proximity of shipping and train lines, and even projected growth of a given area. This section will explore the variables that were weighed when choosing a location.

Marine stations were established on nearly every coast of the American continent, but certain areas of coastline have attracted a larger contingent of investigators (specifically near the Vancouver Islands, Cape Cod, Massachusetts and Beaufort, North Carolina). By examining the reasons for the establishment of laboratories in given locations, and the myriad of reasons why one might abandon a location in which an institution was financially and emotionally invested, we can start to build a better

⁴⁰ See H.V. Wilson, “Marine Biology at Beaufort” *The American Naturalist* 34: 401 (May, 1900): 357. W.K. Brooks, “Johns Hopkins Marine Laboratory” *Science* 19: 465 (Jan. 1, 1892): 10-11.; The Johns Hopkins presence at the USBF laboratory at Beaufort was pronounced, and records show that Brooks tried to fund the laboratory at Beaufort by sending a check for the use of the laboratory to the USBF (although this funding was refused and returned). See Hugh Smith to the Treasurer of Johns Hopkins University, 1902 RU 22 Correspondence Concerning Fisheries Expeditions, etc. 1885-1908 Box No. 1 Folder: Smith Papers “Beaufort Laboratory 1899-1904” RU 22 Records of the US Fish and Wildlife Service. National Archives, Bethesda: MD.

⁴¹ Jeremy Vetter. “Labs in the Field? Rocky Mountain Biological Stations in the Early Twentieth Century.” *Journal of the History of Biology* 45: 4 (2012): 587-611. Not all historians have deemphasized the importance of place in marine laboratory literature. See Keith R. Benson “Summer Camp,” 11-18.

understanding of the strong similarities evinced by seemingly different marine locations at the turn of the twentieth century.

Geography

In the simplest terms, choosing a site can be boiled down to the usual adage about buying real estate: location, location, location. Institutions took several variables into account when choosing sites for their laboratories including water access, natural geographic formations, weather patterns, and proximity to established towns and shipping lines. The importance of the actual land location for a marine station cannot be overstated. To say that a marine station needs to be placed next to a shoreline is a statement that merely scratches the surface of the geographic formations desired by researchers visiting these places.

Water availability was the first major concern. Researchers required both salt and fresh water, and most scientific investigation depended on the purity of available water. These two variables could be complicated by weather, nearby communities, and seasonal differences, but directors and researchers sought locations for permanent stations that could provide them with pure water sources.

Investigators required large amounts of both salt and fresh water. When administrators advertised a newly opened station, or extolled the virtues of a long established laboratory to possible investigators, one of the first aspects mentioned was the ability to provide a constant flow of both fresh and salt water directly into the laboratory aquariums. More commonly, administrators emphasized that they could provide both fresh and salt water to table top aquariums, suggesting that animals could be maintained in aquaria for as long as the investigator desired. When the private Brooklyn Institute

Biological Laboratory (which would eventually merge with the Carnegie Institute and the Eugenics Records office) opened a marine laboratory in 1892, they stated in *Science* that

Into the Laboratory is conveyed a bountiful supply of the water of the Cold Spring for use in the aquaria and troughs. This water is pure, has the same low temperature throughout the year, and is the water used so successfully by the New York State Fish Commission in hatching and growing salmon, trout, and other food fishes. The Laboratory is also supplied with an abundance of salt-water, which is pumped up from the harbor into a reservoir, from which it runs into the Laboratory.⁴²

The requirement for an abundance of both fresh and salt water was compounded by the desire to access relatively pure water sources. Pure water met two requirements: experimental and exploratory. Pure water was the backdrop to successfully maintaining living organisms in aquaria and to monitoring the variables of experimental work. In Charles Atwood Kofoid's introduction to his 1910 United States Bureau of Education bulletin *The Biological Stations of Europe*, he states that

Purity of the water supply, as shown in its freedom of admixture with fresh water and from contamination by sewage, industrial wastes, or considerable quantities of shore detritus due to tidal currents, is a matter of great importance to all stations where experimental work...is carried on, or where varied types, especially pelagic forms, are kept in aquaria.

Kofoid concedes that water can be filtered and decontaminated with the correct equipment, but, "after all is said, purity of water supply is the greatest asset of a marine station."⁴³

In addition to experimental work, water *purity* often translated into *clarity* for investigators. Use of diving apparatus and underwater cameras did not become possible until the second decade of the twentieth century but for investigators interested in

⁴² "The Brooklyn Institute Biological Laboratory," *Science* Vol. 19 No. 481 (April 22, 1892): 225-227.

⁴³ Charles Atwood Kofoid *The Biological Stations of Europe United States Bureau of Education Bulletin No. 40 Whole Number 440*. (Washington: Government Printing Office, 1910), 4.

collecting data with the aid of these technologies, water clarity was a large draw. The amount of clarity needed for the use of underwater investigations was found at the subtropical and tropical marine stations. In 1910, E.A. Andrew reported that the water clarity was so great at the newly established Johns Hopkins laboratory in Montego Bay, Jamaica that “the common water glass or bucket with glass bottom brought the fauna well within observing reach at considerable depths, so that little use was made of the Japanese diving spectacles that enable the observer to see the bottom fauna very distinctly as long as he can hold his head underwater.”⁴⁴ Diving helmets and underwater cameras were utilized frequently at the Tortugas laboratory and it was commonly known to have the best water clarity for the use of this equipment in the field.⁴⁵

The ability for investigators to view organisms in their natural surroundings was considered an added benefit to working in certain areas. Without using extra technologies, a general lack of turbidity meant less separation between the laboratory environment and the surrounding waters. In 1912 and 1913, investigators at Beaufort repeatedly recorded observations of organisms that were seen off of piers and jetties. Lewis Radcliffe wrote a particularly in-depth observation of sharks that appeared in the evening on August 31 and September 1, 1912. Radcliffe records the activity of the sharks, their general coloring, and states that “These sharks appear to be *hypoprion brevirostris poey* [lemon sharks]. If this is correct, this is a new record for the state of

⁴⁴ E.A. Andrews, “A Zoological Laboratory at Montego Bay, Jamaica, B. W. I.” *Science* 32:831 (Dec. 2, 1910) 785-86.

⁴⁵ Klaus Rützler, “Tortugas Marine Laboratory: Threshold to Modern Sponge Biology” in *Field Guide to the Major Organisms and Processes Building Reefs and Islands of the Dry Tortugas: The Carnegie Dry Tortugas Laboratory Centennial Celebration (1905-2005)* edited by Eugene A. Shinn and Walter C. Japp. Key West Florida (Oct. 13-15, 2005): 34-35; Underwater cameras, diving helmets and diving hose were included in the 1923 inventory. Marine Biology L7/15 Tortugas Lab, Buildings, Quarters, Grounds 1904-19. Carnegie Institute of Washington Archives: Washington, D.C.

North Carolina.”⁴⁶ Water clarity allowed investigators to explore the surrounding area of the marine station without the help of water craft or diving technology and to make observations about species outside of the laboratory setting.

Beyond water purity and clarity, an area with a multiplicity of separate water sources and environments was considered ideal. Most marine stations advertised access to both littoral (intertidal/seashore) and pelagic (deep sea) waters. Investigators could be provided with organisms from close to shore, collected either by hand net or by seining from a small boat, and also organisms from a greater depth off of the shelf, usually collected by a larger research vessel or local fishermen. The importance of access to varying salt water depths was not merely that they existed near the marine station, but were easily accessed. The Beaufort, North Carolina area is a particularly good example of the ability to access multiple depths of salt water. Located on the end of a piece of land protected by a group of barrier islands, Beaufort investigators had access to collections from the Core Sound, including the clams, oysters, crabs, and fish that had made Beaufort a populated fishing village from the early 18th century onward. Beaufort had also risen as one of the only Southern whaling villages, and was the only commercial dolphin fishery in the America, proving it had particularly good access to pelagic organisms as well. When J.A. Holmes of the North Carolina Geological Survey assessed the idea of placing a United States Bureau of Fisheries marine laboratory in Beaufort in 1899, he called particular attention to the ease of collecting in multiple depths of salt water, as well as the

⁴⁶ Lewis Radcliffe, William Crozier and Selig Hecht “Log Fishes Taken at Beaufort, NC June-Sept. 1912” Box 16 RU7184 United States Bureau of Fisheries, Records, 1877-1948. Smithsonian Institution Archives: Washington, D.C.

multitude of organisms that were already known to be present in these water sources because of previous fishing activities in the area.⁴⁷

Finally, one of the most important geographical formations needed for a marine laboratory to be built were the existence of natural harbors. Nearby bodies of water, littoral or pelagic, salt or fresh, were potentially useless without the ability to keep research vessels in the area. Research vessels were required for the work that investigators hoped to accomplish at marine stations. The ability to keep multiple kinds, including sail boats, small man-powered skiffs, and large steam-powered research vessels all had to be kept for research. Difficulties navigating surrounding areas, or an inability to keep vessels of a certain size, meant an inability to collect at given depths. When the University of Texas sought to build a Gulf of Mexico laboratory in 1893, they found that the “The low Texas coast is bordered by exceedingly shallow bays, from two to ten miles wide, cut off from the Gulf of Mexico by a very narrow sand-formation. This almost continuous stretch of sand, raised unevenly by innumerable dunes formed by the wind, is broken at eight places by narrow channels into seven islands, and at three other points partially unites with the mainland to form extended peninsulas.” This coast formation made it difficult to find a natural bay for keeping research vessels, and in the end, Galveston Bay was chosen over other locations because, while it was not the most biologically interesting part of the coast, it was accessible by boat and pelagic waters (10-fathoms or more) extended 30 miles “directly off the entrance to Galveston Bay.”⁴⁸

⁴⁷ J.A. Holmes to George M. Bowers. March 27, 1899. RU 22 Correspondence Concerning Fishery Expeditions, Experiments and Research, 1885-1908 Box 1 Folder “Smith Papers- Beaufort Laboratory, 1899-1904” RU 22 National Archives: Bethesda, MD.; See also Douglas A. Wolfe, *A History of the Federal Biological Laboratory*.

⁴⁸ Charles L. Edwards, “The Marine Biological Station of the University of Texas” *Science* 21:538 (May 26, 1893): 284.

Very commonly, directors chose locations known to be commercial fishing areas. While the United States Bureau of Fisheries was interested in these areas because of their connection to and knowledge of local fish stocks, the locations were also established harbors for fishing vessels. Beyond the USBF laboratories, other stations struggled to find natural harbors that could be linked to locations with the correct water access for the work they wished to accomplish. But water and land formations were only two variables taken into account when seeking the perfect place for a marine laboratory.

Weather

Marine stations initially operated on a summer seasonal basis. There were two reasons for this seasonality. The first is that investigators were commonly attached to a university system and therefore could not find the time to visit marine laboratories for extended periods of time until the summer months when their universities went on break for the year. This even held true for USBF investigators, most of whom did field work while on summer break from teaching duties. Secondly, in most locations summer offered the most consistent weather patterns for collecting the largest diversity of marine life, especially larval forms. Naples, one of the oldest European marine laboratories, was held up as the example of perfectly mild weather year-round, making collecting important scientific forms possible throughout the year. While directors and investigators envied this perfect weather, they had difficulties finding locations that offered weather that would be conducive to work year-round in America.

Stations located in the Northeast had mild but sunny weather from mid summer into early fall. This was a short window of seasonal availability from July into September; the first Marine Biological Laboratory season ran from July 10-Sept 22. As

seaside work increased in popularity, the summer season in the Northeast was stretched until the Marine Biological Laboratory and the USBF at Woods Hole were both operating from late May into late October by 1910.⁴⁹ An investigator was generally assured that weather would be amenable for off shore collecting during the summer season and that travel to and from the laboratory would not be impeded by weather restrictions.

While weather for collecting was important, general comfort was also high on the list of weather priorities. Directors of stations established further south in the United States sought to reassure potential investigators that their summers were not too hot and muggy for comfort. According to H.V. Wilson, a member of the University of North Carolina at Chapel Hill biology department and former USBF investigator, the temperatures at Beaufort during the summer hovered between 79 and 81 degrees, “rarely going a degree or two above that, and much more frequently dropping several degrees below.” In addition to the importance of comfortable living conditions, researchers sought comfortable locations to work and spend a “working vacation.” While comfortable weather was important for collecting and work, Wilson also points out that the weather in Beaufort and its nearby resort neighbor Morehead City, “contribute much to the *bien-etre* of naturalists who are spending a working vacation.”⁵⁰

Beyond the importance of collecting in consistent weather and the need to be comfortable, a final weather concern came to the fore work moved further into tropical seas. While Northern stations often dealt with the occasional Nor’easter or blizzard, the movement into the Caribbean pitted permanent stations against a constant threat:

⁴⁹ “The Marine Biological Laboratory” *Science* 11:282 (Jun. 29, 1888): 305-306.

⁵⁰ H.V. Wilson, “Marine Biology at Beaufort” *The American Naturalist* 34: 401 (May 1900): 344; Philip Pauly *Biologists and the Promise of American Life: From Meriwether Lewis to Alfred Kinsey*. (New Jersey: Princeton University Press, 2000). See specifically Chapter 6 “A Place of Their Own: The Significance of Woods Hole.”

hurricanes. The threat and damaging potential of hurricanes can be clearly seen in a letter from Alfred Goldsborough Mayer to Robert S. Woodward of the CIW. According to Mayer, the specially built research vessel *The Physalia* weathered a hurricane in 1906, after nearly being rammed by an unmoored yacht. Not able to resist bragging about the hardiness of the vessel, Mayer pointed out that “this is the third storm of hurricane violence that the *Physalia* has weathered.” This statement might have been more concerning than uplifting to Woodward: The *Physalia* was only two years old at the time!⁵¹ Regardless if a station was built in the Northeast, Northwest, or the tropics, administrators had to weigh the weather advantages against the possible loss or damage of property that natural disasters and consistently bad weather could inflict.

Disease Vectors

Beyond weather disasters, a concern about location of marine laboratories, especially of those located in the tropics, was the insalubrious nature of hot weather and the fevers and health concerns that abounded in these climates. Concerns about disease was not merely conjecture, but had struck the marine science community already. In 1897, The Johns Hopkins University’s first year at their temporary marine laboratory in Port Antonio, Jamaica ended in disaster when yellow fever swept through the researchers. Among the victims of the fever was Dr. J.E. Humphrey, a botanist and the director of that year’s expedition, and Franklin Story Conant, a zoology graduate student finishing his dissertation research on *cubomedusae* (box jellyfish) of the Caribbean. In *Memoirs from*

⁵¹ Alfred Goldsborough Mayer to Robert S. Woodward. Oct. 7, 1906. Marine Biology L7/15 Tortugas Lab, Buildings, Quarters, Grounds 1904-19. Carnegie Institute of Washington Archives: Washington, D.C. Ironically, *The Physalia* would be destroyed the following season by a fire while in harbor in Miami, FL.

the Biological Laboratory of the Johns Hopkins University the story of the quick spreading fever, and the personal sacrifice made by Conant was extolled.

After the sudden and alarming death of the director of the expedition, Dr. J.E. Humphrey, Conant took the burden of responsibility upon himself, and while he fully appreciated his own danger, he devoted himself calmly and methodically to the service of others, who, in their afflictions, needed his help, and he fell in the path of duty, where he had always walked...⁵²

According to the zoologist J.E. Duerden, these deaths effectively halted preexisting plans to build a permanent marine station in Port Antonio, Jamaica- plans that would be taken up again in 1903.⁵³

Concerns about malaria and yellow fever took center stage during the debate about the location of The Carnegie Institution of Washington's proposed marine station. Alfred Goldsborough Mayer favored the Dry Tortugas heavily because, according to him, "The yellow fever quarantine station was abolished at the Tortugas in 1899, and there are practically no mosquitoes on Loggerhead or Bird Keys."⁵⁴ Other scientists involved in the debate agreed with Mayer that a smaller island would afford immunity from tropical diseases, but that the trade off was a generally uninteresting space in which to work. The ornithologist Francis Herrick stated that "The advantages of small islands in affording immunity from tropical diseases are no doubt considerable, yet it must be remembered that a greater land area and a more diversified coast add intensely to the interest of students who go to the tropics for zoological or botanical studies."⁵⁵ Duerden suggested that Jamaica was a better fit for a marine laboratory because it had close medical care and

⁵² William Keith Brooks *Memoirs from the Biological Laboratory of the Johns Hopkins University* (Baltimore: Johns Hopkins Press, 1898), xi.

⁵³ J.E. Duerden, "A Tropical Marine Laboratory for Research" *Science* 17:439 (May 29, 1903): 862-864.

⁵⁴ Alfred Goldsborough Mayer, "The Bahamas vs. Tortugas as a Station for Research in Marine Zoology" *Science* 18:455 (Sept. 18, 1903):369-371.

⁵⁵ Alfred Goldsborough Mayer, "A Tropical Marine Laboratory for Research" *Science* 17: 434 (Apr. 24, 1903): 659.

a larger population that could properly explain to laboratory workers how to protect themselves from harm. According to him “To select any locality of which the general healthiness or climatic conditions are uncertain, or where proper medical advice and attention are not available, would undoubtedly sooner or later result in a sad collapse.”⁵⁶ Explicit in Herrick’s and Duerden’s statements was that the upsides of an isolated marine laboratory did not outweigh the importance of building in an easily accessible and already settled area. But the potentials and pitfalls of building in established communities was very different for temperate versus tropical locations.

Infrastructural support

Finding the perfect balance between established infrastructure and untouched or at least seemingly undisturbed marine surroundings was a constant tightrope walk for administrators. Should one build near an established town or city in the hopes that creature comforts and the accessibility of the location would draw more investigators? Or should you build in a remote location to ensure that urban growth would not encroach on the study of marine organisms and disturb the ascetic quality of a summer spent surrounded by the sea? The distinction between the needs of teaching laboratories and research laboratories cropped up often in debates about the placement of the Carnegie Laboratory. T.H. Morgan suggested Jamaica over the Tortugas because Jamaica was more accessible to students.⁵⁷ But this simple equation for plugging in needs and desires and coming up with location obscures the complicated process of balancing infrastructure with a desire to study untouched nature.

⁵⁶ Duerden (May 29, 1903) 863.

⁵⁷ Alfred Goldborough Mayer, “A Tropical Marine Laboratory for Research?” *Science* 17:434 (Apr. 24, 1903): 659.

The earliest stations depended upon pre-existing transportation and industrial infrastructures; they were built in established fishing villages and were accessible by public roads and railways. Woods Hole, the site of two of the earliest permanent laboratories, had been a fishing village for many centuries, had a permanent population and preexisting housing, and was accessible by railway. This easily accessed laboratory site allowed scientists to rent their own accommodations, come and go throughout the summer months, and to bring multiple graduate student, their own families, and support staff with them to have a “working vacation.”⁵⁸

A lack of infrastructural support may be pinpointed as one of the reasons that southern and sub-tropical laboratories developed more slowly than those in temperate and more populated regions. In 1891 when W.K. Brooks decided that Johns Hopkins required a tropical location, he sent several members of his research team to Jamaica to find the perfect spot. E.A. Andrews declared Montego Bay optimal because of water, weather, natural harbors, and specimen availability, but there was no railway or transportation to that port, so the university chose another location. By 1910 a railway had been built to Montego Bay and it was accessible by steamer directly from Philadelphia, New York and Baltimore. Hopkins immediately relocated to this location.⁵⁹

Some laboratories chose to build in remote locations; the Carnegie Institute of Washington’s Tortugas laboratory required up to a week of travel for investigators to reach the laboratory. Researchers in the first years at Beaufort, San Diego, and Tortugas were housed far off site or in less than desirable conditions during the early years of

⁵⁸ Pauly, *Biologists and the Promise of American Life*, Chapter 6.

⁵⁹ E.A. Andrews, “A Zoological Laboratory at Montego Bay, Jamaica, BWI” *Science* 32: 831 (Dec. 2, 1910): 783.

operations.⁶⁰ This section will examine the arguments for and against building permanent laboratories in areas with preexisting infrastructures and populations.

In established regions, researchers could find suitable housing while waiting for the permanent station to be built. The USBF set up a temporary laboratory in a rented Woods Hole house for their first few seasons; Johns Hopkins continuously rented houses for temporary research laboratories because they shifted locations yearly. In addition, families often accompanied researchers to partake in a summer by the sea. At the Marine Biological Laboratory and the USBF laboratory at Woods Hole, whole families followed researchers, organizing family picnics, sailing trips and other summer revelries. If the location did not contain rentable housing for families, researchers were forced to travel alone and bunk with everyone else.⁶¹

⁶⁰For information on travel to and from the Tortugas laboratory, see individual Carnegie Institute of Washington Grant requests and receipts. For example, M.W. Laubenfels spent a total of 25 days traveling to the Tortugas from Pasadena in 1927, stopping at Oberlin and Beaufort along the way. Laubenfels to W.M. Gilbert. Aug. 26, 1927 Grants Box 12 Folder 12 Carnegie Institute of Washington Archives: Washington, D.C.; Early researchers at Beaufort stayed in a rented house off of the island while the main laboratory was being constructed. Caswell Grave to Hugh Smith May 30, 1902 Ru 22 Correspondence Concerning Fisheries Expeditions, etc. 1885-1908 Box No. 1 Folder Smith Papers "Beaufort Laboratory 1899-1904" RU 222. National Archives: Bethesda, MD.

⁶¹ Pauly, *Biology and the Promise of American Life*, chapter 6. See also Paul Galtsoff's photographs of Woods Hole families taken in the late 1920s. Northeastern Fisheries Science Center photo archives <http://www.nefsc.noaa.gov/cgi-bin/photo.pl> accessed Dec. 15, 2011.



Figure 2 Researchers and Family at a Picnic in Woods Hole, 1925. Northeastern NOAA historical photographs. Northeastern Fisheries Science Center photo archives [available online at <http://www.nefsc.noaa.gov/cgi-bin/photo.pl>] accessed December 15, 2011.

Building in remote locations meant that sleeping quarters were often cramped, and there was little alternative but to live in the rough quarters provided by the station. The lack of a surrounding community meant that families were unable, and most often, unwilling to accompany researchers. A commonly expressed drawback of Tortugas was the inability for researchers to bring their wives and children. Referred to by researchers as “a stag party,” the lack of accommodations for families presented both a personal and a financial problem.⁶² Researchers were forced to maintain a household for their families while they traveled, causing them to complain to directors about the monetary strains.⁶³ Finally, many women were reluctant to spend summers on a poorly outfitted island with poor living conditions. Caswell Grave reported to Hugh Smith that the Beaufort laboratory probably did not need a matron because

⁶² Henry J. Clark quoted in Lester D. Stephens and Dale R. Calder *Seafaring Scientist: Alfred Goldsborough Mayor, Pioneer in Marine Biology* (Columbia, SC: University of South Carolina Press, 2006), 103.

⁶³ De Laubenfels to M.W. Gilbert Dec. 5, 1927 Grants Box 12 Folder 12 Carnegie Institute of Washington Archives: Washington, D.C.

The island is a very poor place for women. No company has time to give them and no one upon whom they feel free to call to row them to and from Beaufort. When they come into the laboratory the men immediately begin to draw on their coats and the visitor makes her visits far apart. For these reasons and others Mrs. Graves is not with me and has no wish to be here.⁶⁴

In addition to the lack of families, remote laboratories denied access to female researchers because of the lack of separate accommodations. When Beaufort opened in 1902, it was announced that women would not be allowed to work there. Without a matron or a separate dormitory for female investigators, it stayed closed to female researchers for almost 5 years. Tortugas never offered table space to female researchers because of its limited facilities.⁶⁵



Figure 3 The Tortugas Laboratory offered little in creature comforts. Alfred Goldsborough Mayer took this photo of his space in 1917. Series 3 Box 7 “Tortugas Folder” Alfred Goldsborough Mayer Papers, Syracuse University Archives: Syracuse, New York.

Laboratories such as Beaufort and Tortugas developed many hurdles stemming from their remoteness from mainland transportation. When the USBF laboratory at

⁶⁴ Caswell Grave to Hugh Smith June 27, 1904 Ru 22 Correspondence Concerning Fisheries Expeditions, etc. 1885-1908 Box No. 1 Folder Smith Papers "Beaufort Laboratory 1899-1904" RU22. National Archives: Bethesda, MD

⁶⁵ H.V. Wilson, “The Laboratory of the United States Fish Commission at Beaufort, N.C.” *Science* 278 (Apr.27, 1900): 674.

Beaufort was built, the railroad had yet to be extended to the area. The railroad was extended to Morehead city in 1858, but those traveling to Beaufort were ferried by boat until 1907. While the Tortugas had access to mainland Key West because of the establishment of a United States military presence on the islands, researchers were forced to take a circuitous route traveling to the island- boats did not go directly from either New York or Philadelphia.⁶⁶ In June 1927, T.H. Morgan and Charles Davenport took the long journey together to visit the Dry Tortugas. They met in New York City at Penn station on June 16, spending two days and nights sharing a railcar (and sleeping car), and arrived in Key West on July 18th to catch the boat to the Tortugas on July 19th. They stayed ten days on the island and the total expense for their travel was \$306.72 each.⁶⁷

Transportation issues caused more than minor travel irritations. Supplies for both the laboratory and the dormitories had to be ordered well in advance. If the researchers ran out of chemicals or needed specialized equipment, it was often impossible to get it in the middle of the season. During the 1902 season, the Beaufort laboratory ran out of alcohol to preserve specimens. Researchers stretched the existing supplies by doubling and tripling specimens in jars, but this fix was only for the short term. The inability for remote laboratories to receive supplies quickly meant that they either ran the risk of over ordering supplies or to go without.⁶⁸

In addition, laboratories struggled to provide isolated workers with pleasing accommodations. A 1902 letter from Caswell Grave stated that he would write to E.B. Wilson and W.K. Brooks that he had hired the services of a cook for Beaufort, because

⁶⁶ Wolfe *A History of the Federal Biological Laboratory*, (2000).

⁶⁷ Box 72 Folder 7 Charles Davenport Papers. American Philosophical Society Archives: Philadelphia, PA

⁶⁸ Caswell Grave to H.F. Moore Aug 18, 1902 Ru 22 Correspondence Concerning Fisheries Expeditions, etc. 1885-1908 Box No. 1 Folder Smith Papers "Beaufort Laboratory 1899-1904" RU 22. National Archives: Bethesda, MD

they both stated that their “coming would depend on the mess.”⁶⁹ Concerns about creature comforts were felt at Tortugas, where the geologist T. Wayland Vaughan explained that he would no longer do work at the station because, among other reasons, the food was so horrible that he would “no longer jeopardize my health, perhaps even my life.” According to Vaughan, when the cook ran out of ham and eggs during the season, he served pickled lamb’s tongues for every meal. The alternative, an abundance of fresh fish, had apparently drawn complaints from other workers.⁷⁰ Regardless of complaints, remote laboratories had to order supplies in advance of the season, and were unable to cater to the desires of individual workers. The 1907 grocery order for the Tortugas laboratory was finalized and paid in February for a season that started in May. The prepackaged foods (including 2 dozen jars of pickled lamb’s tongue) were delivered months before the first investigators stepped onto the island.⁷¹

Finally, the lack of family, supplies, and the poor diet were compounded by a lack of local culture to enliven an endless summer of work. In the discussion of where to place the Carnegie laboratory, many scientists believed that Jamaica or the Bahamas would be a better location than the Tortugas because of the vibrant local communities that existed on those islands. Tortugas had very few residents, and all of them were involved with the small military outpost. While Mayer admitted that the Bahamas were a friendlier place full of English speaking residents who would be great company to researchers, he assured visitors that

⁶⁹ Caswell Grave to Hugh Smith May 27, 1902 Ru22 Correspondence Concerning Fisheries Expeditions, etc. 1885-1908 Box No. 1 Folder Smith Papers “Beaufort Laboratory 1899-1904” RU 22. National Archives: Bethesda, MD

⁷⁰ Quoted in Lester D. Stephens and Dale R. Calder *Seafaring Scientist: Alfred Goldsborough Mayor, Pioneer in Marine Biology* Columbia, SC: University of South Carolina Press, 2006, 107.

⁷¹ S.S. Pierce and Co. to Alfred Goldsborough Mayer . Feb. 1907 Marine Biology L7/15 Carnegie Institute of Washington Archives: Washington, D.C.

Although the community at the Tortugas is small the social conditions are pleasant, for people of culture and education are sure to be found among the naval officers and their families, and indeed, the writer recalls with keen pleasure many most enjoyable hours spent in company with one of the keepers of the lighthouse. The community is sufficiently small not to distract, but yet large enough to render pleasant and profitable the few leisure hours which may be enjoyed by one engaged in marine research.⁷²

While the Spartan lifestyle of researchers at remote stations might seem a particularly good reason to not build in those locations, building near established communities did have its pitfalls. Investigators at Naples and Woods Hole noted that the water quality, one of the most important components of marine work, had declined over the years. Nearby pollutants from growing populations muddied once pristine waters, killing marine organisms and making the collecting difficult. In 1903, the zoologist C.C. Nutting stated that

There being no city or even town in the immediate neighborhood is a decided advantage from this standpoint. Even at Naples, which is now probably the best station in the world, there are many forms that are not successfully kept for any length of time in the aquaria. When the writer was at Plymouth, England, some years ago, the water, although apparently pure, was the cause of much perplexity and discouragement. At the Woods Hole laboratories the condition is even worse, and many problems have to be abandoned that could be solved with the aid of such water as could easily be secured at the Tortugas.⁷³

Even seemingly remote locations, such as Beaufort, experienced water pollution from encroaching industry and populations. During the 1913 season, Beaufort was forced to move their water pump into deeper water because the area that the pump was currently drawing from had become too polluted to properly perform experiments on embryos in the laboratory.⁷⁴

⁷² Alfred Goldsborough Mayer, "The Bahamas vs. Tortugas as a Station for Research in Marine Zoology" *Science* 18: 455 (Sept. 18, 1903): 371.

⁷³ C. C. Nutting, Wm. E. Ritter, David S. Jordan, "The Proposed Biological Laboratory at the Tortugas" 17: 438 (May 22, 1903): 824.

⁷⁴ Lewis Radcliffe, "A Summary of the Work of the U. S. Fisheries Marine Biological Station at Beaufort, N. C." 19: 977 (Sept. 19, 1913): 395-400.

Beyond the issue of water pollution, laboratories built in populated areas ran the risk of being squeezed out by encroaching populations and skyrocketing land prices. Both the Hopkins Marine Station and the San Diego Marine Biological Laboratory were forced to relocate because they inhabited space on a rapidly populating coast; both were unable to expand because they were hemmed in by land prices and new developments.

The San Diego Marine Biological Laboratory was established in La Jolla Park, donated to the San Diego Marine Biology Association by the City of San Diego. As the shipping industry took off in this area, water became polluted, collecting became more difficult, and a lack of available land made it impossible to stay in their current location. The laboratory directors knew that they needed a large swath of coastline in an area where coastline was in high value. A major concern in this move was that in the four years that the city had donated the use of La Jolla Park and the time of the move, a law was passed that all public lands must be put up for auction before it could be sold. Luckily, the city was on the side of the marine laboratory and the Association was the only bidder. If this had turned out differently, the San Diego Marine Biological Laboratory would have been moved further out of the city of San Diego, to a more affordable swath of coastline.

The Hopkins Marine Station suffered a similar problem when their initial location proved to be too small for expansion. After 30 years in one location, they were forced to move to a completely new location because they needed the space that a less populated portion of the coast would allow. In developed areas such as Florida and California, the

cost of land for marine laboratories may have inhibited the establishment of stations in highly coveted areas.⁷⁵

Networks

Directors and researchers seeking to establish marine laboratories took one more variable into account: the location of a marine station in relation to those already established. Researchers interested in evolutionary or comparative biology often utilized facilities at multiple laboratories in order to compare forms found at various locations. For example, Lewis Cary's 1911 paper on sea anemones highlighted species from three separate laboratories: United States Bureau of Fisheries laboratory at Beaufort, NC. , The Carnegie Institute of Washington Tortugas Laboratory, and the New York University and Harvard University Bermuda Biological Station.⁷⁶ In 1927 and 1928, the Carnegie Institution funded M.W. de Laubenfels to work at the MBL, USBF Station in Beaufort, their own Tortugas laboratory, The Plymouth Laboratory in England and even asked the Naples Zoological Station to find a space at a table for him while he was in Italy.⁷⁷ While it was important for laboratories to be founded for easy access for American professors and students, researchers expressed the belief that there should be as many marine stations in the widest configuration as possible for the sake of knowledge of the marine environment.

Marine laboratories, regardless of the organizations that founded them, were seen by researchers as connected points in a global network of investigation. During the 1902 debate regarding the placement of the Carnegie laboratory, many researchers called for a

⁷⁵ W.K. Fisher, "The New Hopkins Marine Station of Stanford University" *Science* 47:1217 (Apr. 26, 1918): 410-412; "The San Diego Marine Biological Laboratory" *Science* 26: 662 (Sept. 6, 1907): 325.

⁷⁶ Lewis Cary, "A Study of Pedal Lacerations in Actinians" *Biological Bulletin* 20:2 (Jan. 1911): 81-108.

⁷⁷ Grants Box 12 Folder 12 Carnegie Institute of Washington Archives: Washington, D.C.

tropical laboratory to complete the “chain” of laboratories spanning the American coastline of the Atlantic. Charles Davenport suggested that the Tortugas laboratory would allow researchers to track and compare species from tropical waters up the Atlantic Coast. His hope was that “marine stations at Jamaica, Porto Rico or another of the Antilles may be considered; and while we are planning a chain of marine stations, certainly the island of Grand Manan or the coast of Newfoundland and Puget Sound should be considered.”⁷⁸ Of course, the idea for a chain of laboratories was not new. In 1899, when the North Carolina Geological Survey advised the United States Bureau of Fisheries on the establishment of a laboratory at Beaufort, one of the reasons given for the location of the station was that

Should the Fish Commission at any future date also establish a marine station on the Florida Keys, the three stations then established (the one at Wood’s Hole, this one at Beaufort and the third one on the Florida Keys) would give a chain of stations for the investigations of the zoologic problems along the Atlantic Coast. And these three stations would answer the purpose for the investigation not only of local problems connected with the Fish Commission but they would also serve for the investigation of such larger problems as the distribution and migration of fishes and other marine forms along the coast.⁷⁹

The USBF sought to fulfill this vision, establishing a marine laboratory at Key West in 1914, but unfortunately, that station ran into financial and logistical problems very early; it did not become fully functional for researchers until after WWI.

The desire of some researchers to develop a fuller picture of migration and distribution of species throughout the ocean led many to travel between marine laboratories. William Ritter, the first director of the Marine Biological Association of San

⁷⁸ C. B. Davenport, Robert Payne Bigelow, B. W. Barton, “The Proposed Biological Station at the Tortugas” *Science* 17: 441 (June 12, 1903): 945.

⁷⁹ J.A. Holmes to George M. Bower May 27, 1899. Box No. 1 Folder Smith Papers "Beaufort Laboratory 1899-1904" RU 22. National Archives: Bethesda, MD.

Diego's laboratory, stated that there was an "inescapably interstate and international character of the scientific problems of the sea." Ritter sought to utilize Canadian, Japanese and American marine laboratories as a network of locations working towards an understanding of a single region: the Northern Pacific.⁸⁰ This movement from laboratory to laboratory was common on both coasts. Many of the researchers that worked at the Tortugas laboratory visited the Beaufort laboratory on the way down the Eastern Coast of the United States. American scientists continued to patronize international laboratories, and to extol the virtues of those laboratories to their fellow researchers, long after marine laboratories were established in the United States. American institutions maintained tables at the Naples Zoological Station throughout the first half of the 20th century. When the Station struggled to rebound after WWI, many American biologists continued to work at the laboratory and to pledge their support for maintaining permanent tables. This continued support resulted in the American Association for the Advancement of Science's subscription to a table, although there were over 30 marine laboratories operating throughout the United States at this point.⁸¹

Marine researchers traveled throughout the world to visit marine laboratories stationed in locations that gave them access to new regions and allowed them to do comparative studies on organisms from multiple locations. The Naples Zoological Station was by far the most popular station for American researchers to visit, but throughout the early 20th century, researchers traveled to stations in France, England, Norway, Russia, and North Africa. According to Edward Gardiner, the Marine

⁸⁰ William Ritter to Benjamin Ide Wheeler. November 21, 1918. Box 2 Folder 1918 William Ritter Papers, Bancroft Library. University of California Berkeley. Berkeley, CA.

⁸¹ Edmund B. Wilson, "Reorganization of the Naples Zoological Station" *Science* 59:1521 (Feb. 22, 1924): 182-183.; Burton E. Livingston, "The Naples Zoological Station and the American Association" *Science* 61:1588 (June 5, 1925): 585-586.

Biological Laboratory in Plymouth, England provided the perfect place to continue work he initiated at Woods Hole the last summer; it had the same temperate water, but was blizzard free in winter.⁸² In 1908, J. Playfair McMurrich suggested that his fellow researchers join him at the Marine Biological Station at Roscoff, France run by the University of Paris. According to McMurrich, the stations organisms and environment complimented the more southerly flora and fauna of the Naples Station.⁸³ And “for biologists who have an interest in the low temperature relationships of organisms,” there was no better place to study than Alexandrovsk Biological Station on the fjord where the Kola River entered the Artic Sea.⁸⁴

Organisms

Availability of organisms was an important criterion in choosing a laboratory site. Both observational and experimental research required easy access to both a wide range of species and a large volume of specimens. Experimental disciplines required a large volume of similar specimens.⁸⁵ Other disciplines required a large range of specimens, including access to as many organismal types as possible, including a wide range of developmental forms and species.⁸⁶

Investigators focused on questions of universal biological development, such as embryologists and morphologists, relied on consistency and volume of specimens.

Common embryological forms used in experimentation, such as the *fundulus*

herteroclitus, were not cultured and raised in the laboratory consistently until the 1960s.

⁸² Edward G. Gardiner, “Plymouth England and its Marine Biological Laboratory” *Science* 9:222 (March 31, 1899): 488-490

⁸³ J. Playfair McMurrich, “The Marine Biological Station of Roscoff. Annex of the University of Paris” *Science* 28: 719 (Oct. 9, 1908): 479-480.

⁸⁴ R.B. Harvey, “Alexandrovsk Biological Station” *Science* 6: 1728 (Feb. 10, 1928): 158.

⁸⁵ Jane Maienschein “History of American Marine Laboratories,”24.

⁸⁶ John P. Wourms, “The Rise of Fish Embryology in the Nineteenth Century” *American Zoologist* 37:3 (June 1997): 269-310.

Before this breakthrough in the cultivation of the species, all *fundulus* used in embryological studies, which was quite a few due to its heartiness and visible developmental cycle, were caught near a marine laboratory and experimented upon in that location. In 1930, the Supply Department of the Marine Biology Laboratory collected *fundulus* twice daily to supply investigators with enough material with which to work.⁸⁷

Investigators who focused on specific species, or whose work was best performed on specific organisms, flocked to specific laboratories for the short period that their specimens would be available for study. The Tortugas Laboratory of the Carnegie Institute of Washington was well known for its access to sponges and coral. These organisms were unavailable in Northern locations, but they were also sparse in other tropical locations. Tortugas became the epicenter of research on sponges and coral in the early 20th century and drew investigators from across the country and around the globe.⁸⁸ When the Johns Hopkins Laboratory spent its first season in Port Henderson Jamaica, W.K. Brooks noted the discovery of *Cassiopea Xamacha*, the first member of the *Cassiopea* branch of *medusae* to be found in the Atlantic. This species became popular with experimental physiologists, especially those studying the physiology of nerves, because of its hardy nature in the laboratory setting. (See Chapter 4) Investigators

⁸⁷ For a history of the *fundulus* as an experimental organism, see James W. Atz, "Fundulus Heteroclitus in the Laboratory: A history" *American Zoologist* 26:1 (1986): 111-120 and Jane Oppenheimer, "Fifty Years of Fundulus" *The Quarterly Review of Biology* 54: 1 (Dec. 1979): 385-395. Merkel Jacobs Collection. Box F Folder 2 "Report Corres. about Supply Depart MBL 1928-1932" Marine Biological Laboratory Archives: Wood's Hole, MA

⁸⁸ Shinn and Jaap (editors) *Field Guide to the Major Organisms and Processes Building Reefs and Islands of the Dry Tortugas*, 34-38.

interested in working with this organism traveled to the Johns Hopkins and Tortugas laboratories each season.⁸⁹

More important than the type or volume of specimens was the emphasis on access to living organisms. Embryologists, physiologists and even taxonomists relied on knowledge of organismal availability, especially spawning and migratory cycles, to plan their research accordingly. An investigator went to a marine laboratory, not because an organism had once been found in the vicinity, but because the laboratory directors could assure them that they would have access at a given time to their organism of choice. Investigators could order preserved specimens from marine laboratories throughout the year, but traveling to a marine laboratory was undertaken with the explicit purpose of working with living organisms.⁹⁰ This section will outline the ways that directors pinpointed and advertised specimen availability for researchers, and also how they made specimens available to investigators throughout their stay at the marine laboratory.

Biological Surveys

Whether an investigator was visiting a station to have access to a large volume of organisms or a specific species, administrators sought to ascertain what specimens would be available at that station. Before or shortly after a marine laboratory was established, a biological survey of the surrounding waters and terrain was undertaken to ascertain the

⁸⁹ W.K. Brooks, "Johns Hopkins Marine Laboratory" *Science* 19: 465 (Jan. 1, 1892): 10. For information on the hardiness of the organism for research and experimental purposes, see Alfred Goldsborough Mayer, "The Relation Between the Degree of Concentration of the Electrolytes of Sea Water and the Rate of Nerve Conduction in *Cassiopea*" *Papers from the Tortugas Laboratory of the Carnegie Institute of Washington Volume IV* (Washington, D.C.: Carnegie Institute of Washington, 1914).

⁹⁰ Even taxonomy work and organism preservation were dependent on access to living organisms. According to Edmond Otis Hovey, "With many forms it is indispensable that they be alive at the beginning of operations; with some it is not so necessary, but with all it is highly desirable. A fish which has been put into alcohol after death looks entirely different from another specimen of the same species which has been put in the fluid while still alive." "Introduction" in *The Methods Employed at the Naples Zoological Station for the Preservation of Marine Animals* by Salvatore Lo Bianco. (Washington, D.C.: Government Printing Office, 1899), 6.

species available to researchers, where they are most prevalent, and perhaps most importantly, when they were available. Every environment contained a separate host of organisms that shaped research in that space. For instance, researchers at Woods Hole did not have tide pools and therefore lacked certain cephalopods. The access to deep sea cephalopods (such as squid) over littoral species (such as octopus) changed the type of research on nerve function performed in these places.⁹¹ Biological surveys continued at these locations and made up the largest continuous project at marine stations during this period (See Chapter 2).

In 1923, the Mount Desert biological laboratory in Maine shifted from a university-based marine laboratory (Tufts) to a private research facility. In order to draw more researchers to the area, the board of trustees suggested that a survey of the surrounding area be undertaken to

Gain knowledge of the flora and fauna of the region, principally the marine forms, which will be of use to the scientific research workers who contemplate coming to work at the laboratory, as well as to present a picture of the ecology of the forms, the numbers as to kinds and individuals, their distribution with regard to season of year and over periods of years, kinds of water and bottoms that they live in, temperature conditions that influence their feeding habits, mating habits and seasons, habits of offense and defense and other ecological relationships.⁹²

These surveys served two separate but equally important purposes: to identify new or rare species endemic to the area and to identify the general flora and fauna of the region.

⁹¹ W.D. Russell-Hunter, "The Woods Hole Laboratory Site: History and Future Ecology" *Biological Bulletin* 168 (June, 1985): 197.

⁹² Ulric Dahlgren. "The Biological Survey of the Mount Desert Island (Maine) region" in *Contributions from the Mount Desert Island Biological Laboratory Vol. I* (Maine: Weir Mitchell Station, 1926), 10. The first request to the USBF from Beaufort was for tidal tables and coastal charts so that the researchers could start plotting flora and fauna locations for the laboratory. Caswell Grave to Henry F. Moore. June 24, 1902. Box No. 1 Folder Smith Papers "Beaufort Laboratory 1899-1904" RU 22. National Archives: Bethesda, MD.; See also W.E. Ritter, "The Marine Biological Station of San Diego: It's History, Present Conditions, Achievements and Aims" *University of California publications in Zoology* 9: 4 (March 9, 1912), 137-248.

W.K. Brooks identified two special organisms available in Port Henderson, Jamaica. The first, a hardy species of medusae, *Cassiopea Xamacha*, was “very abundant and conspicuous.”⁹³ Not yet identified by Western naturalists, but known by the name “Guinea corn blubber” to locals, Brooks felt that the species could greatly contribute to knowledge of the jellyfish physiology. The second species, a *Lucifer* prawn, had previously caught Brooks’ attention in the Beaufort region and he wrote a monograph on its physiology, but had been too scarce in that region for an extensive life history (See Chapter 3). Brooks noted that he was

pleased to find *Lucifer* in abundance, and by going out in a boat and collecting the adults with great care, and taking them carefully home, I was so fortunate as to find some thirty or forty with eggs, and these I kept in aquaria long enough to obtain a tolerably complete series of stages in the embryonic development. I am now engaged in the study of this material, and I hope to have an account of the embryology of *Lucifer* completed within a year. My success in obtaining these eggs is an ample return for the expedition to Jamaica.⁹⁴

In addition to highlighting specialty organisms, early surveys also highlighted the general abundance of materials that could be found in local waters. When Johns Hopkins initially surveyed the waters of Beaufort, North Carolina for their second marine laboratory, they highlighted specimens that would interest the “general student” as well as the “specialist.” Henry L. Osborn listed the large array of organisms found directly off the pier, off the coast, in deeper water, in the shoals surrounding the laboratory, and in the channel and sound near the laboratory. Osborn insisted that there was an abundance of

⁹³ Brooks, 10.

⁹⁴ Brooks, 11. Brooks work on *Lucifer* appeared in 1887 in the *Memoirs from the Biological Laboratory of the Johns Hopkins Laboratory* (Baltimore: Johns Hopkins University, 1887).

crustacean, starfish, echinoids and opihurans throughout the area, as well as individual species of these groups that were special to the Beaufort region.⁹⁵

These surveys served the scientific purpose of identifying new flora and fauna not previously described by naturalists, and as advertisements for marine laboratories seeking to draw more researchers to their establishment. In 1897-98, the United States Bureau of Fisheries was struggling through administrative growing pains. The previous year had seen the death of George Brown Goode, and the new administration was contemplating keeping the station open year-round. Starting in the April 1898 issue of *Science*, H.C. Bumpus, A.D. Mead, W.R. Coe, and M.T. Thompson all wrote articles detailing the general breeding patterns and specimens found in Woods Hole waters throughout the year. Over the course of 12 months, 6 articles gave a laundry list of the organisms caught off the coast. The articles by Bumpus, Mead, and Thompson were divided into sections headed by the taxonomic phyla: cnidaria, ctenophora, mollusca, annelida, anthropoda, and echinoderma.⁹⁶ Coe's article expanded on the availability of a single phylum: Nemerteans. Coe stated that his paper might "prove of interest to some who may desire to carry on researches on the embryology of this neglected group of worms."⁹⁷ Listing the developmental stage (i.e. spawn, young, adult) and the general abundance of each

⁹⁵ Henry L. Osborn, "The Marine Laboratory of the Johns Hopkins University" *Science* 3: 48 (Jan. 4, 1884): 7-10. These surveys were often updated in order to assure investigators that the area still contained the organisms described in earlier studies. See the updated survey of marine life at Beaufort when the U.S.B.F. decided to build a permanent marine laboratory in H.V. Wilson "Marine Biology at Beaufort" *The American Naturalist* 34: 401 (May 1900): 339-360.

⁹⁶ H.C. Bumpus, "The Breeding of Animals at Woods Holl during the Month of March, 1898" *Science* 7: 171 (April 8, 1898): 485-487. "The Breeding of Animals at Woods Holl during the Months of June, July, and August" *Science* 8: 207(Dec. 16, 1898): 850-858 "The Breeding of Animals at Woods Holl during the Month of May, 1898" *Science* 8: 185 (July 15, 1898): 58-61. A.D. Mead "The Breeding of Animals at Woods Holl during the Month of April, 1898" *Science* 7: 177 (May 20, 1898): 702-704. M.T. Thompson "The Breeding of Animals at Woods Holl during the Month of September, 1898" *Science* 9: 225 (April 21, 1899): 581-583.

⁹⁷ W.R. Coe "Notes on the Times of Breeding of Some Common New England Nemerteans" *Science* 9: 214 (Feb. 3, 1899): 167-169

separate species, these articles catalogued experimental organisms that an investigator could count on working with if they visited Woods Hole during these seasons.

Collectors

A common way that laboratory directors sought to assure investigators that they could access the full spectrum of natural resources during their visit was to employ a long standing and trusted collector. The majority of staff at marine laboratories was transient. Laboratory technicians often consisted of undergraduate and graduate students brought by their professors for the summer. Other laboratory workers were hired when needed, but usually stayed for a short time before returning to school or a regular job. Cooks and engineers were a part of daily and yearly life at marine laboratories, and many stayed for years, but they are consistently invisible in laboratory reports. In 1905, the staff of the Beaufort station consisted of Caswell Grave (the director), R.E. Coker (the custodian) and 2 laborers, 5 special assistants, 13 temporary assistants, 1 engineer, 2 firemen in the powerhouse, 3 crewman on the *Petrel*, a janitor, a cook, a kitchen assistant, and the collector, Charles Hatsell.⁹⁸ Against these transient technicians and nearly invisible staff, marine laboratory collectors were integral to the daily operations and yearly success of the scientific investigations at the laboratories.

Collectors' access to local knowledge and their extended careers inextricably linked them with the marine station. Collectors were rarely trained in the academic sciences. Instead, they were men who grew up in the same area as the marine laboratory and who had developed knowledge of the natural surroundings throughout their

⁹⁸ Caswell Grave "The Fisheries Laboratory at Beaufort, Sixth Season" Ru 22 Gen. Corres. Beaufort Lab. 1930-31. National Archives, Bethesda, MA.

lifetime.⁹⁹ One of the most memorable collectors was Vinal N. Edwards. Born and raised in the Woods Hole region, he returned to his home after a stint in the American Navy and was hired in 1871 by Spencer Baird to record specimen collections and weather patterns in the off season. Edwards' local knowledge was considered so extensive H.C. Bumpus reported it to be the impetus for the original "Biological Survey of the waters of Woods Hole and Vicinity" to "incorporate in a permanent form the valuable but unpublished data in the possession of this indefatigable collector and observer."

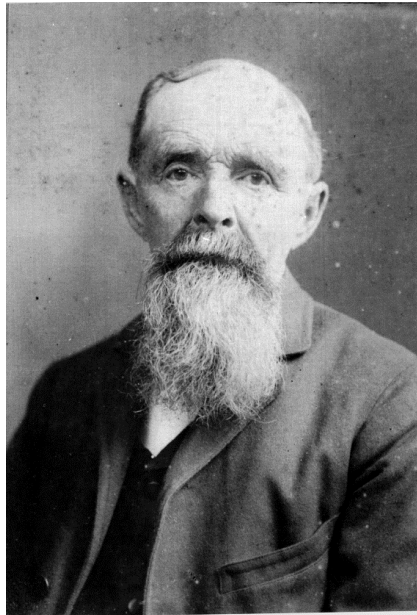


Figure 4 Vinal Edwards Collector at the United States Bureau of Fisheries laboratory at Woods Hole. Northeastern NOAA historical photographs. Northeastern Fisheries Science Center photo archives [available online at <http://www.nefsc.noaa.gov/cgi-bin/photo.pl>] accessed December 15, 2011.

⁹⁹ Herman C. Bumpus *Vinal N. Edwards* unpublished biography (1919). American Museum of Natural History. OCLC Number 31835328. The Naples Zoological Station's collector, Salvatore Lo Bianco, was known as a man who could find an investigator whatever specimen they requested. His specialty was in the preservation of laboratory specimens, especially *Medusae*. Christine Groeben "The Stazione Zoologic: A clearing house for marine organisms" in *Oceanographic History: The Pacific and Beyond* eds. Keith Benson and Philip F. Rehbock. Seattle: University of Washington Press, 1993. Another well known collector was John Veeder at the Marine Biological Laboratory. See Maienschein "History of American Marine Laboratories," 15-25.

Collectors' knowledge was continuously incorporated into academic understandings of ichthyology by their association with marine stations. Osborn and Cole stated in the introduction to "A biological survey of Woods Hole and the Vicinity" that the lists of specimens that were utilized by the authors for the survey were provided by Edwards from those he collected himself. Of course, stated Osborn and Cole, "The descriptions, and in large measure, the determination of species have, however, been the work of others."¹⁰⁰ Edwards' observations and collections were reported yearly to the Director of Scientific Inquiry, and the lists of fish and special specimens listed in *Science* articles and Reports of the Commissioner passed from Edwards through an academically trained scientist into publication. In an 1890 letter to Director Richard Rathbun, Tarleton Bean states that, "I give below a synopsis of interesting fishes collected and observations made by Vinal N. Edwards during the fiscal year ending June 30, 1889."¹⁰¹ This list of observations is over 10 pages long and contains information on new species, volume of fish caught in a given period, and observations about volume regularity based on knowledge of previous seasons.

Although collectors' information was tempered by translation, directors and investigators acknowledged these men as integral parts of the station staff. Investigators considered both Edwards and the collector at the Beaufort station, Charles Ives Hatsell, indispensable to the running of the station. Investigators often thanked collectors in their published work for procuring organisms.¹⁰² Upon his death in 1919, a scrapbook of reminiscences of his contribution to science was created "In order that the life and work of

¹⁰⁰ *Bulletin of the Bureau of Fisheries*, 30:1 (1911): 14.

¹⁰¹ Tarleton H. Bean to Richard Rathbun May 9, 1890. Box 1 Folder "Woods Hole, 1885-1900" RU 22 National Archives: Bethesda, MA.

¹⁰² For an example of a scientist acknowledging Hatsell's collecting, see Howard Edward Enders, "A Study of the Life History and Habits of *Chaetopterus Variopedatus*" *Journal of Morphology* 20:3 (Oct. 1909): 480.

Vinal N. Edwards may not become forgotten.” In the work, the leading scientists of the day, including T.H. Morgan, E.S. Conklin, Robert Bigelow and E.B. Wilson, catalogued the many ways that Edwards had contributed to the scientific environment and work at the USBF Woods Hole laboratory. Five copies were made and sent to the libraries of the USBF, MBL, The American Museum of Natural History, The Library of Congress and the National Museum. The reliance of visiting investigators on the knowledge of the collector is made clear in the final sentence of Morgan’s piece. He writes “How the young fellows nowadays know when the water is warm enough to go swimming, when the tide is at a standstill in the “hole” and whether there will be a storm, I cannot imagine without Vinal to ask about such things.”¹⁰³

Establishing a marine station in an area known to be rich in flora and fauna was only the first step in drawing investigators. Retaining a well-known and trusted long-term collector demonstrated to investigators that they would be able to obtain the organisms that they required and desired each summer when they visited. A thorough and ongoing survey of local waters, a printed record of any new developments and species found within those waters, and retaining an experienced local collector helped to assure investigators that they would not be disappointed by a visit. While the vast marine environment remained largely unexplored, these three variables helped to make the organisms around laboratories as known as possible in order to facilitate continuous scientific investigations.

¹⁰³ T.H. Morgan *Vinal N. Edwards* unpublished biography (1919). American Museum of Natural History. OCLC Number 31835328.

Technologies

In Charles Atwood Kofoid's 1910 *Biological Stations of Europe*, he listed two types of technologies that were needed to assure that a station could function: large amounts of aquaria and "ample field equipment."¹⁰⁴ Technological requirements far exceeded this simple statement, and the equipment required grew exponentially throughout the early 20th century. For example, when the Hopkins Marine Laboratory was built in 1891, there was a single room dedicated to photographic work. In 1917, when Stanford moved the laboratory north to a larger location, the plans still called for only one photographic darkroom, but by 1929 a newly renovated Hopkins announced "five dark-rooms, one for general photographic use, three for spectroscopy, polarimetry and photometry, and one heliostat room which derives its light directly from the roof of the building."¹⁰⁵ Photographic techniques and equipment were only one source of increase in required technology. The rising demands of chemistry equipment prompted stations to undergo extensive and costly expansions. Specialized equipment for physiological and chemical work increased the number of private laboratories and slowly, the space of the marine laboratory changed from an open air communal laboratory to a warren of specialized spaces, each dedicated to specific equipment and scientific investigations in seemingly separate disciplines.

With the increase in technologies utilized for research, stations lacked the ability to provide every technology that a researcher might require. Instead, they provided a

¹⁰⁴ Kofoid *The Biological Stations of Europe*, 6.

¹⁰⁵ W.K. Fisher, "The Hopkins Marine Station of Stanford University" *The Scientific Monthly* 29: 4 (Oct. 1929), 301.

baseline of equipment, including all those required for collecting and storing specimens, and advised those needing specialty equipment to send it to the laboratory, either on loan from their home institution or purchased with financial assistance. This section intertwines the dual needs of space and technology to try to ascertain the base pieces of technology that were required for working at marine stations before 1930.

Nets and Vessels

Collecting equipment were the most integral technologies to station function. They rarely relied on one type of collecting, but utilized varied techniques from hand seining to pelagic dredging. In the first few months of operation, the USBF's Beaufort station's director Caswell Grave requested two skiffs, and stated he would also require a sail boat for collecting as soon as funds became available.¹⁰⁶ By the 1905 season, Grave reported that "the equipment for collecting and general field work, which was available to all, consisted of a steam launch, a 33-foot sharpy, nine rowboats, a pound net, a fyke net, seines, serape nets, tow nets, dredges, a trawl and implements for digging."¹⁰⁷ Marine stations supplied researchers with a wide range of collecting apparatus. Based on the 1923 inventory of the equipment of the Carnegie Institute's laboratory in the Tortugas, the laboratory operated six separate collecting boats, including an unnamed 14 foot no engine flat bottom boat, the 10 horsepower engine 25 foot *Veleva*, 8 horse power 25 foot *Darwin*, 2 horse power 17 foot long *Bull Pup* and the 50 horse power 70 foot *Anton Dohrn*.¹⁰⁸ While steam launches and large research vessels such as the *Anton Dohrn* were

¹⁰⁶ Caswell Grave to Hugh Smith. May 27, 1902 Box 1 Folder "Beaufort Laboratory 1899-1904" RU 22 National Archives: Bethesda, MD.

¹⁰⁷ Caswell Grave "The Fisheries Laboratory at Beaufort, Sixth Season" *Science* 21: 541 (May 12, 1905): 732.

¹⁰⁸ Bursar to John W. Mills Aug. 1, 1923 Marine Biology L7/15 Carnegie Institute of Washington Archives: Washington, D.C.

a luxury, and signaled to researchers that they would have access to collecting in a wide array of marine environments, many investigators operated only the simplest vessels for collecting.

The simplest form of boat utilized for collecting was the flat bottom boat or skiff. A small number of people could fit comfortably in this boat as it was rowed up and down the coast with either small hand nets or seine nets dragging in the water. W.E. Castle described the process at Alexander Agassiz's Newport laboratory thus:

About ten o'clock each evening "Thomas" Mr. Agassiz's faithful man-of-all-work, rows slowly up and down the cove skimming the surface of the water with a net. From time to time he lifts the net of fine cheesecloth carefully from the water, turns it inside out and dips it repeatedly in a bucket of water.¹⁰⁹

Thomas brought these buckets back to the laboratory and emptied them into the main sorting aquarium to await the investigators who arrived every morning at 9am. Castle explains that these catches from the rowboat form the basis for most material investigators worked with- occasionally supplemented by dredging from steam-launches and shore combing at low tide.

¹⁰⁹ W.E. Castle, "Summer Work in Maine Zoölogy at Newport" *Science* 548 (Aug.4, 1893): 60.



Figure 5: George Browne Goode (standing in the boat) and Spence Fullerton Baird (nearest to shore) help with collecting at the USBF laboratory in Woods Hole. Northeastern NOAA historical photographs. Northeastern Fisheries Science Center photo archives [available online at <http://www.nefsc.noaa.gov/cgi-bin/photo.pl>] accessed December 15, 2011.

Beyond the simple, human powered flat bottomed skiffs, and the wind powered sail boats, larger launches were required for deep water collecting. Steam powered collecting boats could go long distances and hold many researchers. At the Beaufort laboratory, the *USBF Fish Hawk* and *Petrel* collected directly from the Gulf Stream in deeper water off the coast.¹¹⁰ At the USBF laboratory at Woods Hole, the investigators utilized the *Phalarope* not only as a collecting vessel but to take visitors and family on day cruises. At the Tortugas laboratory, the *Anton Dorhn* was reserved for longer collecting trips and for ferrying investigators to and from Key West: during the 1923 season, the laboratory planned several trips on the *Anton Dorhn* to Jamaica to collect. But the expense of large steam launches, along with local laws that required an engineer on board while the ship was active, made it a large expense for the stations. John Merriam wrote to Asa Schaffer in 1924 that the Tortugas laboratory would be utilizing the *Anton Dorhn* much less than in previous years, but that they hoped to make at least a

¹¹⁰ Wolfe A *History of the Federal Biological Laboratory at Beaufort*, 11-12.

few trips throughout the season. Similarly, the Fish Commissioner, Henry O'Malley, admonished Elmer Higgins for over utilizing the *Phalarope*.¹¹¹

Steam launches were expensive for two reasons: fuel and employees. Steam launches required large amounts of fuel. The earliest launches utilized from 5-15 pounds of coal per Indicated Horse Power per hour. Beyond fuel use, American laws required that an engineer be present on the launch during voyages, and laboratories also kept firemen on launches due to the history of fire on steam launches.¹¹² To keep cost of collecting down, naphtha launches were more commonly utilized in collecting than full sized steam powered boats. Naphtha launch engines resembled small steam engines, but ran off of naphtha (a by-product of oil refinery techniques). Naphtha launches were able to be taken out without an engineer onboard and they were also commonly smaller and took less costly energy to power. The upsides of the naphtha launch were stated thus:

No steam is used in this motor, therefore no licenses of any sort are required, and explosion is practically impossible...An 18 foot launch with a 2-4 horsepower engine will carry from six to ten persons...at a speed of 6 to 8 miles an hour, at a cost of six cents per hour.¹¹³

To minimize costs, most day trips for collecting were taken on sail boats or naphtha launches. But, these smaller launches could not hold as many people, nor could they take collectors on longer collecting trips, and therefore a steam launch was still desired by marine laboratories.

¹¹¹ John Merriam to Asa Schaffer. January 4, 1923. Box 33 Folder 4. Grants. Carnegie Institution of Washington Archives: Washington, D.C.; Henry O'Malley to Elmer Higgins. May 25, 1927. Folder Woods Hole 1919-1931 RU 22 General Correspondence. National Archives: Bethesda, MA.

¹¹² Charles P. Kunhardt *Steam Yachts and Launches; their machinery and management* (New York: Forest and Stream Publishing Company, 1887), 22.; Beaufort hired local men as engineers and firemen. Caswell Grave to Hugh Smith. June 2, 1902. Box No. 1 Folder "Beaufort Laboratory 1899-1904" RU 22 National Archives: Bethesda, MD.

¹¹³ Kunhardt, *Steam Yachts*, 229.



Figure 6 The Steam Launch "Anton Dohrn" at the Carnegie Institution of Washington marine laboratory in Tortugas, Florida. Series 3 Box 7 "Tortugas Folder" Alfred Goldsborough Mayer Papers, Syracuse University Archives: Syracuse, New York.

Collecting also required many varieties of nets. In 1905, Beaufort boasted “a pound net, seines, serape nets, tow nets, dredges, a trawl and implements for digging” that, along with the boats available, put “the entire harbor and adjacent sounds...within easy reach and, during calm weather, trips were made outside the inlet, where dredgings and towings were frequently made.”¹¹⁴ Investigators utilized smaller dip nets, labeled the “handiest and most indispensable piece of equipment that can be used for many purposes and under a great variety of conditions” on daily collecting trips on foot while wandering the shoreline. The dip net had netting that could range from 1 inch mesh to specialized netting made from silk for collecting smaller organisms, such as larval forms and plankton.¹¹⁵ Bigger hauls throughout the season required larger, specialized nets. Not all net types were utilized at every station, a pound net was not a common form of

¹¹⁴ Caswell Grave “The Fisheries Laboratory at Beaufort, Sixth Season” *Science* 21:541 (May12, 1905): 732.

¹¹⁵ Paul S. Galtsoff “General Methods of Collecting, Maintaining, and Rearing Marine Invertebrates in the Laboratory” in *Culture Methods for Invertebrate Animals* Frank E. Lutz, Paul L. Welch and Paul S. Galtsoff (eds.) (New York: Dover Publications, 1937), 6

technology in tropical waters, but marine laboratories sought to provide basic collecting implements so that investigators could have their pick.¹¹⁶

The pound or fyke is a form of net fishing that is fixed throughout a single season in a given location. The nets, which funnel live fishes into an inner chamber to be counted and collected at the discretion of the investigator or fisherman, was often utilized to get an accurate idea of fish stocks available in a given location, as well as to capture new species that might accidentally wander close enough to be trapped within the pound net. In 1913, the Beaufort pound net was fixed at the mouth of the Newport River between Morehead City and Beaufort. Investigators checked it throughout the season, the frequency depending on how many fish were being caught throughout the week. The first boat trip to check the seine for the 1913 season was on June 19, when 138 fish were identified, logged and preserved. By July 12, over 3,000 fish were reported at 9am during the check and investigators were checking the pound net twice a day.¹¹⁷

The pound net served as a point of survey for the station. Fish were caught constantly and could give accurate counts of fish without constant effort from staff. Another advantage is that it caught living fish and held them until they could be processed. While the majority of fish were either released or preserved, several unknown or interesting species were brought back to the laboratory and placed into the aquarium for future study. While the pound was not always successful in catching organisms

¹¹⁶ For an introduction and in depth description of nets, especially those utilized at marine laboratories for collecting smaller organisms closer to shore, see Galtsoff "General Methods of Collecting, Maintaining, and Rearing Marine Invertebrates." For information on pound and seine nets, see Joseph E. Taylor, *Making Salmon: An Environmental History of the Northwest Fisheries Crisis* (Seattle: University of Washington Press, 2001), Chapter 1.

¹¹⁷ "Fishes Taken at Beaufort, N.C. 1913" Box 16 Folder 20 RU 7184 Smithsonian Institution Archives: Washington, D.C. 23, 56.

required for experimentation, it served the purpose of constantly updating surveys of the waters surrounding laboratories.

The seine net was the most widely used net. Weighted on the bottom and buoyed on the top, the seine was a highly flexible collecting technology. During the 1912 and 1913 seasons at Beaufort, log entries of fish catches detail the use of at least five different seine sizes, ranging from a small 12 foot seine operated completely by hand from shore to a 125 foot seine utilized off of the steam launch. Investigators or collectors could utilize seines in any body of water and it could be carried to any location they desired to sample. On June 28, “one haul was made with the 20 ft. [seine] net in the salt pond west of the life saving station. The tide was high and the pond water very muddy. The catch was poor.”¹¹⁸ Seines gave all the advantages of the pound net with the added advantages of mobility and the ability to be operated by a single individual on foot. With the seine net, investigators could focus their collecting on a particular spot and could personally refresh their stock of organisms without the aid of a boat.

Finally, the tow or dredge was a larger net for collecting bottom dwelling organisms, either by hand in shallow water or by winch and tow on steam launches. Tow nets operate exactly as it sounds; a net was dragged behind a moving vessel for a period of time and then collected onto the deck. The dredge is a heavy net usually lowered by winch into the water and dragged behind a steam launch. Dredge technology could be modified to capture specific organisms. The tangle or mop dredge consists of a mop-like grouping of cotton strands attached to an iron bar. The bar is then dragged from the launch for a distance. The cotton strands capture echinoderms and crustaceans that might

¹¹⁸ “Fishes Taken at Beaufort, N.C. 1913” Box 16 Folder 20 RU7184 Smithsonian Institution Archives: Washington, D.C. 33.

otherwise be missed with regular nets. Another modification is the grapple- which consisted of long steel wires bent upward at a 45 degree angle. When utilized during a dredging operation, the grapple dredge could pick up flora, worms, crustaceans and other organisms that were commonly missed by the net dredge.¹¹⁹

Glassware

Jars and bottles were the simplest but most versatile glassware in marine stations. Jars served multiple purposes: preserving, maintaining living species, and even experimenting. When the Carnegie Institute of Washington's Tortugas laboratory #2 was inventoried in 1923, there were over ten varieties of jars and bottles on the inventory sheet, including specimen bottles, museum jars, aquarium jars, water sample bottles, experiment jars, specimen bottles, specimen jars, and tincture bottles. The number of empty bottles and jars in each of the laboratory could number in the thousands.



Figure 7 Alpheus Hyatt Mayer standing in front of glass jars at the Tortugas Laboratory, 1912. Series 3 Box 7 "Tortugas Folder" Alfred Goldsborough Mayer Papers, Syracuse University Archives: Syracuse, New York.

¹¹⁹ Galtsoff, "General Methods of Collecting," 11.

While these jars were categorized for different purposes, the main difference between these pieces of equipment was size. For instance, in the case of aquarium jars- a jar that was utilized to hold a specimen that was either waiting for necropsy or did not need running water to be kept alive- researchers had the choice of five different sizes, ranging from 1.5 to 5 gallons with the most prevalent being 2 gallons. Most jars that were meant to hold specimens were utilized for short term holding cells- there was no circulation in the jars and water quickly became fouled by organisms. Experiment jars were, again, utilized for short term experimentation and were especially useful because they contained an organism in a small space, but were highly mobile. A researcher could carry a jar quickly from room to room if an experiment required mobility.¹²⁰

Aquaria

By the late 1890s, American marine laboratories contained several variations on the balanced and circulating aquarium, including table top, portable, and experimental aquaria. Simply stated, aquaria are equipment for maintaining a living organism in its natural state for an extended period of time. The difference between a simple jar and an aquarium is the amount of time or room one wishes to give a particular organism. Time, in effect, is purchased through a creation of a stable and livable environment. But aquariums were not easily kept. According to Asa Schaeffer, who commonly worked at the Tortugas laboratory and hoped to be able to maintain aquaria while teaching:

A successful aquarium is a very rare object in undergraduate biological laboratories. The difficulties to be overcome in running an aquarium are generally thought to be so great that few are ever started; and if an animal happens to survive, it is usually considered an exceptional or an accidental case.¹²¹

¹²⁰ Bursar to John W. Mills Aug. 1, 1923 Marine Biology L7/15 Carnegie Institute of Washington Archives: Washington, D.C.

¹²¹ Asa A. Schaeffer, "A Simple and Economical Aquarium Aerator" *Science* 31:807 (June 17, 1910): 955.

According to Schaeffer, organisms in aquariums died for two reasons: a lack of food or a lack of oxygen. But, Schaeffer suggests that if the oxygen content of the water is stabilized, minute organisms will grow and survive in the environment as well, providing food for the inhabitants to feed. Therefore, the largest issue in aquarium keeping was providing oxygen to organisms in the aquarium while maintaining livable water purity.

Several forms of aeration were utilized to provide oxygen and fresh water to an aquarium. The simplest form of aeration was either by hand or by a line that pushed oxygen directly into the tank. If a researcher wished to aerate water by hand, they merely dipped something into the water of the aquarium, lifted some water up and then let it gently drop back down. This type of aeration was commonly used by collectors who put their specimens in buckets to be transported back to a laboratory. This type of aeration works temporarily, but eventually, the water will become soiled by the organism and no amount of aeration will keep it alive.

The oxygen pump delivered air directly to the organism by keeping a steady supply of oxygen available. When Johns Hopkins first moved their laboratory to the Beaufort area, they occupied a temporary laboratory in a rented space. Instead of establishing and laying down permanent or semi-permanent pumps to introduce a constant flow of water to aquarium, Henry L. Osborn states that “In their place was used the cheaper and very effective device of aeration by means of a stream of fresh air constantly forced through the aquaria by a Sprengel pump.”¹²² This was also a temporary

¹²² The Sprengel pump was only one of many air pumps utilized by investigators. There were an almost limitless varieties and brands of air pumps- many of the companies listed in the journals went out of business within 5 years. Henry L. Osborne, “The Marine Laboratory of the Johns Hopkins University” *Science* 3: 48 (Jan. 4, 1884): 9. For more information on aeration with compressed air pumps, see Galtsoff, “General Methods,” 19.

solution for keeping organisms alive in an aquarium; while the water would remain oxygen rich, it became filled with the waste of whatever occupied the space, and the organism would die. There was also a fear of over- or under- oxygenating an organism with this method; without further study it was very difficult to know the oxygen requirements of specific organisms. Both hand aeration and oxygen pumps were temporary fixes for keeping organisms alive in aquariums.

The longer term solution was to continuously pump fresh water through the aquarium system. Water lines, made of lead, rubber, wood, or glass, brought fresh or salt water directly to an aquarium. Water was brought into the aquarium by hooking the aquarium attachment to the water line on either the nearest work table, or in a given room (if the aquarium was portable). The aquarium would then have an overflow valve or a separate pipe, which funneled water out of the aquarium and into recirculation or filters. In this way, the tank was constantly supplied with oxygenated water, and toxins released by the living organisms were not able to build up in the tank, keeping the specimens alive for a longer period of time. This system also allowed investigators to feed the organisms they needed to be kept alive for extended experimentation. The excess food and waste would be washed out of the tank with the old water. Most laboratories advertised the ability to pump fresh water into aquariums, either directly from their water source, or from a cistern stored on the laboratory grounds. The ability to supply both fresh water and salt water directly to aquariums was also highly coveted by researchers.¹²³

¹²³ Galtsoff, "General Methods," 13-26.

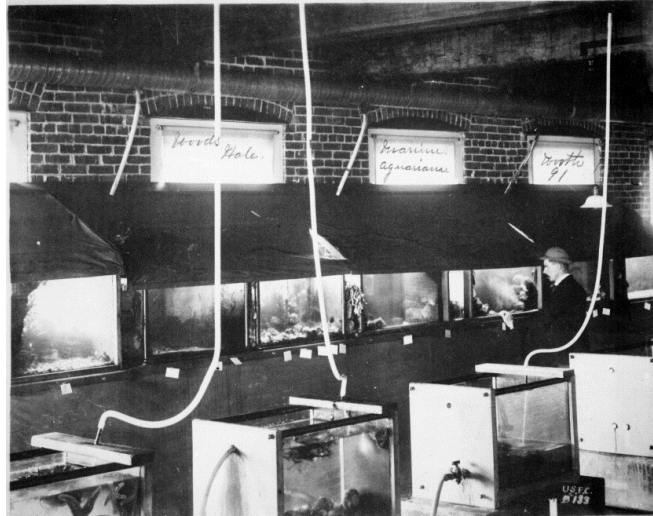


Figure 8 Water was transferred from pipes in the ceiling into the aquaria, and evacuated out of the bottom through another pipe. In this photo you can see a large water supply pipe near the beams on the back wall. Circa 1920. Northeastern Fisheries Science Center photo archives [available online at <http://www.nefsc.noaa.gov/cgi-bin/photo.pl>] accessed December 15, 2011.

Researchers utilized several types of aquaria in their daily work. The first aquarium that they might encounter was a large, free standing aquarium placed in the center of the laboratory to hold the specimens caught by the laboratory collector. The center salt water tank at the Tortugas laboratory was 25'X 12'X 3'.¹²⁴ This aquarium, usually the largest standing aquarium in the laboratory, was hooked up to a constant supply of running water. Throughout the day, organisms could be added to the tank. Commonly, organisms that were secured in the field that were either unknown, or that investigators desired to further examine while living, were placed into the main tank for observation. On July 12, 1930, Lewis Radcliffe found a male *felichtys felis* (sea catfish) with 6 young arranged in his mouth. The adult was necropsied that day, but the six young fish were taken back and kept in the main laboratory aquarium for almost a week

¹²⁴ Bursar to John W. Mills Aug. 1, 1923 Marine Biology L7/15 Carnegie Institute of Washington Archives: Washington, D.C.; For other examples of the setup and size of main aquariums, see the blueprints of the Beaufort Laboratory. *Report of the U.S. Commissioner of Fishes* (1902), 11-16

when “they died because the water was accidentally turned off overnight.”¹²⁵ If a particular specimen was desired by a researcher, they could then transfer that organism from this larger tank to a smaller table tank at their particular work station.

Another type of aquarium that researchers encountered at the marine laboratory was the individual table tank. Each researcher occupied a table in the laboratory, and each table held an aquarium with running water that held whatever organisms that the researcher planned to work on that day. These tanks usually contained only the organism that one researcher was working on at that time. When T.H. Morgan worked with *Ilyanassa Obsoleta* (Eastern mudsnail) at Woods Hole, he kept 30-40 snails in a “large aquarium of running sea water and fed [the snails] daily on 1 or 2 clams broken into pieces.”¹²⁶ Morgan needed to keep the snails at his work station to be watched closely for the moment when they would deposit their eggs.¹²⁷ By providing investigators with their own individual table aquariums, laboratories allowed each researchers space to closely observe their organisms or to create their own experimental systems.

There were two specialty aquariums that were often utilized in the laboratory space. The first was the portable or movable aquarium. In 1868, Anton Dohrn and David Robertson modified the circulating aquarium (see the introduction) to create a portable aquarium. The portable aquarium was mounted on the beach and provided living specimens with a constant flow of sea water through tubing extended into the ocean and a small pump.¹²⁸ These aquaria were often utilized to take specimens into specialized

¹²⁵ Lewis Radcliffe, William Crozier and Selig Hecht “Log Fishes Taken at Beaufort, NC June-Sept. 1912” Box 16. RU7184 Smithsonian Institution Archives: Washington, D.C., 57.

¹²⁶ T.H. Morgan “The formation of the antipolar lobe in *Ilyanassa*” *The Journal of Experimental Zoölogy* 64:8 (1933): 433.

¹²⁷ Morgan, “The formation of the antipolar lobe,” 434.

¹²⁸ Christiane Groeben, “The Naples Zoological Station and Woods Hole” *Oceanus* 27 (1984): 62; Maienschein “History of American Marine Laboratories,” 17.

rooms of the laboratory. Studies on phosphorescence in fishes often meant taking animals in and out of dark environments, either to stimulate different times of day or to view organisms' reactions to light conditions. Before installing a heliostat in the laboratory during a 1929 renovation, the Hopkins Marine Laboratory stated that "from the third floor a stairway gives access to the flat, parapeted roof" where movable aquariums could be set up as needed.¹²⁹ Utilizing mobile tanks allowed the investigators to transfer organisms to different locations within the laboratory without having to take them out of water that was a similar temperature and causing them undue distress.

The final type of specialty tank that investigators might utilize was not a piece of glassware, but was instead known as a floor tank. Floor tanks were constructed out of cement, usually on the bottom floor of a laboratory. Not every station had an indoor floor tank but many had holding tanks of a similar size located outside of the laboratory. These tanks were more prevalent where researchers and collectors were likely to bring in large organisms that might still be living. In Beaufort, the floor tank on the first floor of the laboratory building often contained sea turtles or large fishes that researchers wished to observe before they preserved the animal. At Hopkins the cement floor tank was 6 by 14 feet located in the physiology laboratory for observing and maintaining experimental organisms.¹³⁰ These tanks often served as a catch-all for larger organisms or for experiments that required large amounts of swimming space. The downside to cement tanks was that the contents were only visible from above, meaning that they were often a last resort for experiments that required the constant observation of organisms.

¹²⁹ W.K. Fisher, "The New Hopkins Marine Station at Stanford University" *Science* 47: 1217 (Apr. 26, 1918): 411.

¹³⁰ *Report of the U.S. Commissioner of Fishes* (1902): 11-16; Fisher, "The New Hopkins Marine Station," 411.

Visual Apparatus

One of the most common technologies utilized at marine laboratories, and one of the least commonly provided, was the microscope. Marine laboratories suggested that people who would need microscopes for their daily work, especially if they needed microscopes that were high powered, should bring their own. When the MBL opened its doors in 1888, they stated that “Microscopes will not be provided, but it is believed that investigators will find most of their indispensable wants satisfied.”¹³¹ In 1928, M.W. de Laubenfels wrote the Carnegie Institution of Washington to request \$250.00 for a microscope to take with him to the Beaufort, MBL and Tortugas stations that summer. The Carnegie Institution, who had agreed to fund de Laubenfels’ work on sponges through a \$2,000 fellowship that year, believed that he should utilize an old microscope at the laboratories. But de Laubenfels reminded the administrative secretary that neither Beaufort nor Tortugas provided adequate amounts of microscopes to investigators and those provided were of the meanest sort. In the end, Gilbert granted de Laubenfels the \$250.00 for a new microscope- a huge expense given that his family was expected to live off of \$150.00 a month throughout the year.¹³² Microscopic work required specialized chemicals to fix specimens and to bring certain structures into view; these chemicals were provided and stocked for researchers, but microscopes were not.¹³³

Another specialized form of equipment was the camera and dark room. The need for multiple types of dark rooms rose in the early twentieth century- progressing from a simple darkroom to six separate rooms with four different uses. Marine laboratories

¹³¹ “The Marine Biological Laboratory” *Science* 11: 282 (June 29, 1888): 306.

¹³² M.W. deLaubenfels to W.M. Gilbert. Jan.3-10, 1928. Box 12 Folder 12 Grants. Carnegie Institute of Washington Archives: Washington, D.C.

¹³³ “The Annisquam Seaside Laboratory” *Science* 5: 110 (March 13, 1885): 211-213; Bursar to John W. Mills Aug. 1, 1923 Marine Biology L7/15 Carnegie Institute of Washington Archives: Washington, D.C;

provided darkroom space and camera equipment for visiting researchers. When the Tortugas laboratory was inventoried in 1923, the laboratory owned an 8 by 10 century view camera, a press graflex camera without lens, four camera tripods, two Eastman Kodak trimming boards to edit photos, and an underwater camera apparatus.¹³⁴ If researchers wanted unrestricted access to photographic equipment, or required specialized equipment for their purposes, they were expected to bring it with them.

In a combination of the previous two specialized technologies, the photomicrographic camera- a camera that could be attached to a microscope to take pictures- was not provided by most laboratories. Asa Schaeffer, who received a grant for the Carnegie Institute in 1925, was able to purchase a photomicrographic camera for his work on amoebas. While this particular funding was for a trip to Labrador, Schaeffer wished to keep the equipment for future work at the Tortugas laboratory. In all, he spent nearly \$75.00 of his \$700.00 budget on camera equipment.¹³⁵ X-rays, which became very popular in marine science in the 1920s, were provided by larger marine laboratories but were uncommon at the smaller stations.¹³⁶ Investigators utilizing specialized visual equipment, such as microscopes, cameras, and photomicrographic cameras were expected to bring their equipment with them, but the space and chemicals to operate these technologies was provided by the station.

¹³⁴ Bursar to John W. Mills Aug. 1, 1923 Marine Biology L7/15 Carnegie Institute of Washington Archives: Washington, D.C This reference to an underwater camera is somewhat confusing. The first underwater picture is said to be completed by Longley in 1927 with the help of a glass box to protect the camera and an enormous magnesia flare for underwater illumination. Before this photo (published in National Geographic), scientists at Tortugas and elsewhere were experimenting with taking photos through panes of glass perched just atop the water, but I am still unaware of why they would have listed this camera as an “underwater camera complete.”

¹³⁵ Asa Schaeffer to W.M. Gilbert Nov. 5, 1925. Box 33 Folder 4 Grants. Carnegie Institute of Washington Archives: Washington, D.C.

¹³⁶ Frank R. Lillie “Plans for the Enlargement of the Marine Biological Laboratory” *Science* Vol. 59 No. 1530 (Apr. 25, 1924) 371-372.

Conclusion

Investigators could shift from one marine laboratory to another with the knowledge that each institution provided both a singular experience into a slice of the ocean environment and also the baseline equipment required for research with living organisms. Historians of science have continuously called attention to the impact of the Naples Zoological Station to the development of the Marine Biological Laboratory at Woods Hole. This importance has been examined, but there is no question that investigators who sought to found new marine laboratories to explore new coastlines and waters were influenced by their work at other institutions. When Alfred Goldsborough Mayer proposed and planned the Tortugas Laboratory, he consulted directors of other marine laboratories. As a student he visited marine laboratories with his mentor Agassiz, and even after the opening of Tortugas he continued to visit other locations, including the Johns Hopkins laboratory at Port Royal, Jamaica and the New York University-Harvard laboratory in Golden Cay, Bahamas. William Ritter worked at the NZS and visited the laboratory at Misaki, Japan before planning his own station. He continuously referred to Naples and the Johns Hopkins Stations during the construction of the marine station in San Diego.¹³⁷ The first cohort of researchers that founded and utilized marine laboratories created a coherent network of institutions that served to connect them to individual locations and also facilitated study of the larger marine environment.

The multitude of seemingly disparate marine stations founded in the United States shared common goals: each was committed to finding the optimum location from which to observe, collect and maintain living marine organisms for scientific study. Each station

¹³⁷ William Ritter to unknown, Feb. 10, 1893. Box 1 Folder 1879-1904. William E. Ritter Papers. Bancroft Library. UC Berkeley: California.

maintained baseline technologies and living conditions that allowed researchers to perform experiments with similar equipment at each location. Those founded in the United States at the end of the 19th century looked to European and Japanese stations such as the Naples Zoological Station (1872), the Marine Biological Station at Misaki (1887) and the Plymouth Laboratory in England (1888) to model their facilities. By examining the criteria involved in choosing a location for permanent laboratories, and the techniques and technologies for studying the flora and fauna at those locations, we are able to view these marine laboratories as pieces of a coherent scientific network. These laboratories, and their similarities in practice if not place, form the institutional basis for 20th century biology and marine science in America (and internationally) at the turn of the twentieth century. The following chapters will highlight work done at these stations and trace the exchange of information and research between these institutions.

Chapter 2

Imagining the Ocean: the importance of field work on marine scientific portraiture

In the December 1934 issue of *National Geographic Magazine* readers were introduced to startling creatures living over a mile below the ocean's surface. Eleven color plates painted by Else Bostelmann accompanied William Beebe's description of organisms encountered from his Bathysphere on the deepest manned-dive accomplished at that time. Bostelmann's illustrations depicted newly discovered species in startling color and motion. These seemingly alien organisms appeared life-like in their cold and lifeless environment. But these polished illustrations belied their creation-story: the images accompanying the article were created through collaboration between Beebe and Bostelmann that relied more on memory and imagination than traditional taxonomic tools of extensive observation and preserved specimens. Many of the organisms in the paintings had yet to be captured through trawling practices and there was no capture mechanism on the Bathysphere. The newly described *Bathysphaera intacta* or 'untouchable Bathysphere fish' was so named because it was only seen by Beebe for moments and had yet to be caught in a net. Beebe explained to the reader that the finished images of these organisms were cobbled together using his sketches, communications with the boat during dives, and eventually, from Else Bostelmann's imagination.¹³⁸

¹³⁸ Bostelmann illustrated ten of the eleven colored plates included in the article. The final illustration was done by E.J. Geske. William Beebe. "A Half Mile Down: Strange Creatures, Beautiful and Grotesque as Figments of Fancy, Reveal Themselves at Windows of Bathysphere" *National Geographic Magazine* (Dec. 1934) 661-704.

Bostelmann did not accompany Beebe in the Bathysphere, nor did she personally examine many of the creatures she became famous for illustrating. This does not mean she had no reference for her work; through extensive training and field work she developed the skills required of marine taxonomic illustrators during this period. Bostelmann was born in Leipzig and trained as an artist at the Grand-Ducal Academy of Fine Arts (renamed Bauhaus in 1919) before immigrating to America in 1909. She accompanied Beebe on four expeditions to the New York Zoological Society's marine station at Castle Harbor, Bermuda between 1929 and 1934.¹³⁹ In the field, Bostelmann expanded her understanding of the underwater environment and its inhabitants. During Beebe's 1932 expedition, she donned a bathing suit and diving helmet to paint living fishes in their underwater environment. Bostelmann used underwater research to develop an understanding of the natural movement of marine animals and sketched impressions of their movements with oil paints on slate during her dives.¹⁴⁰ Her 1934 collaboration with Beebe drew upon both her formal artistic training and her time in the field.

¹³⁹ "Else Bostelmann, Artist, Dies at 79: Painter of Sea Life Served on Beebe Expedition" *New York Times* (Dec. 29, 1961) 24.

¹⁴⁰ T.C.L. "Sketches Made on Sea Bottom" *New York Times* (Dec. 21, 1932) 17.



Photograph by John Tee-Van

Figure 9: Photograph of Else Bostelmann working on illustrations at Castle Harbor, Bermuda. Similar to portraits of scientists during this period, artists are commonly pictured next to the scientific apparatus they utilized in their work. The most common technologies included in these portraits are microscopes and aquariums. William Beebe “A Half Mile Down” *National Geographic Magazine* (Dec. 1934): 686.

The establishment of stable marine stations allowed scientific illustrators access to a new form of natural knowledge that enhanced their craft. Naturalists and collectors had long relied on trained draftsmen to transform field notes and hastily preserved specimens, or “actual specimens,” into scientifically accurate and artistically striking marine images, or “virtual specimens.”¹⁴¹ Marine portraits¹⁴² presented special difficulties; the inability of field naturalists to visually access the submarine environment from which their subjects originated meant that they relied more heavily on the discretion and imagination of their artists in choices of background, coloring, and depictions of movement. Marine field

¹⁴¹ Anne Larsen, “Not Since Noah: The English scientific zoologists and the craft of collecting, 1800-1840” (PhD diss. Princeton University, 1993) 37.

¹⁴² Isabel Cooper referred to her work as “living portraiture” as did some marine photographers. I have adopted this term over “taxonomic illustration” to encompass a wider swath of images that appear, not only in scientific peer-reviewed journals, but also in more mainstream publications such as *National Geographic* and more widely distributed sources such as field guides. Isabel Cooper, “Artist at Large,” *The Atlantic Monthly* (July 1926) 85.

work facilitated a deeper understanding of the inaccessible environment by allowing artists to both view organisms for extended periods with aquaria and to work in field locations close to the their subjects' origins.

Marine stations and the aquarium technologies therein provided space for artists to view living marine specimens for extended periods. Previous marine exploration relied primarily on sampling or sounding off a ship or distant shoreline. Specimens collected were recorded and preserved, but they often remained the sole example of their species and became default type specimens. The specimen was often mangled or partially destroyed from seining and dredging methods; preservation in alcohol caused discoloration or even dissolution in the case of many ctenophores. Often the specimen described by naturalists was the only example of that species available; issues with collecting and preservation limited both taxonomic description and the accompanying illustrations.¹⁴³

Seaside stations were close enough to the source of collection and survey that specimens could be transferred from collecting vessel to aquaria for extended viewing. This simple extension of lifespan in the laboratory was essential to all of the experimental life sciences in these spaces (as we will see in the rest of this dissertation) and it had a profound impact on scientific illustration.¹⁴⁴ Instead of working exclusively with field notes and preserved specimens, illustrators could view live subjects for extended periods. Increased access to freshly caught living specimens gave illustrators an idea of the

¹⁴³ For a history of deep sea exploration see Helen Rozwadowski, *Fathoming the Ocean: The Discovery and Exploration of the Deep Sea* (Boston, MA: Harvard University Press, 2008). Anne Larsen, "Equipment for the Field" in *Cultures of Natural History* ed. N. Jardine et al. (Cambridge, UK: Cambridge University Press, 1996) 358-377

¹⁴⁴ Hannah Landecker, has discussed the importance of lifespan extension in the laboratory on 20th century life sciences. See *Culturing Life: How Cells Became Technologies* (Boston: Harvard University Press, 2007).

movements and habits of marine organisms that informed not only individual portraits but their entire *oeuvre*.

In addition to organismal access, artists in these stations experienced and constructed conceptions of the natural world. Few illustrators claimed the type of access to the marine environment that collectors did during this period; many came from urban areas and, if they had ever visited the shore, had done so on vacation in resort locations. At the turn of the 20th century, beach visitation was still a limited form of leisure, and although it was growing more popular, it was not as culturally pervasive as it is today.¹⁴⁵ The ability to spend extended periods of time experiencing the ocean, illustrating from shore, and sometimes diving below, allowed artists to form ideas of the natural environment from which their subjects had originated. While not every artist used diving gear to literally immerse themselves in the experience of the marine environment, other artists spent up to 7 years in the field, studying fish both in the laboratory and as they swam lazily under docks or wriggled in nets.

The experiences afforded artists at marine laboratories impacted their scientific illustrations and in turn, the portrayal of scientific knowledge in ichthyology. Pamela Smith has emphasized the importance of natural experiences in the production of knowledge of craftsmen and artisans during the scientific revolution. Smith's work highlights the impact on scientific knowledge production by artisans. Historians tend to privilege the "theorizer" over the "maker" but the author seeks to place artisans in the center of knowledge production to examine their impact on the finished product. Smith examines the importance of artists' own naturalistic understandings and their traditional

¹⁴⁵ Alain Corbin, *The Lure of the Sea: The Discovery of the Seaside, 1750-1840* (New York: Penguin Books, 1995)

training in printing techniques to produce some of the most iconic images of the Early Modern Period. According to Smith, these illustrations, which highlight collaboration between the naturalist and the artisan, conveyed important knowledge claims during this period.¹⁴⁶ Smith's focus on the experiences of the artisan, and its impact on knowledge production, can be applied to illustrators working at marine laboratories at the turn of the twentieth century.

Field work, and the experiences of a place from both a scientific and personal perspective, affected the products of naturalists and scientists during this period. Field work gave illustrators access to what Anne Larsen has labeled the “content” and “context” of their subjects. *Content* refers to “internal anatomy, its living colors, the forms it assumed at different points in its life cycle, whether it was sexually dimorphic and what its hunting techniques were, how it selected a mate, and so on.” Field experience helped illustrators pair understandings of biology and behavior with *context*: an understanding of the environment where it was collected. Both Larsen and Robert Kohler highlight the importance of thinking about “residential science” as a significant experience in a scientist's life that impacted the type of work produced. The process of living in and coming to know a given environment was essential in certain types of scientific understandings during this period.¹⁴⁷ According to Larsen, “In order to learn an animal's content and context, one needed to see the living creature—preferably several of them—in its natural habitat, and to record one's observations on the spot. In addition, the zoologist could learn a great deal about an animal from the local people who dealt with it

¹⁴⁶ Pamela H. Smith, “Art, Science, and Visual Culture in Early Modern Europe” *Isis* 97:1 (March 2006): 83-100; Pamela H. Smith, *The Body of the Artisan: Art and Experience in the Scientific Revolution* (Chicago: University of Chicago Press, 2004).

¹⁴⁷ Robert E. Kohler, *All Creatures: Naturalists, Collectors, and Biodiversity, 1850-1950*. (Princeton: Princeton University Press, 2006); Robert E. Kohler, “Paul Errington, Aldo Leopold, and Wildlife Ecology: Residential Science,” *Historical Studies in the Natural Sciences* 41:2 (Spring 2011): 216-254.

routinely because they ate it, used it for decoration, avoided its poison, and so on.”¹⁴⁸

According to Larsen and Kohler, extended work in the field was integral to the naturalist’s process. If we shift the focus from naturalists and scientists at marine stations to the artisans who were also present, we can see that “residential art” was also important and that it impacted the scientific knowledge eventually produced.

This chapter will examine the impact of artistic field work, and especially work done at marine station, on scientific illustrators during this period. Marine stations became a shared space, not just for scientific researchers, but for multiple professional groups that worked to make the marine world visible to both the public and scientific communities. The new laboratories gave artists access to not just fresh and living specimens, but to the larger field experience. Artisans flocked to these spaces to illustrate newfound species for the scientific community. There, they developed visions of the marine environment through extensive research and field work, and applied this experience to their scientific portraits. By adding artisans into our picture of the professional groups who worked at marine stations, and by acknowledging that taxonomic portraits were the combined effort of both researchers and individual artisans, we can see that permanent stations impacted not just the way that marine science was conducted during this period, but also the development of a wider vision of the marine environment.

Survey Work

Before examining the impact of field work on scientific illustration, it is important to understand the larger scientific endeavor to which these artists were engaged. The

¹⁴⁸ Anne Larsen, “Not Since Noah,” 38-39.

proliferation of marine stations at the turn of the twentieth century opened up large stretches of previously unexplored shoreline for biological survey and exploration. Robert Kohler's work explores the rise of biological surveys at the end of the twentieth century, and finds that the proliferation of field stations facilitated this form of scientific knowledge production. The biological survey can be distinguished from previous biological exploration and collecting by its methods and goals: they were "methodical, systematic, and disciplined" long-term collecting expeditions meant to provide a nearly complete inventory of animal life in a given location.¹⁴⁹ Surveys were socially complex scientific endeavors that relied on the expertise or "cosmopolitan knowledge" of professional groups such as collectors, taxonomists, artists, and support staff and also the "local knowledge" that these individuals gained, both from locals who lived in these remote areas and from exposure to a particular locality during the survey. Kohler's work focuses on terrestrial surveys, and states that the majority of surveys focused on vertebrate organisms during this period.¹⁵⁰ 'Wet' specimens, or invertebrates such as mollusks, polyps, and medusa that needed to be preserved in an alcohol solution, were more difficult to preserve for museum or personal collection displays. For this reason, Kohler may have found fewer instances in which marine surveys were undertaken to collect specimens for these types of displays.¹⁵¹ However, multiple private and government agencies sponsored surveys of large swaths of the American coastline during this period, the largest being the United States Bureau of Fisheries.

¹⁴⁹ Kohler, *All Creatures*, 2006.

¹⁵⁰ *Ibid.*

¹⁵¹ See Larsen, "Equipment in the Field," 359-360. For a more in depth discussion of preservation issues, see Chapter 3 "A Bundle of Nerves: Jellyfish and Neurophysiology at Marine Laboratories, 1850-1930."

The United States Bureau of Fisheries funded major surveys of the American coastline throughout the early twentieth century. The U.S. Fish Commission (renamed the USBF in 1902) was founded in 1871 to arbitrate fishing disputes between states regarding diminishing stocks in the North Atlantic. Investigations of species availability and methods of capture integrated research scientists' academic knowledge with understandings of fishes and perceived changes in their habits based on local observations by fishermen and residents. Spencer Baird, the head of the Commission, deemed this initial survey ineffective and suggested a more extensive and intensive study of fish stocks and general aquatic resources in U.S. waters.¹⁵² Baird's vision of a more complete survey of marine resources led to the founding of the USFC laboratories at Woods Hole, MA, and Beaufort, NC. Each year, researchers conducted systematic surveys along the Atlantic coast of the United States. During off seasons, collectors such as Vinal Edwards and Charles Hatsell continued surveying by recording daily catches and monitoring the area for changes only visible over the course of the year.¹⁵³ But government biological surveys at USFC laboratories accounted for just a slice of marine surveys occurring during this period. The USFC in conjunction with local marine stations supported a wide array of surveying along the American coastline.

Biological surveys were typically performed to ascertain the suitability of a location for the establishment of a permanent field laboratory. Locations were scouted for specimen availability; a short part of a summer collecting season was usually devoted to

¹⁵² Dean C. Allard, *Spencer Fullerton Baird and the U.S. Fish Commission* (New York: Arno Press, 1978);

¹⁵³ Dean C. Allard, "The Fish Commission Laboratory and Its Influence on the Founding of the Marine Biological Laboratory," *Journal of the History of Biology*, 23:2 (1990) 251-270.; Paul S. Galtsoff, *The Story of the Bureau of Commercial Fisheries Biological Laboratory Circular 145* (Washington, D.C.: Department of the Interior, 1962);

Douglas A Wolfe, *A History of the Federal Laboratory at Beaufort, North Carolina 1899-1999* (Washington, D.C.: U.S. National Oceanic and Atmospheric Administration, 2000).

surveying a potential area. After a site was chosen, labs commonly published yearly surveys that highlighted both the most consistently available specimens in the area and the discovery of new species. Throughout the season, graduate students and collectors recorded daily catches at stations around the laboratory. In 1904, William E. Ritter, the head of the San Diego Marine Biological Association Laboratory, described their long-term survey plans to Alexander Agassiz. They included dredging and sounding from 500 to 2000 fathoms, year-round plankton collecting and analyzing, and collecting and recording the movements and behaviors of the “simplest pelagic organisms.” After outlining their plan for research, Ritter highlighted the expense of extensive surveying, stating “You will readily see that our aims are quite comprehensive and that they can be carried out only at the expenditure of considerable sums of money, and by the organized effort of a rather large number of scientific people.”¹⁵⁴

The social complexity of surveying that Kohler describes can be seen on the institutional level with multiple groups contributing resources to a single survey. The San Diego Marine Biological Association was comprised of a group of citizens bankrolling research on their local marine environment, but their financial support was not enough to fully fund the coastal survey that William Ritter wished to perform around San Diego. Ritter contacted the US Fish Commissioner George Bowers in 1902 to ask for additional funding. The Commission had yet to secure a permanent laboratory location on the West Coast and Ritter hoped that there could be a coordinative or cooperative effort between them.¹⁵⁵ Bowers replied that, at the time, there were few funds for a West Coast

¹⁵⁴ William Emerson Ritter to Alexander Agassiz. April 11, 1904 Box 1 Folder Outgoing Letters 1879-1904. William Emerson Ritter Papers Bancroft Library: Berkeley, CA.

¹⁵⁵ William Emerson Ritter to George M. Bowers Nov 7, 1902. Box 1 Folder Correspondence 1902 William Emerson Ritter Papers 1893-1944 Scripps Oceanographic Institution: La Jolla, CA.

survey, but by 1904 H.M. Smith, Bowers' successor, wrote to Ritter to coordinate a survey between the Stanford Hopkins Marine Laboratory in Palo Alto, the University of California Laboratory in Monterey, and the USFC. The USFC provided the *USS Albatross* to facilitate deep sea dredging and collection, and offered Ritter's researchers onboard accommodations during the survey. In addition, they paid for publication of results.¹⁵⁶ Ritter also sought collaborative work with E.H. Harriman, the wealthy railroad magnate and funder of the Harriman Alaska Expedition in 1899 in which Ritter had participated.¹⁵⁷

But surveys were not merely collaborative on the institutional level; these endeavors required a wide range of staff. Ritter actively recruited researchers to San Diego to work on collections taken during the survey. In April, 1904, he invited G.H. Parker to spend 6 weeks in San Diego working on copepods collected during the survey. In addition to compensation, Ritter promised Parker a capable person to help sort the collection and assist in illustrations.¹⁵⁸ Biological surveys required at least one illustrator; many times researchers brought several individuals with different styles (this will be explored later in the chapter). Researchers often sought to capture specimens at their freshest with crude field drawings or quick photographs, but these forms of imaging were inadequate for capturing pertinent information about the specimen and for eventual

¹⁵⁶ Hugh Smith to William Emerson Ritter Jan. 9, 1904. Box 1 Folder Correspondence, January-May 1904 William Emerson Ritter Papers 1893-1944 Scripps Oceanographic Institution: La Jolla, CA.

¹⁵⁷ William Emerson Ritter to the President and Board of Trustees of the Carnegie Institution of Washington Feb. 7, 1902; William Emerson Ritter to E.H. Harriman April 20, 1902 Box 1 Folder Correspondence 1902 William Emerson Ritter Papers Scripps Oceanographic Institution: La Jolla, CA. See also William Emerson Ritter to E.H. Harriman Feb. 20, 1901 Box 1 Folder Outgoing Letters, 1879-1904. William Emerson Ritter Papers Bancroft Library: Berkeley, CA.

¹⁵⁸ William Emerson Ritter to G.H. Parker. April 11, 1904. Box 1 Folder Outgoing Letters 1879-1904. William Emerson Ritter Papers Bancroft Library: Berkeley, CA.

publication: to do both of these, a professional draftsman was required.¹⁵⁹ The importance of the artist to the success of a survey cannot be overstated: illustrations that were completed quickly and accurately helped maintain costs and ensure that work need not be redone. And although artists could work with preserved specimens and field notes, it was optimal if the artist could see live specimens and experience the marine environment for themselves. Several variables, including survey location, financial compensation, and artistic style, constrained the process of choosing an illustrator.

Location was a particularly large constraint because of the varied locations and extended time of surveys. If the survey was taking place in a particularly remote region, a female artist might be unacceptable. Neither the USBF laboratory at Beaufort, NC nor the Carnegie Laboratory in the Tortugas had facilities for women; although a large amount of marine illustrators (and scientific artists in general) were female, their sex still constrained their career choices and especially access to field work.¹⁶⁰ This does not mean that women were not allowed at marine stations. The New York Zoological Society Station in Bermuda employed Else Bostelmann and Isabel Cooper and David Starr Jordan relied heavily on the work of Chloe Lesley Starks at the Hopkins Marine Station in Palo Alto, CA. But the remote nature of much of the field work was time consuming and required an artist able to travel for large stretches of the year. In 1914, Alfred Goldborough Mayer hired Stanley J. Rowland for a three month survey of aquatic

¹⁵⁹ Investigators often used photography in the field to supplement their sketching. J.I. Hamaker to Hugh Smith, Sept. 5, 1902 Box No. 1 Folder Smith Papers "Beaufort Laboratory 1899-1904" RU22 NARA II: Bethesda, MA.

¹⁶⁰ There were some female illustrators who traveled with male researchers, but they commonly visited these remote marine laboratories for short periods and were not in residence without those researchers. For general information on female scientific illustrators during this period, see Sally Gregory Kohlstedt, "In from the periphery: American women in science, 1830-1880." *Signs* 4:1 (Autumn, 1978): 81-96.; Barbara T. Gates, *Kindred Nature: Victorian and Edwardian Women embrace the Natural World*. (Chicago: University of Chicago Press, 1998).

organisms in Jamaica.¹⁶¹ Working in the field meant travel to a remote location, time in the field, and then travel home. In 1901, Charles Bradford Hudson traveled from Washington, D.C. to Hawaii to work on a USBF survey of the newly acquired Hawaiian Islands. He left D.C. for California in mid-May, and left California for Hawaii by June first. He painted fishes in Hawaii for June and July and then returned to the states in August.¹⁶² Other illustrators relocated to marine stations for years; Isabel Cooper spent seven years on various expeditions for the Tropical Research Station of the New York Zoological Society, much of that time spent at the Society's marine station in Kartabo Point, Demerara (now Guyana).¹⁶³

In addition to location, artists expected different levels of compensation. It is difficult to find records of how much illustrators were paid, and the rate and rubric vary. A common form of compensation seems have been monthly payment, including room, board, and traveling expenses. Alfred Goldsborough Mayer recorded in his notebooks that he “agreed to give him [Rowland] \$80 per month and traveling expenses and board for 3 months.”¹⁶⁴ Charles Bradford Hudson was given \$60 a month for his work with Barton Evermann surveying Golden Trout in the Grand Tetons and also received compensation for each finished illustration.¹⁶⁵ Other artists were paid according to finished products. In a 1901 letter from David Starr Jordan to Henry Fowler, Jordan invites Fowler to the Hopkins Station, telling him that “there are about 200 species here

¹⁶¹ Notebooks Series 4 Box 9 Alfred Goldsborough Mayor Papers Syracuse University Library Manuscripts Collections: Syracuse, NY.

¹⁶² Victor G. Springer and Kristin A Murphy, “Drawn to the Sea: Charles Bradford Hudson (1865–1939), Artist, Author, Army Officer, with Special Notice of His Work for the United States Fish Commission and Bureau of Fisheries” *Marine Fisheries Review* 71:4 (2009): 18.

¹⁶³¹⁶³ Isabel Cooper, “Artist at Large,” *The Atlantic Monthly* (July 1926): 85.

¹⁶⁴ Notebooks Series 4 Box 9 Alfred Goldsborough Mayor Papers Syracuse University Library Manuscripts Collections: Syracuse, NY

¹⁶⁵ Springer and Murphy, “Drawn to the Sea,” 18.

to be drawn, and the Smithsonian pays fifty cents a square inch, multiplying the greatest length by the greatest depth. The drawings are usually made large and then reduced.”¹⁶⁶

Another system involved paying for each individual drawing. Later in his career, Hudson often received between five and ten dollars for each drawing he completed for the USBF.¹⁶⁷ The variability of payment might suggest that researchers would try to hire the cheapest illustrator, but this was not necessarily the case. Certain artists were considered more capable than others, and particular styles developed by these individuals contributed to the final project. In the next section, we will examine the education of the artist and why it was important to match specific artistic visions with scientific researchers.

The Artist’s Education(s)

The process of becoming a scientific illustrator incorporated both traditional artistic training and investigation of the natural world through personal exploration and field work; this combination of experiences created illustrators that were technically accurate and also artistically distinct in their naturalistic depictions. Although there were many struggling artists willing to travel into the field, certain individuals were highly valued and courted for their specific style. This section will examine how illustrators developed their individual perspectives on the marine environment.

Most scientific illustrators received some formal artistic training. Isabel Cooper, a staff artist for the New York Zoological Society who worked with Beebe in Bermuda, attended one year of college at Bryn Mawr and another at Cornell. She eventually shifted

¹⁶⁶ David Starr Jordan to Henry Fowler Feb. 20, 1901 as quoted in William F. Smith-Vaniz and Robert McCracken Peck, “Contributions of Henry Weed Fowler (1878-1965), with a Brief Early History of Ichthyology at The Academy of Natural Science of Philadelphia,” *Proceedings of the Academy of Natural Science of Philadelphia* 143 (1991): 181.

¹⁶⁷ Springer and Murphy “Drawn to the Sea,” 19.

her focus to art and studied at an art school in New York before her work with the New York Zoological Society. Cooper's family can recall few details of her early education, including the name of the art school in New York City she attended, but their recollections parallel those formally reported by other artists.¹⁶⁸ This mixture of educational sources is mirrored in the biographies of Charles R. Knight and Charles Bradford Hudson. Knight, best known for his portraits of dinosaurs, was encouraged to begin painting by his stepmother and was enrolled in the Metropolitan Art School in the basement of the museum. At fifteen he was hired by a stained glass company to illustrate commissioned designs for clients, and he chose to extend his art education by attending evening classes at the Art Students League (ASL) in Manhattan.¹⁶⁹ The ASL offered evening classes to all ages and sexes in a wide range of techniques, including sketching and painting. Charles Bradford Hudson, staff artist at Stanford's Hopkins Marine Station and long-time USBF illustrator, also took advantage of these courses. Hudson graduated from Columbian College in Washington, D.C. in 1887 (now Georgetown University) and continued his art education outside of the university system. In 1889, Hudson traveled to New York to take evening sketch classes at the ASL with George deForest Bush, a prominent artist who painted in a romantic but naturalistic style.¹⁷⁰

In addition to both formal and informal art education, scientific illustrators relied on access to subjects from local aquariums, zoos and museums as subjects for naturalistic research. Knight's autobiography describes his search for subjects throughout New York City. While a student at the Metropolitan Art School and during his tenure at the stained

¹⁶⁸ Personal correspondence between Charles Mahaffie (Cooper's son) and the author April 21, 2013.

¹⁶⁹ Charles R. Knight, *Autobiography of an Artist: Selections from the Autobiography of Charles R. Knight* (New York: G.T. Labs, 2005) 18-19.

¹⁷⁰ Springer and Murphy, "Drawn to the Sea," 7.

glass company, Knight visited the Central Park Zoo to draw live animals. He also visited the American Museum of Natural History to draw the taxidermied specimens. Knight links the two by saying that the Zoo sent all of their dead specimens to the AMNH to be put on display- he was welcomed into the taxidermy studio at the Museum to watch the recently deceased animals be prepared for preservation and display. Knight calls his study at the CPZ and AMNH a “real anatomy course” and pointed to this portion of his study as one of the most important for producing naturalistic drawings later in his career. He states that “it’s a very difficult thing even under the best circumstances to make a good drawing of a living animal but without this preliminary study it is certainly impossible to produce a satisfactory picture.”¹⁷¹ Illustrators suggested that viewing all animal life, not merely the specimens they were commissioned to illustrate, helped them render organisms more naturalistically. Other artists left the cities and public institutions to view organisms in their native environment. In an *Atlantic Monthly* article entitled “Artists at Large” Isabel Cooper calls attention to the “peripatetic existence of the scientific illustrator.” Cooper stated that she, like Knight, spent her winters sketching and painting in exhibition halls and museums, her summers on the shores painting any animals that she could find, and seeking out “good models, old-fashioned gardens, and rock bound coasts” all the time.¹⁷²

Survey work at marine stations allowed artists to immerse themselves in an environment filled with foreign and exotic creatures, and in some cases, in the marine environment as well. Isabel Cooper described her work in Kartabo Point and Georgetown in a 1924 *The Atlantic Monthly* article entitled “Wild Animal Painting in the Jungle.” In

¹⁷¹ Knight, *Autobiography*, 39.

¹⁷² Isabel Cooper, “Artist at Large,” 85.

it, Cooper outlined the process of ‘living portraiture’ and the importance of environmental immersion to her work, which

Necessitates travel to some of the most wonderful places in the world, and it has used and developed my artistic tendencies...I have had to work out for myself many of the details of my profession. For instance, there is no such thing as a school of snake artists, so when the problem of making a portrait of a snake presented itself I had to think up a technique for myself.¹⁷³

Residency in the field during survey work helped artists develop their own techniques for rendering naturalistic images, and they sought experiences that would help them develop these techniques. Else Bostelmann took advantage of her time in Bermuda, and the diving suits Beebe himself was using for research, to experience as much of the marine environment as possible. She donned a diving helmet and took oil paints underwater to study the movements of aquatic organisms.¹⁷⁴ Of course, not every artist could spend seven years in the field, nor could they access the submarine environment directly, but field work helped artists develop individual techniques and naturalistic visions.

These separate but intertwined educational paths resulted in artists that claimed both technical accuracy and a personalized vision of the natural environment. Each artist brought their own imagination of the aquatic environment to a commission, and this individual vision was noted by scientists. William Beebe hired Else Bostelmann as his resident illustrator after firing two previous artists and finding fault with a third; one artist’s style did not fit with Beebe’s vision, another was deemed adequate, and Helen Tee-Van (his longtime scientific assistant) was labeled mediocre at best. Bostelmann’s work, on the other hand, was technically beautiful and Beebe felt that she was particularly gifted at visualizing specimens as living creatures. Bostelmann was entrusted

¹⁷³ Isabel Cooper, “Wild-Animal Painting in the Jungle,” *The Atlantic Monthly* (June, 1924): 732.

¹⁷⁴ T.C.L., “Sketches Made on Sea Bottom,” 17.

initially with Beebe's field notes and over 600 photographs from his surveys of Bermuda; during his bathysphere dives she worked almost exclusively from his personal observations and her own imagination.¹⁷⁵ Working together, "little by little, each new species materialized, refined by the imagination of both scientist and artist, the proportion, color, and size exactly right." While Beebe called upon Isabel Cooper and Helen TeeVan to illustrate the *Arcturus* organisms, he trusted his bathysphere finds only to Bostelmann's skill and "imagination."

The marriage of accuracy and a personal vision distinguished individual artists and led some artists to be favored as scientific illustrators. Hashime Murayama, one of the most popular and respected marine artists of this period, was recognized as being both extremely scientifically accurate and classically artistic. He was known to study specimens extremely closely, sometimes spending days at the New York Aquarium studying live specimens for illustration, and his bosses at the *National Geographic* believed he "counted scales" for accuracy.¹⁷⁶ David Starr Jordan and Barton Warren Evermann favored Charles Bradford Hudson's style and Jordan stated that he believed Hudson to be one of the top two scientific illustrators in the country.¹⁷⁷ Through formal training, artists developed proficiency in specific mediums- some excelled at watercolors, others oil or line drawings. While most of these artists worked with multiple mediums, many times a laboratory or researcher required proficiency in all of these modes of depiction. For instance, Charles Bradford Hudson worked primarily with paints- oil paints with fresh water and water colors for salt water organism. His fellow artist at the

¹⁷⁵Brad Matsen, *Descent: The Heroic Discovery of the Abyss* (New York: Pantheon, 2005), 63-64.; Alice Carter and Chris Sloane, *The Art of National Geographic: A Century of Illustration* (Washington, D.C.: National Geographic, 1999), 16-17.

¹⁷⁶ Carter and Sloane, *The Art of National Geographic*, 95.

¹⁷⁷ Springer and Murphy, "Drawn by the Sea," 28.

Hopkins Marine Station, Chloe Lesley Starks, preferred working with pen and ink for line drawings.¹⁷⁸

One of the simplest ways to see the expression of style in marine illustration is to examine background composition and perspective in these images. Scientists worked with the illustrator to assure scientific accuracy, but they often allowed the artist to make choices regarding the rest of the image. These choices could be quite small, such as background color. Else Bostelmann's signature was her use of black backgrounds for pelagic specimens. Charles Bradford Hudson also favored a dark background behind his fish portraits. While this variable seems minor, in reality the artist's choice of background color might change the tenor of the entire portrait.

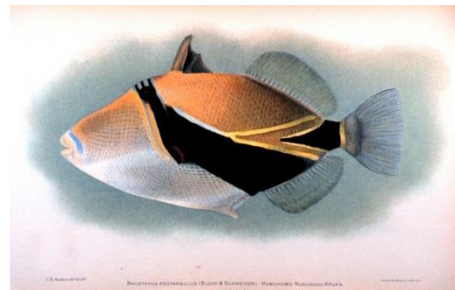
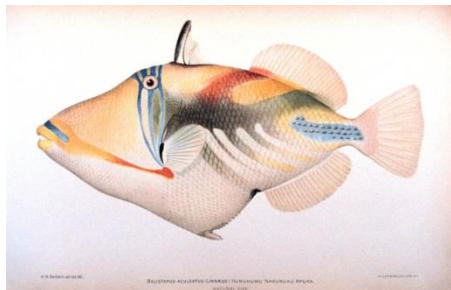


Figure 10: Fish portrait with a white background by A.H. Baldwin. "The Shore Fishes of the Hawaiian Islands, with a General Account of the Fish Fauna", by David Starr Jordan and Barton Warren Evermann. *Bulletin of the United States Fish Commission, Vol. XXIII*, (Washington, D.C.: Government Printing Office, 1903), 574, Plate LXII.

Figure 11: Fish portrait with a dark background by C.B. Hudson. "The Shore Fishes of the Hawaiian Islands, with a General Account of the Fish Fauna", by David Starr Jordan and Barton Warren Evermann. *Bulletin of the United States Fish Commission, Vol. XXIII*, (Washington, D.C.: Government Printing Office, 1903), 574, Plate LXIII.

¹⁷⁸ Springer and Murphy, "Drawn by the Sea," 17.

Larger artistic choices involved the inclusion of extra content or context, such as floral details, perspective, and portrayal of movement or family groupings in a single portrait. Charles Townsend chose paintings from four separate illustrators for his 1929 work *Records of Changes in Color Among Fishes*. Townsend asked his illustrators to portray every color variation of a single species in the same portrait, but it appears he did not place any restrictions on the illustration of the background. Each illustrator had a different background style: Herbert B. Tschudy highlighted flora, Olive Earle shows a slightly naturalistic but non-specific backgrounds, Charles R. Knight presented a romantic, dark background to more clearly highlight the fishes and Hashime Murayama's paintings present all his organisms from the perspective of looking up from an ocean bottom strewn with legible rocks, pebbles, and technically stunning floral elements.¹⁷⁹ All of these portraits were scientifically accurate but stylistically different based on the artist's vision of their subject and the natural world.

¹⁷⁹ Charles H. Townsend, *Records of Color Changes Among Fishes* (New York: New York Zoological Society, 1929)



Figure 12, 13, and 14: These three portraits demonstrate the choices artists made regarding background. Charles Knight (left) preferred a dark, romantic background, Helen Tschudy (middle) used a light, blank background to highlight color changes and patterns in the fishes, and Hashime Murayama (right) depicted flora and ground cover such as pebbles in his portraits. Charles Haskins Townsend *Records of Changes in Colors Among Fishes* (New York: New York Zoological Society, 1929).

Artists utilized traditional art education and personal experience with the natural world, in the city and in the field, to develop individual naturalistic style. This style helped them render lifelike illustrations from both preserved and living specimens.

Illustration

The end result of scientific collection was the description of specimens discovered in a geographical area. Collectors, naturalists and taxonomists produced written descriptions of their collections, but images were equally important. Extensive descriptions detailing coloring, body shape, and distinctive characteristics helped taxonomists differentiate between species, sub species, and sexual maturity and dimorphic features; images illuminated these descriptions and operated as both a proxy specimen and shorthand for quicker field identification.¹⁸⁰ Naturalists often developed a deft hand at illustration, and many utilized their own drafting skills during field research and collection processing, but the eventual publication of research commonly involved working with professional draftsmen.¹⁸¹ The working relationship between naturalist and artist varied depending upon the disciplinary parameters of scientific illustration and the personal vision of both individuals involved. The artist worked with sketches, field notes,

¹⁸⁰ The literature on taxonomic illustration is sparse, but covers a wide swath of historical periods and scientific discipline. For an example of the breadth of the information, see Pamela H. Smith, "Art, Science, and Visual Culture in Early Modern Europe" *Isis* 97:1 (2006): 83-91.; Kärin Nickelsen, "Draughtsman, Botanists, and Nature: Constructing eighteenth-century botanical illustrations." *Studies in History and Philosophy of Biology and Biomedical Sciences* 37 (2006): 1-25; Ann Secord, "Botany on a Plate: Pleasure and the power of pictures in promoting early nineteenth-century scientific knowledge" *Isis* 93:1 (March 2002): 28-57; Martin Rudwick, "Picturing Nature in the Age of Enlightenment" *Proceedings of the American Philosophical Society* 149:3 (Sep. 2005): 283. Rudwick utilizes Mark Himeline's concept of "proxy specimens" laid out in Chapter 2 of Himeline's dissertation "The Visual Culture of the Earth Sciences, 1863-1930" (PhD dissertation, University of California, 1993). The rise of popular natural history, and especially botany and bird watching, resulted in a proliferation of field guides for amateurs.. For information on these illustrations, and the ongoing debates about them, see Mark Barrow, *A Passion for Birds: American Ornithology after Audubon* (Princeton, NJ: Princeton University Press, 2000); Thomas R. Dunlop, *In the Field, Among the Feathered: A history of birders and their guides* (Oxford: Oxford University Press, 2011); Sara T. Scharf, "Identification keys, the "natural method," and the development of plant identification manuals" *Journal of the History of Biology* 42:73 (2009): 73-117.

¹⁸¹ Some ichthyologists were known for illustrating their own works for publication, especially Henry Reed Fowler. See Smith-Vaniz and Peck, "Contributions of Henry Weed Fowler," 173-191.

preserved specimens and open conversation with the collector to produce a usable image.

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Illustrating marine collections presented a very specific set of difficulties. Aquatic organisms appear different when submerged, and their coloring changes drastically when exposed to air. In addition, death causes rapid color changes. Finally, the most commonly used preservation liquids cause further deterioration of color and morphological characteristics. The earliest collectors of marine organisms dredged and netted these organisms from a dry location; they never saw the specimen alive in its native habitat, and only briefly glimpsed its colors before death. These variables placed limitations on marine illustration from the outset. But marine stations, and the expansion of biological surveys combining stable locations with trawling and traditional boat collecting, made it possible for both researchers and the illustrators they depended upon to describe and depict these organisms.¹⁸³ Marine laboratories provided a space where both collectors and illustrators could view marine specimens alive for extended periods. Both researchers and artists took advantage of the stable location and the technologies that extended life in the laboratory to lengthen the period in which they could study living specimens; this extension of viewing time greatly changed the process of marine illustration.

¹⁸² Historians have highlighted the importance of field drawings for scientific knowledge production. For an example see Isabelle Charmantier, “Carl Linnaeus and the Visual Representation of Nature” *Historical Studies of Natural Sciences* 41:4 (Fall 2011): 365-404. For information on the working relationships between naturalists and artists, see Julia Voss’s *Darwin’s Pictures: Views of Evolutionary Theory, 1837-1874* (New Haven, CT: Yale University Press, 2010), 15-60. See also Matthias Bruhn, “Life Lines: An Art History of Biological Research Around 1800” *Studies in History and Philosophy of Biological and Biomedical Sciences* 42 (2011): 368-380.

¹⁸³ Larsen, “Equipment in the Field,” 358-377.

From Type or Specimen: Illustrating from Description

The captions of scientific illustrations offer clues to the process of image production. Images of marine species commonly contain two annotations: “from type or specimen” and “from life.” Illustrations “from type or specimen” were produced utilizing a combination of field notes, field sketches, and the preserved and accessioned specimen; artists working “from life” viewed the specimen in an aquarium or during a dive. The rise of marine stations meant that many more illustrations were done “from life,” but working in the field also changed the way that illustrators worked “from type or specimen”. This section highlights inherent issues in all forms of marine illustration: visibility, access, and time limitations all constrained image production. These limitations forced illustrators to find alternate means of personally and professionally accessing the marine realm to complete their work.

Collectors often called upon illustrators to produce scientifically acceptable images based exclusively on field notes and preserved specimens. The process of marine exploration meant that new or interesting specimens were accessed in distant locations. An organism of interest could be obtained at an outdoor market, fishing dock, or on board a scientific vessel in the middle of the ocean. The artist combined the notes of the researcher with preserved specimens and their own artistic skill set to produce acceptable illustrations. This kind of illustration was termed “drawn from type/specimen” in the caption because the artist utilized a first-hand description and preserved specimen, not a live model, to create the illustration.

Researchers recorded pertinent details about specimens in field notebooks, both for easy identification in collections and use by artists. Marine field notebooks contained

several integral pieces of information about a specimen. A thorough field note included place captured, date, species (if already identifiable), and a tag number. The tag number was the number utilized to identify the fish after accession to a collection. The importance of this number was especially important to illustrators: it allowed researchers to match up preserved specimens with field descriptions- something made incredibly difficult because of the problem of color. Marine field work required rapid recording of details; the problem of color required quick work to produce accurate descriptions that would later guide both taxonomists and illustrators.¹⁸⁴

The Problem of Color

Marine organisms quickly lose color after being removed from their native habitats. Organisms that appear one color while submerged take on a completely different hue when exposed to air. In addition, stress and tissue death cause color changes in fishes. The most common form of specimen preservation, submersion in alcohol, caused color to fade further. Isabel Cooper elegantly described the problem of color change in fishes in her *Atlantic Monthly* piece entitled “Artists at Large”:

But it was a great mistake to spend much time upon reflection, because rage and discomfort had a strange effect on their color schemes. Right before my eyes the gleaming steel and gunmetal of their visors and armored plates would dim and darken and film over with streamers of purple mist, or jagged patterns of ultramarine, or shadows of leaden grayness. And I would be left guessing, somewhere between the myth of what they had been and the myth of what they were rapidly becoming, with nothing remaining of the truth which the scientists most earnestly desire.¹⁸⁵

Artists tasked with rendering lifelike images from preserved specimens required additional details for accurate coloring.

¹⁸⁴ Ibid., 363.

¹⁸⁵ Cooper, “Artists at Large,” 91.

Rapidly taken field notes worked to combat color change in specimens.

Commonly, the observer of the specimen would record color in two separate but corresponding methods: a written description of the coloration followed by a quick sketch of the specimen. The field notebooks from David Starr Jordan and Barton Warren Evermann's 1901 survey of the waters off the newly acquired Hawaiian Islands offers a good example of this form of field notation. On June 13, 1901 the notebook records that Jordan and Evermann received a *Chaetodon lunula* (raccoon butterfly fish) from a Portuguese fisherman. The specimen was recorded under the number 03313 and described thusly:

Upper parts of side rich greenish olive, covered by about 9 or 10 reddish brown bars; lower part of side rich lemon yellow covered by about 5 reddish orange bars; the two under pectoral breaking up into reddish orange spots; tip of snout pale rosy, rest of snout pale yellow; a broad black saddle overhead and through eye to upper edge sub operculum about one half broader than orbit. Back of this is a broad white saddle of about same width extending to near lower part of operculum and enveloping part of the shoulder girdle; back of this is a yellowish-green space, then a black saddle at anterior (?) of dorsal and extending along (?) until the 5th spine; a large oblong black spot beginning on humeral region and curving (?) and backwards (?)...a jet black spot on caudal peduncle¹⁸⁶

The description of the coloring and markings of this specimen go on for another half a page.

In addition to written color descriptions, researchers might quickly draw a diagram of the specimen. On July 27, collectors observed specimen 035030 alive at the Honolulu market. No written description of the specimen was recorded; instead, a diagram was drawn. As you can see below, the observer included a rough sketch of the fish with indications of color placement. While it is labeled as *Pachynautus brusus* in the

¹⁸⁶ Color Notes on Hawaiian Fishes Box 19 RU 7184 United States Bureau of Fisheries Records; Smithsonian Institutional Archives, 87.

notebook, the fish was later identified in the publication as *Balistaopus aculeatus* and was painted by A.H. Baldwin from the preserved specimen and field notation.

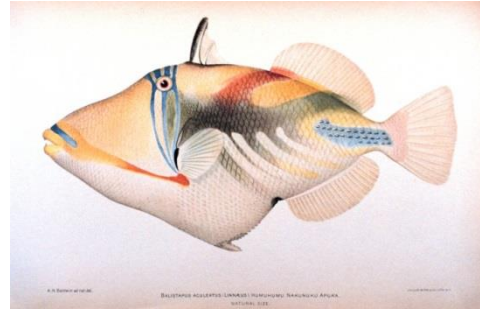
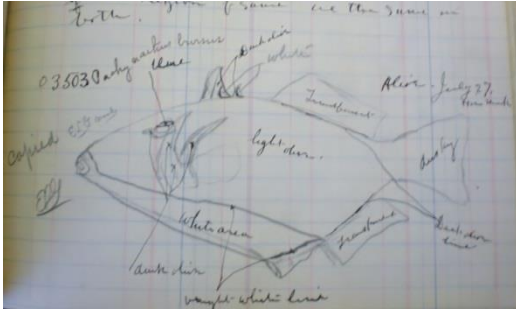


Figure 15: A quick field coloring of living fish at Honolulu docks. Color Notes on Hawaiian Fishes Notebook p. 157 RU7184 US Fish Commission Papers, Smithsonian Institution Archives. Washington, D.C.

Figure 16: A.H. Baldwin's published illustration based on the field sketch in Figure 2. "The Shore Fishes of the Hawaiian Islands, with a General Account of the Fish Fauna," by David Starr Jordan and Barton Warren Evermann. *Bulletin of the United States Fish Commission, Vol. XXIII* (Washington, D.C.: Government Printing Office, 1903), 574, Plate LXII.

As the technology developed, these quick field sketches were sometimes replaced by field photographs. Although photography could capture the specimen quickly, colored photography had yet to be developed so researchers were still required to take extensive notes about markings and body color. These images were meant to serve as another form of field data that could eventually be turned over to the illustrator for incorporation into the final illustration.¹⁸⁷

¹⁸⁷ Many researchers used photography as a form of field notation. William Beebe had a personal interest in photography, he was an amateur wildlife photographer, and utilized the medium as field notation on many of his voyages. See Carol Grant Gould, *The Remarkable Life of William Beebe: Naturalist and Explorer* (New York: Island Press, 2004), 67-68; Matsen, *Descent*, 63.

“From Life”: Living Portraiture

The importance of aquariums to aquatic illustration cannot be overstated. Because of color changes upon death, and the inability to ascertain those colors from preserved specimens, the optimum time for illustrating organisms and capturing their living color was for artists to view fresh or living specimens in person. Logistical difficulties and the cost of shipping live specimens inland meant artists traveled to marine stations or sailed on research vessels to access their subjects. Illustrators utilized aquariums in tandem with field work; fishes were kept alive for a very short time in aquaria, long enough for artists to paint their portrait. After the artist had finished with the portrait, the organism was assigned a number, preserved, and shipped to an institution to be stored as part of a collection for future study. But the introduction of aquarium technology did not necessarily make illustrating organisms easier; it merely changed the process.

Illustrators found new difficulties illustrating from life. Just as human portraiture is difficult because of the need for proper lighting and the cooperation from the subject, so too was fish portraiture difficult for these reasons. Artists in the field set up their studios in any location that would afford them enough space for their aquarium and the proper lighting. Charles Bradford Hudson’s studio during his work on the Jordan and Evermann Hawaiian expedition was described as

An interesting den. It is not in at [sic] attic or under a eucalyptus tree. He is perched on a bench at the outer end of a pier seaward from the Moana hotel. He has before him a glass aquarium, full of sea water. Here he poses his models.¹⁸⁸

¹⁸⁸ Springer and Murphy. “Drawn to the Sea,” 71.

Isabel Cooper wrote about a multitude of locations that she used as studios during her career, including spaces in the bamboo forest of Guyana and the deck of the *Arcturus*. Cooper describes her floating studio on board the *Arcturus* as an “exciting, and disturbing place to work.” The rolling of the boat made it difficult for her to paint, and waves forced her to stabilize both herself and her subject while painting. But she also found the experience exhilarating:

A web of difficulties, indeed, in which to enmesh an artist and her inadequate physique! But it was interesting, nevertheless, to work away at my strange job, sketching the queer creatures that were fished up from the depths and rushed-alive, preferably-to my rolling, rocking studio, to float for an hour or so beneath the concentration of a human being’s senses, and the lenses and mirrors which make up the sensitive glass eye of civilization.¹⁸⁹

The illustrator had to be able to work in a multitude of environments and to be able to work rapidly.



Figure 17: Charles Bradford Hudson painting "from life" in his makeshift studio on the end of the dock in Oahu. Photography by John N. Cobb. Springer and Murphy, "Drawn to the Sea," 71.

¹⁸⁹ Cooper, “Artist at Large,” 91.

Field illustrators had to work quickly with organisms dumped into temporary aquaria. While color faded quickly after death, change of environment elicited fright responses from many organisms. Beebe recalled the difficulties of keeping certain specimens, especially squid, in temporary aquariums. He stated that he needed to transfer the organism three times because it inked up the water so badly from fright. Other fear responses included color change or even death, both of which could have serious impact on the final coloring depicted in the portrait. Aquariums in the field allowed a new way of visualizing aquatic organisms, but it was not sufficient in all cases.



Figure 18: Isabel Cooper painting a living fish in an aquarium aboard the *Arcturus*. Beebe, *The Arcturus Adventure*, 396.

Cooper and other researchers working from live specimens in the field had to work quickly to capture the color and mannerisms.

Long term study of organisms in permanent aquariums added a new depth to the artists' ability to capture color, mannerisms, and other characteristics that might go unnoticed during rushed examination in the field. The ability for illustrators to study fishes in aquariums actually allowed multiple portraits of the same specimen. Juvenile fishes could be captured daily during development to depict juvenile and adult forms

through portraits. Mary Fish seined unidentifiable larval forms from the ocean surface as the *Arcturus* traveled through the Sargasso Sea. Fish placed the forms in an aquarium and drew them every day, tracking their development through portraits.¹⁹⁰ In addition, fishes that could change color could be studied, and illustrated multiple times before preservation. Charles Townsend's work examined color changes from fright, light, and environmental surroundings; the four artists he employed for his work on fish coloration painted multiple portraits of the same specimens- each time focusing on a specific color change in the organism. The visibility afforded by the aquarium helped taxonomic artists depict multiple colorations of the same species in the same portrait, thereby offering a set of descriptions for naturalists and collectors who may encounter only one coloration in the field at a given moment.¹⁹¹

In addition to capturing coloration of freshly caught organisms and observing the life cycle of individual specimens, aquariums could be utilized to enhance an illustrators' knowledge of a species when illustrating "from type or specimen." Hashime Murayama traveled from Washington, D.C. to New York to view living trout for illustrations for *The National Geographic*. Murayama's illustrations were intended to portray all of the scientifically important aspects of trout, and in addition to working with preserved specimens he tried to capture their color and movement by viewing living specimens. Unfortunately, the trout shipped to the New York Aquarium for this specific purpose died almost immediately when introduced to the aquarium water. Murayama stayed in residence until more could be shipped and kept alive for an extended period. This story illustrates another difficulty, one that is a major theme of this dissertation: it is difficult to

¹⁹⁰ C.J. Fish to Willis H. Rich. May 3, 1925 and C.J. Fish to William H. Rich May 25, 1925 Woods Hole Plankton Studies, 1925 RU 22 NARAH: Bethesda, MA

¹⁹¹ Townsend, *Records in Changes of Color*.

keep organisms alive in aquariums- and this difficulty impacted not only researchers but also artists working with specimens.¹⁹²

Separate difficulties arose when illustrating “from specimen/type” and “from life.” Optimally, artists could utilize both of these forms- in the field the artist could illustrate the living form, but still have the preserved specimen for reference. In less optimal circumstances, when the artist worked from hastily assembled field notes or the specimen was not immediately preserved (often the case when illustrating at public aquaria or if organisms were kept in aquaria for further study), artists relied on personal knowledge garnered from extensive study of forms in natural history establishments and the field. Even in optimal drawing conditions, with extended access to both living and preserved forms, artists utilized personal vision to embellish and enhance scientific portraits.

New Visualization Techniques and Scientific Portraiture

In the mid nineteenth century, amateur and professional photographers’ subjects began to intersect with the scientific community. Photography became a useful medium for scientific information gathering and distribution in meteorology, medicine, and other fields. Some believed that the mechanical objectivity achieved by the camera outstripped the ability of artists to portray natural phenomena.¹⁹³ One of the earliest proponents of photographic illustration was R.W. Shufeldt. His early experiments photographing live fishes produced a photo of a large pike that differed from previous taxonomic drawings.

¹⁹² Carter and Sloane, *The Art of National Geographic*, 95.

¹⁹³ Jennifer Tucker, *Nature Exposed: Photography as Eyewitness in Victorian Science* (Baltimore, MD: The Johns Hopkins University Press, 2006) Early marine photographers expressed the belief that photography could be beneficial to marine taxonomists. See Fabre-Domergue, *La Photographie des Animaux Aquatiques* (Paris: Georges Carré and C. Naud, 1899); R.W. Shufeldt, “Photographing Living Fishes Under Water” *Outing* 38 (Jan. 1, 1901): 543-547.

This prompted Shufeldt to remark that “In time, with the most suitable subjects taken under the most favorable conditions, pictures of fish (as in the case of other animal forms) produced by half-toning processes from faultless photographs, will surely supersede in biological literature the often inaccurate figures that now illustrate it.”¹⁹⁴ But this goal took longer to accomplish than Shufeldt predicted due to limitations in camera technology. Early cameras lacked the ability to accurately capture living organisms because of low light and animal movement; color photography was in its infancy. While some photographers believed that cameras could enhance taxonomic methods by picking up on details overlooked by researchers and artists, artist-rendered illustrations still continued to accompany photographic illustrations in taxonomic publications and remained the optimal form of presenting scientifically accurate taxonomic images of specimens throughout the 20th century.

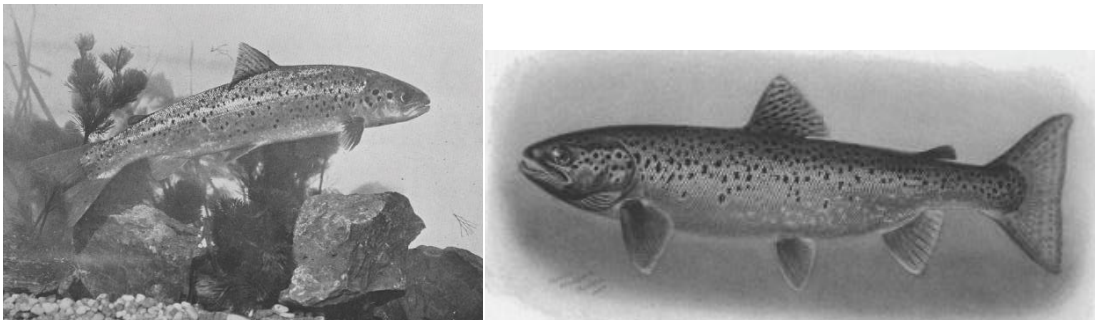


Figure 19 and 20: Both of these images appeared side by side in David Starr Jordan and Barton Warren Evermann’s seminal work *American Food and Game Fishes*. Jordan and Evermann were some of the first ichthyologists to utilize photographs in taxonomic work, but did not publish them as stand-alone images.

They still used illustrations to portray scientifically pertinent information. *American Food and Game Fishes* (Garden City, NJ: Doubleday, Page, and Co., 1920), 154-155.

¹⁹⁴ R.W. Shufeldt, “Experiments of Photography of Live Fishes” *Bulletin of the United States Fish Commission* (1899): 3.

Photography did become a useful tool in survey work as a form of short hand field notation. Collectors and researchers photographed specimens in the field in place of rough sketching. Until color photography developed, they still made color notations, but the convenience of photography allowed researchers to reproduce the image of the specimen accurately, and to send that image with preserved specimens to other scientists. On July 26, 1912, collectors at the USBF marine laboratory in Beaufort, North Carolina found what they believed to be a stranded bottle-nosed whale. Dr. Albert Kuntz, of the University of Iowa, working at Beaufort on the embryology of pelagic fishes, recorded pertinent information about the specimen, including coloration and measurements, and performed a necropsy on the specimen before shipping the bones along with the photo and information to Frederick True at the Smithsonian in Washington, D.C.¹⁹⁵ True identified the bones as a new species *Mesoplodon mirus*, commonly known as True's Beaked Whale, and replicated Kuntz' field notes and photograph in his paper announcing the new species.¹⁹⁶ The species, and most beaked whales, have never been netted nor are they commonly seen in the wild; by 1940 only eight living specimens had been seen in the Atlantic

¹⁹⁵ "Fishes taken at Beaufort, N.C. 1912" page 51. RU 7184 United States Bureau of Fisheries Records, 1877-1948. Smithsonian Institutional Archives: Washington, D.C.

¹⁹⁶ Frederick W. True, "Description of *Mesoplodon mirum*, A Beaked Whale Recently Discovered on the Coast of North Carolina" *Proceedings of the United States National Museum* 45 (Nov. 29, 1913): 651-657.



Figure 21: This field photograph of a stranded unknown whale species taken by Albert Kuntz at Beaufort, NC in 1912. The photograph, along with the skeletal remains and measurements of the organism, were sent to Frederick True at the Smithsonian for identification. Frederick W. True “Description of *Mesoplodon mirum*, A Beaked Whale Recently Discovered on the Coast of North Carolina” *Proceedings of the United States National Museum* 45 (Nov. 29, 1913): plate 52.

The scarcity of eye witness accounts and field notes did not stop A. Remington Kellogg from commissioning Else Bostelmann to illustrate True’s Beaked Whale for his 1940 *National Geographic* article entitled “Whales: Giants of the Sea.” Neither Bostelmann nor Kellogg had ever seen the species alive- they worked together to create illustrations that were both life like and scientifically accurate based on the field notes, photographs, and information sent to True by Kuntz.¹⁹⁷ Once again, Bostelmann was called to use her imagination and personal experience of the aquatic world to render lifelike drawings of animals she herself had never encountered. Bostelmann’s final illustration portrayed two beaked whales frolicking in an imagined ocean; while the image portrayed vitality and movement, it also focused on pertinent taxonomic details, including jaw and fin shape and coloring.¹⁹⁸

¹⁹⁷ D. Graham Burnett, *The Sounding of the Whale: Science and Cetaceans in the Twentieth Century* (Chicago: University of Chicago Press, 2012), 314-315.

¹⁹⁸ Remington Kellogg, “Whales: Giants of the Sea” *The National Geographic Magazine* 77:1 (1940): 35-90.



Figure 22: Else Bostelmann and Remington Kellogg's combined imagination of the True's Beaked Whale in the wild. "Whales: Giants of the Sea" *The National Geographic Magazine* 77:1 (1940): Plate X.

Scientific artists remained important collaborators in marine taxonomy throughout the twentieth century. Even with the integration of new visualization techniques into field work, collectors and researchers continued to rely upon the personal and professional skills of illustrators to transform actual into virtual specimens. Marine stations and field work provided these illustrators with reference points for content and context and helped them depict unknown environments and the movements of newly discovered organisms through them; these spaces were integral in the training of marine artists and therefore in the creation of marine scientific illustrations. Artists played a significant role in the knowledge production of American marine surveys during this period and the imagination and skills they developed during their time in the field had an impact on the way both scientists and the public came to imagine the ocean.

Chapter 3

Crossing the lab-field border: working with embryological materials at marine stations

The spring and summer of 1880 found W.K. Brooks keeping odd laboratory hours. At the end of April, 1880, Brooks found a single specimen of *Lucifer ancestra* with two eggs attached to its appendage. After examining the eggs, Brooks believed that the development of *Lucifer*, a small crustacean, could hold the key to the evolutionary history of arthropods and sought to trace its developmental stages in the laboratory. Between April and the end of August, Brooks sought more embryological material with little success, but in the first week of September he collected several advanced larvae and by the end of that month had succeeded in not only collecting multiple stages of development, but hatching a larval form from a collected egg in the laboratory. Brooks' publication on this research highlighted his limited findings on the tracing of the life history of the organism. According to Brooks, new findings would only be accomplished when it became possible to rear and maintain the crustaceans in artificial conditions, a feat he labored at unsuccessfully throughout the summer.¹⁹⁹

Brooks' embryological research on the crustacean *Lucifer* required a refinement of both field and laboratory techniques. In order to find fresh embryological material, Brooks had to ascertain the exact location of the *Lucifer* spawning ground and visit that location at the exact right time to collect fertile females. On clear evenings precisely as the tides turned, Brooks set out to trawl the salt marsh near Beaufort, North Carolina to collect as many of the tiny creatures as he could in hopes of finding spawning females.

¹⁹⁹ W.K. Brooks, *Lucifer: A Study in Morphology* (London: Trubner and Co. 1882),62.

The spawning females proved so delicate and rare that Brooks did all the collecting himself; he felt he could not trust the job to the station's paid collector. After hours of painstakingly separating the tiny, nearly translucent, fertile females from their non-fertile and male brethren, Brooks carefully transferred his few usable specimens to the laboratory on Pivers Island and sat down to wait for the release of eggs. Females released fertilized ova between 9 and 10pm and work was started on the eggs immediately, as they proved as delicate and perishable as their progenitors. Brooks personally followed development in each egg, trying unsuccessfully to rear a mature form in the artificial laboratory environment. While he failed to accomplish this goal, his extensive collecting and laboratory work resulted in the publication of illustrations of normal embryological development and the general physiology and natural history of the species.²⁰⁰

²⁰⁰ Ibid. 64-65.

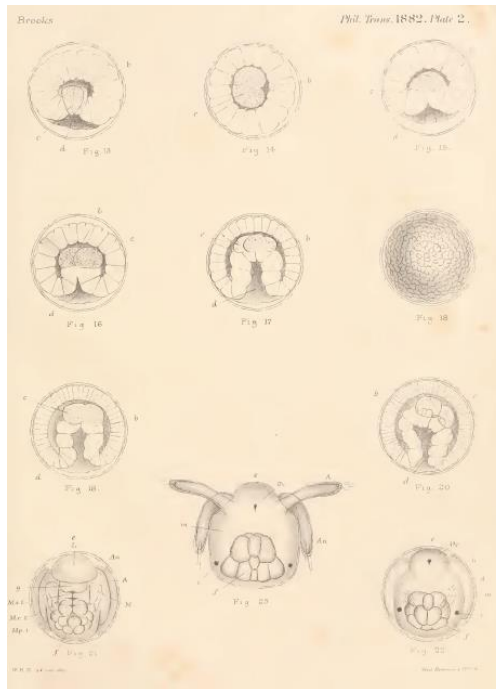


Figure 23 W.K. Brooks' illustration of Lucifer's development. *Lucifer*, Plate 2

Marine stations gave researchers interested in embryological problems access to a wide variety of local forms. But the mere accessibility of live organisms did not guarantee usable specimens for scientific work. While they were granted access to a wide variety of species surrounding the environment, few of these were easily incorporated into laboratory studies. The species that were most commonly utilized were those that were easily collected, reared in artificial conditions, and abundantly available throughout the entire summer research season. But these materials, such as those of various species of sea urchin, shark, and game fish, were not always the best for studying specific embryological questions.²⁰¹ More scientifically interesting materials were difficult to

²⁰¹ W.K. Brooks, *Handbook of Invertebrate Zoology: For Laboratory and Seaside Work* (Boston: S.E. Casino), 99.

collect and maintain, meaning that few marine species were consistently represented in the embryological laboratory.²⁰²

Working with and maintaining embryological forms took a wide array of knowledge and the growth of skills that required intensive labor both inside laboratory walls and throughout the surrounding marine environment. Researchers developed intimate knowledge of the normal life history of their organisms around which they built laboratory techniques to maintain them in artificial conditions. The inherent difficulty of combining these two skill sets meant that a large majority of embryologists chose to work primarily with reliable terrestrial species such as frogs or chickens.²⁰³

In spite of the difficulties surrounding collecting and maintenance, the use of marine organisms for embryological research rose in popularity at the turn of the twentieth century. Researchers consistently sought out new species in the untapped and unmapped marine environment and the establishment of stable stations in new locations provided new specimens for description.²⁰⁴ In addition to descriptive embryology, many marine species, including echinoderms (sea urchin), elasmobranchs (shark), and teleosts (fish) had hard, nearly translucent eggs that facilitated teaching and experimentation on

²⁰² James W. Atz, "A Working Bibliography on Rearing Larval Marine Fishes in the Laboratory" in *Sea Water Systems for Experimental Aquariums* eds John R. Clark and Roberta L. Clark, Research Report 63 (Washington, D.C. : Bureau of Sports Fisheries, 1964), 95-102; John P. Wourms, "The Rise of Fish Embryology in the Nineteenth Century" *American Zoologist* 37:3 (June 1997): 269-310.

²⁰³ Adele E. Clark, "Research materials and reproductive science in the United States, 1910-1940" in *Physiology in the American context 1850-1940* ed. Gerald L. Geison (New York: Springer, 1987), 323-350; Adele E. Clarke, "Embryology and the rise of American reproductive sciences, circa 1910-1940" in *The expansion of American biology* eds. Keith Benson et al (New Jersey: Rutgers University Press, 1991), 107-132.

²⁰⁴ John P. Wourms, "The relationship between comparative embryology, morphology, and systematics: An American Perspective" in *From Embryology to Evo-Devo: A History of Developmental Evolution* eds. Jane Maienschein and Manfred Laubichler (Boston: MIT Press, 2007), 215-266. Keith Benson calls attention to the link between embryology, morphology, and embryology in *William Keith Brooks (1848-1908): A Case Study in Morphology and the Development of American Biology* (PhD Dissertation: Oregon State University, 1979); Nick Hopwood, "Visual Standards and Disciplinary Change: Normal Plates, Tables and Stages in Embryology" *History of Science* 43 (2005): 239-303.

development in the laboratory.²⁰⁵ Finally, while aquaculture of fresh-water species had been successful for years, researchers were still struggling to understand the development and life cycle of edible, and rapidly declining, marine species such as cod and lobster. They adopted space in newly established marine stations to work out these stages and to experiment with aquaculture techniques for producing bulk fishes for human consumption.²⁰⁶ Descriptive and experimental embryologists relied on fresh specimens and a combination of field and laboratory space in order to achieve their research goals.

Marine stations provided an outpost that allowed researchers to live close enough to the shore to explore the life history of their embryological materials in the field and to utilize that information during observation of and experimentation upon fresh specimens in the laboratory. Historians of American biology have consistently emphasized the role of the marine laboratory in the rise of experimental embryology. Jacques Loeb and other experimentalists' work is often held up as an example of the embryological investigation performed at marine laboratories during this period. But these narratives rarely explore the techniques, either in the field or the laboratory, which made embryological investigation in these spaces possible.²⁰⁷ It was not enough to simply be in a location that granted access to fresh embryological material. Researchers required in depth information on the organisms' life history, how to collect them, fertilize them, and maintain them in the laboratory before any research could be performed.

²⁰⁵ James W. Atz, "Fundulus heteroclitus in the laboratory: a history" *American Zoologist* 26:1 (1986): 111-120; John P. Wourms, "The Rise of Fish Embryology in the Nineteenth Century" *American Zoologist* 37:3 (June 1997): 269-310.

²⁰⁶ Robert Stickney, *Aquaculture in the United States: A historical survey* (New York: John Wiley and Sons, Inc., 1996)

²⁰⁷ Garland Allen, *Life Science in the Twentieth Century* (Cambridge, UK: Cambridge University Press, 1978); Jane Maienschein, "Shifting assumptions in American Biology: Embryology, 1890-1910," *Journal of the History of Biology* 14:1 (Spring, 1981): 89-113. Philip Pauly, *Controlling Life: Jacques Loeb & the Engineering Ideal in Biology* (Oxford: Oxford University Press, 1987).

This chapter will examine the common difficulties encountered while working with marine embryological material and highlight the choreography balancing field and laboratory procedures that investigators developed to stabilize their research programs. Investigators working with marine embryological material encountered difficulties during each step of the process of collecting, fertilizing, maintaining, and rearing in the liquid laboratory. Moving to marine locations allowed continuous access to *some form* of embryological material, but working with *specific forms* required extensive knowledge of life cycles, behavior, normal embryological development, and mature physiology and morphology. All of this knowledge was brought to bear when researchers sought to transfer organisms from the field to the laboratory.

The growth of experimental embryological investigations at marine stations has long been used as an example of the type of laboratory-based experimentation that kept researchers removed from the field during this period. While it is true that some advanced investigators relied primarily on the station's official collectors for a consistent supply of research specimens, and that they operated primarily from the bench, not the beach, for students and many researchers throughout the liquid laboratory network, working with embryological forms bound them inextricably to their surroundings. Researchers desiring to build viable artificial environments in which to house their subjects required knowledge of those organisms' natural milieu; this knowledge could only be built through intimate experiences with the marine environment. These experiences, and the consequent knowledge of specific marine surroundings, not only facilitated in-depth embryological investigation, but also contributed to the ongoing development of general marine biology.

Collecting

Historians have emphasized the importance of consistently available material when explaining the link between the study of embryology and marine laboratories. While it is true that embryological material, including fertilized eggs and spawning mature forms, was available at marine stations, the image of an easily accessible catalogue of specimens is somewhat misleading. Researchers and teachers often required or at least requested specific forms for their needs, but spawning and fertilization is dependent on uncontrollable conditions such as local weather, lunar calendars, and seasonal and yearly fluctuations. To avoid gaps in specimen availability and to achieve optimum productivity during the season, researchers worked with multiple species as they became available. This section highlights the process of collecting embryological material at marine laboratories. Collecting viable specimens relied on the development of specialized knowledge of environmental variables and their interactions with a wide variety of species.

The study of embryological development necessitated access to viable reproductive material; this necessity brought researchers to marine stations and it also linked them intimately with the surrounding area and the organisms with which they worked. Understanding spawning behavior and the lifecycle of an organism was one way that investigators were assured that they had access to viable material. While professional collectors played a large role in delivering fresh embryological material to the laboratory (see Chapter 1), some researchers working with embryological forms felt it was important that they collect their own materials in order to both follow natural development in nature and to properly handle their material. According to Ernest Everett

Just, an experimentalist working with embryological forms at Woods Hole, Naples, and Roscoff in the early 20th century, the knowledge gained from collecting your own specimens and viewing them in their natural environment was extremely important for further research. Just states that “the experimental embryologist should as far as possible know his animal personally and directly through work in the field, never resting content to become what Kropotkin in another sense denominated a “desk-biologist.””²⁰⁸ Students in the MBL invertebrate course each summer were strongly urged to do their own collecting. According to the course description

The field work is one of the most important aspects of the entire course; even the anatomy cannot be clearly understood until the animal has been seen in its native haunts. Gross collecting methods are avoided as far as possible and the student is urged to observe carefully while collecting where the animals are found and what they are doing.²⁰⁹

Field work served two purposes for embryological researchers: the collector was able to ascertain the normal development of their experimental organism in their natural surroundings, and they also pinpointed the exact place and time that viable specimens could be taken near the laboratory.

²⁰⁸ E.E. Just, *Basic Methods for Experiments on Eggs of Marine Animals* (Philadelphia: P. Blackiston's Son & Co: Philadelphia, 1939), 8.

²⁰⁹ W.C. Allee, “The Invertebrate course in the Marine Biological Laboratory. A Contribution to the technique of teaching zoology.” *Biological Bulletin* 42:3 (Mar. 1922): 112.



Figure 24 Mr Davis digging *Balanoglossus* circa 1920 Folder Unidentified Pictures 71/3 Carton 14 William E. Ritter Papers. Bancroft Library Archives, University of California, Berkeley: Berkeley, CA.

The importance of recognizing normal development cannot be overstated when discussing the study of embryology. Regardless of the ultimate goal of the research, it was important to ascertain if the embryo being studied was developing along a “normal” path (how a sexually mature specimen would develop in its native environment) or if it was developing abnormal characteristics (teratology). In his 1939 embryological laboratory manual, Just suggests that researchers should spend time in the field observing their experimental organisms in the wild in order to note their natural behaviors; collecting should also be done personally for the same reason. According to Just, the basis and the control of any experiment was the perfectly normal egg; the investigator needed to be able to recognize abnormalities in developing eggs. “The best source for this knowledge lies in the most thorough acquaintance of the normal egg in its normal surroundings. Whenever possible the normal development of the egg in nature should be followed.” Just believed that if a researcher had never seen their subject in their original milieu, they should reconsider working with that organism in the laboratory.²¹⁰

²¹⁰ Just, *Basic Methods*, 7-8.

Not all researchers needed extensive field work to pinpoint normal developmental stages in their embryos; many could rely on ‘normal plates’ and developmental information already worked out by previous embryologists. The MBL invertebrate zoology course studied embryological development with several types of echinoderma eggs; they referenced Christianna Smith’s previous observations on the normal development of these eggs under July conditions.²¹¹

<i>2. Arbacia punctulata.</i>	
Two celled.....	1 hr., 30 minutes.
Four celled.....	2 hrs., 30 minutes.
Eight celled.....	2 hrs., 45 minutes.
Sixteen celled.....	3 hrs., 45 minutes.
Sixty-four celled.....	4 hrs., 15 minutes.
Early blastula.....	7 hrs., 15 minutes.
Late blastula.....	14 hours.
Early gastrula.....	23 hrs., 30 minutes.
Pluteus	Two days.
<i>3. Echinarachnius parma.</i>	
Two celled.....	1 hr., 35 minutes.
Four celled.....	2 hrs., 45 minutes.
Sixteen celled	3 hrs., 15 minutes.
Sixty-four celled.....	4 hrs., 15 minutes.
Early blastula.....	6 hrs., 15 minutes.
Late blastula.....	10 hours.
Early gastrula	21 hours.
Late gastrula.....	38 hours.
Pluteus	Two days.

Figure 25 Christianna Smith's timetable of echinoderm development in Woods Hole in July. Allee, "The Invertebrate Course," 121.

In 1937 Jane Oppenheimer worked out the normal developmental stages of *fundulus heteroclitus*, a popular embryo for teaching and experimental purposes. In her publication, she explains that she worked out the normal stages of the embryo “to facilitate the work of students who may find *fundulus* eggs favorable experimental material for morphological or experimental investigation.”²¹² Publications on normal development often included extensive illustrations of the embryonic and larval growth entitled ‘normal tables.’ Oppenheimer’s paper contained three photomicrographic plates

²¹¹ Allee, “The Invertebrate Course,” 120-121.

²¹² Jane M. Oppenheimer, “The normal stages of *Fundulus heteroclitus*.” *The Anatomical Record* 68.1 (1937): 1.

with 33 figures illustrating the growth of the *fundulus* embryo from fertilization to larval form. These illustrations served as a reference for researchers as they viewed their specimens' development in the laboratory. While surveys continuously expanded the number of normal tables available, many of the most widely available and popular species did not have accurate published normal plates. For instance, the dogfish, a species of shark with reproductive materials that proved incredibly useful for teaching and experimentation, did not have an accurately timed, widely distributed normal table in publication until 1993.²¹³ Locally specific species available at varying points of the season often had no normal table available, forcing researchers to rely on Just's method of field work and extensive observation.²¹⁴

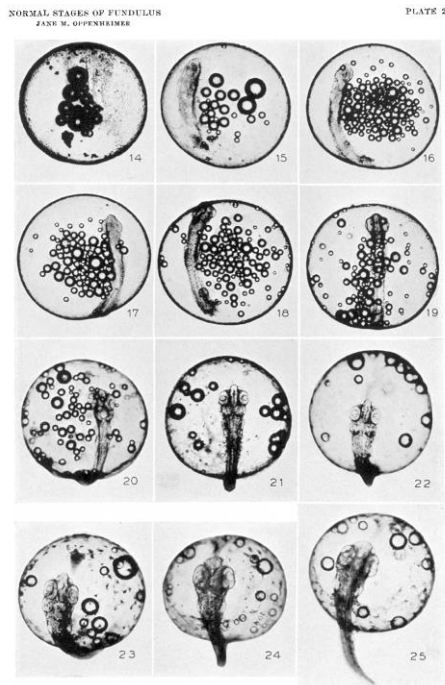


Figure 26 The normal table for *Fundulus heteroclitus*. Oppenheimer, "Normal Stages," Plate 2.

²¹³ William W. Ballard, Jean Mellinger, and Henri Lechenault "A Series of normal stages for the development of *Scyliorhinus canicula*, the lesser spotted dogfish (*Chondrichthyes: Scyliorhinae*)," *Journal of Experimental Zoology* 267 (1993): 318-336.

²¹⁴ For information on normal plates, see Nick Hopwood, "Visual Standards," 239-303.

There were two ways to collect embryological material at marine stations: as naturally fertilized ova or by collecting mature spawning adults and inducing shedding or artificially fertilizing the eggs in the laboratory. Often, fertilized embryos were found in trawls or net catches by survey collectors during their daily trips. While trawling off of the Arcturus, Marie Fish recovered several fertilized eggs which she believed were those of the American eel- a species of eel about which little developmental knowledge was known at the time. These embryos appeared in the trawl without a mature or even intermediate form, making it difficult to ascertain the species to which it belonged. Fish was forced to observe her specimens over the course of several days to tentatively identify the resulting larva.²¹⁵ Lewis Cary encountered an unknown embryo at the Beaufort laboratory over the course of several seasons, and eventually worked out the normal development and breeding period of the *Epizoanthus Americana* in the Beaufort region.²¹⁶

Not all fertilized eggs were free-floating or mysterious. Many researchers hoping to examine the earliest developmental stages of arthropods found that they could only obtain reproductive materials by collecting adult forms that contained internally fertilized ova. D.R. Crawford found that even collecting sexually mature spiny lobsters did not assure usable reproductive material. Females had to contain fertilized eggs before capture, and in most instances if they were not prepared to spawn within 24 hours of capture, they would not do so nor would the embryos be viable if forcibly removed.²¹⁷

²¹⁵ Marie Poland Fish, "Contributions to the embryology of the American Eel (*Anguilla rostrata* Lesueur) *Zoologica* 8:5 (1927): 1-36.; Marie Poland Fish, "Preliminary report on the egg and larva of the American Eel (*Anguilla rostrata*) *Science* 64: 1663 (Nov. 5, 1926): 455-456.

²¹⁶ L. R. Cary, "Notes on a peculiar Actinozoan larva." *The Biological Bulletin* 7.1 (1904): 75-78; Caswell Grave, "The Fisheries Laboratory at Beaufort, Sixth Season" *Science* 21:541 (May 12, 1905): 732-737.

²¹⁷ D. R. Crawford, "Spawning Habits of the Spiny Lobster (*Panulirus Argus*), with Notes on Artificial Hatching," *Transactions of the American Fisheries Society* 50.1 (1921): 312-319. D.R. Crawford and

William Bateson encountered a similar problem with the acorn worm *Balanoglossus*. Attempts at laboratory fertilization only produced abnormal embryo development but naturally fertilized ova were often available in the muddy sand near the laboratory.²¹⁸

Investigators utilized naturally fertilized embryos collected in the field, but this system of collecting contained certain drawbacks. If one wanted to study the earliest stages of embryological development, collecting already fertilized materials provided less control over the stage that could be observed. Gaps in developmental stages could be missed if researchers failed to collect materials in varying stages of development. The earliest stages were the most commonly absent, often because development started even before fertilized material was actually released into the surrounding waters. Lewis Cary lamented the inability to find the earliest stages of certain actinians (sea anemone) he wanted to study and eventually chose to manually fertilize eggs in the laboratory in order to circumvent this impediment.²¹⁹ If researchers could collect spawning adults to bring into the laboratory for artificial fertilization or shedding, this was considered the optimum form of collecting. But this process also involved major obstacles.

Spawning behavior greatly influenced the ability of researchers to consistently access the same specimen for research. While marine laboratories called attention to easy access to some sort of embryological material available at all times, if a researcher sought out a particular species, the window of opportunity for research was often limited to specific months, weeks, and even days throughout the summer season. E.E. Just, working with Frank Lillie on the embryology and development of various forms of *Nereis*

William JJ De Smidt. *The spiny lobster, Panulirus argus, of southern Florida: its natural history and utilization* Vol. 921. (Washington, D.C.: Govt. Print. Off., 1922), 306.

²¹⁸ William Bateson, "The early stages of *Balanoglossus*" *The Quarterly Journal of Microscopical Science* 2:94 (1884): 208-236.

²¹⁹ Lewis R. Cary, "A study of pedal laceration in actinians." *The Biological Bulletin* 20:2 (1911): 81-107.

(polychaete worms) at the MBL, published several articles describing the collecting details of these organisms in both Woods Hole and at the Naples Zoological Station. In one article, Just outlines the difficulties involved in the process of collecting *Nereis limbata* (*Alitta succinea*), an organism on which he had been performing fertility experiments and embryological investigations for several seasons. According to Just, the mature spawning forms appeared after sunset on the “dark of the moon” in the months of June, July, August, and September. No individuals swarmed during the “light of the moon” meaning that there were four runs in four months corresponding to a lunar calendar. The runs had two sub runs that allowed the collector access to spawning males and females for about a week each month.²²⁰

²²⁰ Frank R. Lillie and Ernest Everett Just, "Breeding habits of the heteronereis form of *Nereis limbata* at Woods Hole, Mass." *Biological Bulletin* 24.3 (1913): 148.

TABLE II. 1912.

Moon Phase.	Date.	Number of Females.	Number of Males.
	June 4 to July 2	None	None
	July 3	0	1
	4	0	0
	5	0	0
	6	0	0
Third Quarter	July 7	0	0
	8	0	0
	9	0	0
	10	1	3
	11	3	3
	12	3	3
	13	0	2
New Moon	14	2	2
	15	0	2
	16	0	1
	17	0	0
	18	0	0
	19	0	0
First Quarter	20	0	0
	21	0	0
	22	0	0
	23	0	0
	24	0	0
	25	2	1
	26	1	0
Full moon	27	0	1
	28	0	0
	29	0	0
	30	15	30
	31	2	30
	August 1	4	30
	2	3	30
	3	0	20
Third Quarter	4	0	0
	5	8	20
	6	14	20
	7	0	0
	8	12	10
	9	10	50
	10	12	100's
	11	15	1000's
New Moon	12	18	30
	13	0	0
	14	0	0
	15	3	6
	16	0	0
	17	0	0
	18	0	0
First Quarter	19	0	0
	20	0	0
	21	0	0
	22	0	0
	23	0	0
	24	0	0
	25	0	0
	26	0	0

Figure 27 Table 2 for the year 1912; spawning of *P. megalops* E.E. Just "Habits of the Heteronereis," 204.

In his paper on the spawning behavior of *Platynereis megalops*, a polychaete pelagic worm closely related to *N. limbata*, Just published data detailing the number of mature males and females observed spawning during the 1911-1913 summer research periods at Woods Hole.²²¹ He found that, similar to *N. limbata*, *P. megalops*' spawning was correlated with lunar cycles but had a more pronounced yearly variability. In addition to correlations with lunar cycles, Just and Lillie isolated other factors that contributed to differential spawning behaviors, including time of day (spawning only

²²¹ E.E. Just, "Breeding Habits of the Heteronereis Form of *Platynereis megalops* at Woods Hole, Mass." *Biological Bulletin* 27:4 (Oct. 1914): 201-212.

occurred for one to two hours after sunset), weather (inclement weather sometimes lessened or completely halted spawning), and overall lighting conditions. Other conditions, known to influence spawning behavior, such as tide (high or low) and water temperature, seemed to have little or no effect on the spawning of *N. limbata*.²²²

W.K. Brooks outlined the tiny window of opportunity for collecting *Lucifer aestra*, a small prawn found near the Beaufort station. Similar to other anthropoda, reproductive materials were collected from mature spawning adults. Brooks found females in great numbers near a large marsh “during the first hour of ebb tide, on calm evenings when the tide turned between 7 and 8pm.” Three variables-- calm water, a turning tide, and sunset--all needed to be in place in order for Brooks to find his specimens. This caused Brooks to opine that “owing to this singular limitation there are only a very few favourable evenings for procuring the eggs in a single season.”²²³ The small window of collecting transferred to a small window for experimentation: researchers needed to work with the freshest specimens available in order to assure normal development.

Collecting usable embryological forms involved more than understandings of their spawning periods; quality was also key. In Just’s 1939 laboratory manual *Basic Methods for Experiments on the Eggs of Marine Animals*, he calls attention to the importance of using the freshest sperm and eggs available. This corresponds to both a collecting and a fertilization issue. According to Just, while many species shed reproductive materials throughout the summer research season, there are periods when the eggs and sperm are of higher quality, meaning that more fertilized eggs develop into

²²² Lillie and Just “Breeding Habits,” 154.

²²³ W.K. Brooks, *Lucifer: A Study in Morphology* (London: Trubner and Co., 1882), 60.

embryos and that those embryos are more robust and follow a normal developmental path. For example, Just suggests that a researcher should not work with *Arbacia* (sea urchin) at the end of the season because of low fertilization rates and *Echinarachius* (sand dollar) are in better condition and are more robust in the early season as well.²²⁴ In addition to qualitative changes in reproductive materials and the resulting embryos, transferring the mature spawning forms into the laboratory for artificial fertilization added additional complications to the process of collecting and utilizing these forms.

Fertilization

Inducing shedding or artificially fertilizing ova in the laboratory allowed researchers to consistently work with earlier developmental stages, but it was not a stress free process. Even though organisms were in the laboratory environment, their spawning and shedding behaviors still followed a natural cycle and researchers had to work within the parameters of these behaviors. Researchers working with collections of spawning adults had to work within these behavioral constraints to have access to embryological material. One way to do this was to utilize species from which reproductive material could be harvested, artificially fertilized, and reared as normal embryos. But the species for which this was simplistic were not guaranteed to be the most scientifically interesting.

As shown in the previous section, spawning patterns differed greatly between species and these patterns affected the laboratory work built around them. Researchers wanted to utilize both the freshest material and also to examine the earliest stages of development, and for this they had to bend their work to the timeline of the spawning organism. The best example of this is William Keith Brooks' work with the prawn

²²⁴Just, *Basic Methods*, 20.

Lucifer. The organism, which Brooks felt might hold the key to understanding the evolution and phylogeny of early arthropods, presented “unusual difficulties” when working with its embryological materials. Firstly, Brooks found so few spawning adults that he could not even sacrifice one for necropsy to outline its actual reproductive physiology. The spawning individuals he did find contained so few eggs, and they were so delicate, that he could not work with any one embryo for more than 2 hours. These difficulties alone were enough to stall research progress, but a larger concern was working around the spawning time of *Lucifer*. Brooks described the difficulties thus:

When we add to this that the eggs are laid about 9 o’clock in the evening, and must be studied between this time and daylight, after several hours of laborious collecting, by eyes that have already been severely taxed when looking over the collections and picking out the transparent and almost invisible adults by an artificial light, and examining each one of them with a lens to find those which carry eggs, the difficulty of the subject will be appreciated.²²⁵

Brooks’ work with these delicate embryos is outlined in his manuscript, and it demonstrates, not just the knowledge that he gained from the organism, but how his work schedule was changed in order to accommodate working with it. Brooks collected the prawns in the evening, sorted them in the laboratory, and waited for their spawning between 9 and 10 pm. After the spawning, Brooks detailed their development through 9am. E.B. Wilson described a similar time sensitivity while working with *Renilla* (sea pansy): the eggs were laid between 5:30 and 7am (most consistently at 6am) every day and Wilson had to be present during this period to view the earliest developmental forms.²²⁶

²²⁵ Brooks, *Lucifer*, 63.

²²⁶ E.B. Wilson, “The development of *Renilla*” *Philosophical Transactions of the Royal Society of London* 174 (1883): 729.

Other organisms were not quite so time sensitive, but this did not mean that intense concentration and knowledge of spawning behavior were not required. T.H. Morgan worked with a common shore snail, *Ilyanassa obsoleta*, at Woods Hole and in his labs at Columbia University.²²⁷ Unlike Brooks' *Lucifer*, *Ilyanassa* could be kept in captivity and relied upon to lay eggs daily between June and August. But even the shore snail's consistent egg laying did not guarantee consistent embryological material without additional requirements of time sensitivity and watchfulness. Morgan states that in order to obtain examples of early developmental stages, the snails crawling on the glass walls of the aquarium were closely watched throughout the day.

When a capsule is about to be deposited it can be seen at the opening of the oviduct. As soon as it is fixed, the snail is gently pulled away or pushed off, leaving the capsule attached to the glass. The capsules of newly laid eggs are much softer than are those that have been laid some hours and are more easily opened.²²⁸

Time sensitivity was two-fold when working with *Ilyanassa*: the capsules were easier to open without damaging the eggs if harvested right immediately after depositing and researchers interested in the earliest moments of development required access to the eggs as quickly as possible. According to Morgan, even catching the capsule at the oviduct did not guarantee the earliest starting point for developmental events- the egg may have already started to develop before it was deposited.²²⁹ *Lucifer* and *Ilyanassa* are examples of mature forms that had internally fertilized eggs when brought into the laboratory, but mature forms did not always shed fertilized ova in the laboratory. Collecting spawning

²²⁷ NYA Director's Office, C.H. Townsend. NYA Day Book 30 Oct. 1913- 20 Aug. 1918. RG 7 1009 Box 24. C.H. Townsend Papers. Wildlife Conservation Society Archives. Bronx: New York.

²²⁸ Thomas Hunt Morgan, "The formation of the antipolar lobe in *Ilyanassa*," *The Journal of Experimental Zoology* 64:8 (1933): 434.

²²⁹ *Ibid*, 435-436.

males and females prepared to release their eggs into the water allowed researchers to manually fertilize embryos in the laboratory.

Researchers utilized two methods for fertilizing ova in the laboratory: inducing shedding or stripping the reproductive material and excising the material from the mature forms. Inducing shedding required knowledge of the organism's spawning behavior. The methods employed to induce the shedding of reproductive materials depended upon the organism. In his 1913 paper, Just outlines his method for inducing shedding for the worm *Neiris limbata*. After collecting spawning adults at dusk, males and females were placed in separate dishes in a cool, dark place overnight. To induce shedding and fertilization, the male and female were placed together in a clean tank.

If a male and female be placed together in a bowl of fresh sea-water they appear to stimulate one another very quickly, but it is usually several minutes, at least in the case of animals that have been kept in the laboratory overnight, before the male begins to shed sperm; and the female never sheds her eggs until after the male has begun to shed sperm.²³⁰

In addition to inducing shedding, researchers working with fishes commonly stripped the milt and roe from mature adults and manually fertilized the material in a separate dish.

Stripping (or milking) fish for their eggs was a common practice in aquaculture during this period. The practice was so common, many researchers state that they “stripped” eggs from fishes for artificial fertilization, but it is difficult to find a paper that explains the process. To strip the milt (sperm) and roe (eggs) from mature fishes, the researcher pressed firmly near the anal fin of the fish; if the fish was a ripe male the milt would begin easily flowing and could be caught in a clean, shallow dish. The same procedure was repeated with a ripe female and the roe was also transferred to the dish

²³⁰ Lillie and Just “Habits of the Heteronereis form of *Nereis limbata* at Woods Hole, Mass.” *Biological Bulletin* 24:3 (Feb. 1913) 150.

containing the milt. The researcher then gently mixed the milt and roe and placed the now fertilized eggs in water until they were ready to work with them.²³¹ Embryologists exploring fisheries issues perfected the art of stripping milt and roe from common food and game fishes such as trout and salmon, but researchers working with newly discovered teleosts had to develop reliable techniques to assure viable and normally developing embryos for their research.

Fundulus heteroclitus (mummichog) were the most commonly utilized teleost eggs in embryological study during this period. The fish were abundant on the East coast and the eggs were large, nearly translucent, and contained a hard outer coating that allowed rough handling without damage. Because researchers did not develop a way to maintain and breed mummichogs in the laboratory until the 1950s, all fishes during this period were collected during their spawning period, stripped by hand, and artificially fertilized.²³² Stripping was not a fool-proof process- sometimes stripped eggs developed abnormally due to rough handling, so monitoring development was especially important after this process.²³³ Stripping milt and roe from fishes did not require destroying the mature specimen, but retrieving reproductive materials from other species, such as lobster and sea urchin, required cutting open the adult forms to extract the reproductive materials.

²³¹ Sylvia R. Black, "Seth Green: Father of Fish Culture" *Rochester History* 6:3 (1944): 9-10; John Wheelock Titcomb, "Fish Cultural Practices in the United States Bureau of Fisheries," *Bulletin of the Bureau of Fisheries* 28 (1908): 734.

²³² James W. Atz, "*Fundulus heteroclitus* in the Laboratory: A History," *American Zoologist* 26:1 (1986):111-120;

H. H. Newman, "Spawning behavior and sexual dimorphism in *Fundulus heteroclitus* and allied fish," *The Biological Bulletin* 12.5 (1907): 314-348; Warren H. Lewis, "Experiments on the localization of eggs in a teleost fish (*Fundulus heteroclitus*)" *The Anatomical Record* 1 (1912): 1-6.

²³³ Researchers stripped eggs from organisms other than fishes. Crawford "Spawning Habits of the Spiny Lobster," 316.

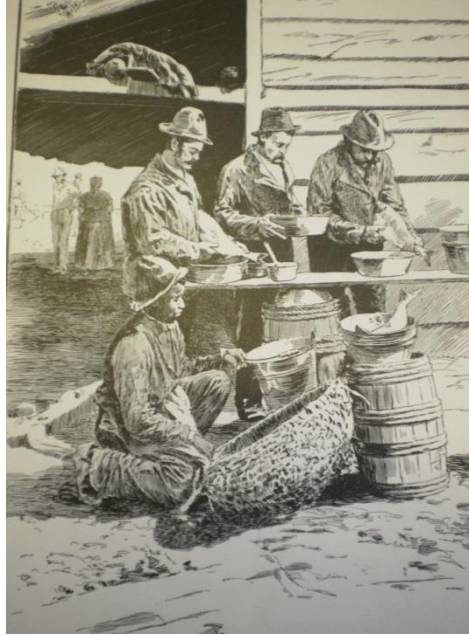


Figure 28 Woodcut of fisheries' workers stripping roe and milt from fish. Box 21 Folder 17 Bureau of Fisheries Records "1877-1948" Smithsonian Institutional Archives: Washington, D.C.

Extracting reproductive material from mature specimens was a two-step process: determining the reproductive readiness of the collected organisms and fertilizing the ripe materials in the laboratory. In his laboratory manual *Handbook of Invertebrate Zoology for Laboratories and Seaside Work*, W.K. Brooks outlines these two steps when working with *Arbacia* eggs. These sea urchins proved especially useful for teaching embryology at marine stations because their breeding season on the southeastern coast of the United States extended from early spring until the end of August. This continuous spawning meant that a collector could potentially find a ripe female and male every day during the summer, but not every specimen would have usable materials. To find a usable specimen, the student collected several adult sea urchins and transferred them to the laboratory. Once inside the lab, a strong knife was used to open the shells and ascertain the sex; females have brown reproductive organs and males white. The next step was for the

student to find reproductive materials ripe for fertilization. The ovaries were cut open and the eggs retrieved and placed under a microscope.

If the eggs are of uniform size and color, they are probably ripe, and ready for fertilization, but if they vary much in size, and if some are more transparent than others, other specimens should be examined until one is found in which the eggs are more uniform. Place this specimen on one side, where it can be recognized, and keep it until a ripe male is found.²³⁴

Testes of mature males were then cut up and examined under the microscope for uniform and robust sperm. Once located, the sperm and egg were combined in a dish and rinsed repeatedly until the water ran clear. The fertilized material was then ready for examination under a microscope to teach embryological development, or it could be placed in a bright location out of direct sunlight until it matured into larvae (approx. 24 hours) to teach later stages of physiological development in the mature form.²³⁵

While it might seem as if embryologists would be uninterested in cultivating and maintaining the embryo into larval and mature forms in the laboratory, there were multiple reasons to try to rear specimens through the mature and spawning stages of their lifecycle. Researchers often found embryological forms, especially pelagic forms, collected during survey work difficult to taxonomically identify if they could not link the embryo and larval forms to the often drastically different mature specimens.

Understanding the embryological development of specimens was merely the first step in establishing a viable fisheries program capable of producing large amounts of fry and larvae for restocking. And finally, researchers and teachers interested in specific forms attempted to propagate these in the laboratory to shortcut the collecting and fertilizing

²³⁴ Brooks, *Handbook of Invertebrate Zoology*, 100.

²³⁵ Ibid., 103. For other examples of excising reproductive materials, see Lewis R. Cary "The Formation of Germ Layers in *Actinia bermudensis verr*" *Biological Bulletin* 19:6 (Nov. 1910): 339-346.

issues discussed in the last two sections. But rearing marine organisms from their earliest developmental stages to maturity in the laboratory was, and still is, one of the most delicate and difficult processes.

Rearing from Embryos in the laboratory

Of all the difficulties encountered in embryological work at marine stations, rearing specimens from their earliest stages into maturity was considered both critical to research and extremely difficult for the researcher. Marie Poland Fish's study of mysterious eel eggs taken from a tow on *The Arcturus* proved difficult to identify because they could not be reared past the leptocephalus stage (larval stage). Fish believed that the developing embryos were those of the American eel, but her successive attempts at extending their life in the laboratory failed and she could only make a tentative taxonomic identification. In her subsequent publications, she stated that definitive identification of the eggs, and a full description of the developmental cycle of the American eel, required the ability to rear the species in the lab. At the time of publication, Fish had failed several times to rear additional eggs in artificial conditions.²³⁶ In addition to taxonomic difficulties, fisheries researchers found that a thorough understanding of embryological development did not necessarily facilitate the use of that species in the laboratory; they needed to know how to rear embryos into mature forms to use them consistently.

D. R. Crawford had great success in stripping fertilized ova from spiny lobsters and rearing them through their earliest developmental stages in the laboratory, but all his

²³⁶ Marie Poland Fish, "Contributions to the embryology of the American Eel (*Anguilla rostrata* Lesueur) *Zoologica* 8:5 (1927): 1-36.; Marie Poland Fish "Preliminary report on the egg and larva of the American eel (*Anguilla rostrata*) *Science* 64: 1663 (Nov. 5, 1926): 455-456.

larval lobsters eventually died. Crawford knew of no successful attempt at rearing mature spiny lobsters in the laboratory, and stated baldly that “it is a very easy to place a spawn bearing female in any sort of floating contrivance and allow the eggs to hatch for they will hatch readily under such conditions, but there is no gain or improvement over natural conditions unless many of the young can be reared beyond the larval stages.”²³⁷ W.K. Brooks also lamented the inability to rear and maintain *Lucifer* in the laboratory. The difficulty in procuring usable reproductive material for study led Brooks to state that “until the animals can be made to thrive and multiply in confinement, it must always remain an extremely difficult matter to procure the eggs in abundance.”²³⁸ Without the ability to rear and maintain specimens in the lab, researchers were hard pressed to work out physiological details and to obtain enough normally developing organisms for extensive study.

Calibrating the artificial environment to the developing organism’s needs proved extremely difficult for marine specimens. Many species inhabited vastly diverse environments during their multiple life stages. Pelagic forms often float near the surface of the ocean during embryological development and retreat into deeper waters when mature. Other organisms, such as the American eel studied by Marie Poland Fish, drift thousands of miles in their lives, maturing in wildly different environments and returning to warm water estuaries to spawn. Multiple environmental conditions proved difficult to recreate in the laboratory, especially at the exact time in the lifecycle needed to maintain normal development. Researchers failed to maintain many of these more difficult organisms, including eels and Brooks’ *Lucifer*, but those specimens with more consistent

²³⁷ Crawford, *Spiny Lobsters*, 319.

²³⁸ Brooks, *Lucifer*, 60.

environmental needs might be reared if other considerations, such as water temperature, lighting concerns, and feeding schedules, could be overcome.

The largest hurdle when rearing embryos in the laboratory involved their feeding. A fertilized embryo did not require food immediately; it could survive on its yolk sac for much of its developmental period. But researchers were at a loss of when and how to feed emerging larvae after the yolk sac had been consumed. Larvae were often too small to consume artificial food utilized in the fisheries industry such as liver.²³⁹ Even small copepods proved too large for many larval forms. In addition to figuring out *what* to feed organisms, researchers also ran into the issue of *when* to feed their specimens: feed a larva too early or late in their development and they died or developed abnormally. The first step was to find a reliable food source and then to figure out when to dispense it.

Researchers sought a food source that was cheap, accessible, and easily dispensed. In 1902, Caswell Grave published a short article in *Science* detailing the method he developed for feeding larval forms of echinoderms in the laboratory. The method, perfected over two years of research at the Beaufort laboratory at North Carolina, was fairly simple. After fertilization and waiting for the larvae to swarm to the surface of the water, the researcher placed the larvae in a jar of fresh seawater.

At the same time there are also added a dozen or more pipettefuls of the surface sand from an aquarium containing a culture of diatoms. (Prepared by putting a liter or more of sand, dredged from the ocean bottom, in an aquarium of sea water and allowing to stand several days.) The jar thus stocked is now covered and set before a window, where it is well, but indirectly, lighted.²⁴⁰

²³⁹ F.H. Herrick *Natural history of the American lobster* (No. 747). (Washington, D.C.:US Government Printing Office, 1911), 318.

²⁴⁰ Caswell Grave, "A Method of Rearing Marine Larvae" *Science* 15:380 (April 11, 1902): 580.

The addition of the diatoms to the jar performed multiple functions: they kept the water pure through natural filtering, provided food for the larvae, and through the balance of the aquarium kept the oxygen level consistent so that fewer water changes were needed and thus fewer interventions were required by the researcher to maintain a livable environment.²⁴¹

Grave's method was quickly adopted by other researchers seeking to rear larval forms in the laboratory environment. The method traveled quickly for several reasons: diatoms were readily available in multiple locations and because of their size they were highly mobile. Initially, the method was utilized by junior researchers working under Graves at Beaufort, and they traveled with diatoms cultured from sand at Beaufort. Eventually, it was found that diatom cultures collected at other laboratories in the network could also be used. In 1926, Benjamin H. Grave reared the larvae of the bivalve *Cumingia tellinoides* at the Marine Biological Laboratory on *Nitzschia* diatoms cultured at the Plymouth laboratory in England. According to Benjamin Grave, the diatoms in the Woods Hole area were not suitable for feeding to the embryos because of a danger of a bacterial infection, but the Plymouth culture worked nicely. Grave also remarks on Caswell Grave's culture

The Beaufort species first used by Caswell Grave, on the other hand, grows in great abundance in aquarium jars and may be fed without difficulty. This diatom has the advantage over *Nitzschia* in being relatively short and thick instead of long and slender. Both of these species should be propagated at marine laboratories for the use of investigators.²⁴²

In addition to being readily available and extremely compact and mobile, the diatom culture worked on a multitude of marine organisms. The method worked, not only for the

²⁴¹ Ibid.

²⁴² Benjamin H. Grave, "The Natural History of *Cumingia tellinoides*" *Biological Bulletin* 53:3 (Sept. 1927): 208.

echinoderm larvae Grave was cultivating, but also a wide variety of species both naturally and artificially fertilized. R.P. Cowles used the method to rear “well-developed larvae taken from the tow” demonstrating that the method worked for both artificially and naturally fertilized larvae.²⁴³ Lewis Cary reported utilizing the Beaufort diatoms to rear separate actinian species in laboratories at Beaufort, the Harvard laboratory in Bermuda, the Carnegie Laboratory in the Dry Tortugas.²⁴⁴ R.P. Cowles reared the marine worm *Polygordius appendiculatus* at Beaufort and in Baltimore with Grave’s original diatom culture as well.²⁴⁵ But the uptake of Grave’s method of diatom culture and larval feeding did not solve all of the issues inherent in rearing marine organisms in the laboratory; researchers still needed to pinpoint the proper time to start feeding and this proved to be a substantial hurdle.

Grave’s diatom method facilitated the extended development of fertilized specimens in the artificial environment, but it also led to further difficulties in maintenance of these advanced forms, including complications with feeding. Rearing embryos into sexually mature adults required close observation of the developing organism. In 1913, E.E. Just succeeded in rearing sexually mature polychaete marine worms (*Neiris limbata* and *Platynereis megalops*) in the laboratory utilizing a culture of the Beaufort diatoms. His paper concentrates, not on his method for procuring diatoms, but instead on establishing precision in feeding his larval forms. At the time of fertilization, the embryos contained a large number of “oil drops” which were reduced through each successive division of the cell from embryo into larval form. “It is thus

²⁴³ R.P. Cowles, “Notes on the Rearing of the Larvæ of *Polygordius appendiculatus* and on the Occurrence of the Adult on the Atlantic Coast of America” *Biological Bulletin* 4:3 (Feb. 1903): 125-128.

²⁴⁴ Cary, “A Study of Pedal Lacerations,” 82.

²⁴⁵ Cowles, “Notes on the Rearing of the Larvæ” 125-128.

possible to follow the history of the oil drops very fully in these creatures that make veritable living test tubes in a fat-digestion experiment.”²⁴⁶ In addition to understanding this process for its own sake, watching fat-digestion was important for knowing the exact moment that the developing organisms required feeding. When the larvae gained segmentation, they were watched closely; when they reached the three-segmented free swimming stage, diatoms could be introduced into the aquarium.

*The criterion for the initial feeding is the complete disappearance of the oil drops from the entoderm cells... If food is given the worms before the oil has been completely used, they are killed in large numbers. On the other hand, food must not be withheld too long after the disappearance of the oil. The first feeding consists of ten c.c. of a diatom culture known by previous examination under the microscope to be free of metazoa or larvae strained through three thicknesses of bolting silk of very fine mesh. As the larvae add segments more food is given.*²⁴⁷

The “critical period” for feeding marine larvae differs in each species required careful observation by the researcher in order to reduce mortality of experimental subjects.²⁴⁸

Whereas the oil drop or yolk sac was readily visible in some species, such as the worms utilized by Just, it was not visible in many popular species such as echinoderms and required timed experiments to identify the proper time for feeding.²⁴⁹

By combining knowledge of collecting, fertilizing, and rearing, some species were successfully brought into the marine station laboratory- and some even migrated into terrestrial laboratories. However, the most popular species continued to be those that were abundantly available and required as little extra attention as possible. Sea urchin

²⁴⁶ E.E. Just, “On Rearing Sexually Mature *Platynereis megalops* from Eggs” *The American Naturalist* 56:646 (Sept-Oct. 1922): 472.

²⁴⁷ *Ibid.*, 472-473.

²⁴⁸ The term “critical period” was applied to the problem of laboratory rearing by James Atz, “A working bibliography on rearing larval marine fishes in the laboratory,” 96. For more information on how the term is used in fisheries biology and the debate surrounding the existence of a “critical period” in nature, see R.W. Morris, “Some considerations regarding the nutrition of marine fish larvae” *ICES Journal of Marine Science* 20:3 (1955): 255-265; R. C. May, “Larval mortality in marine fishes and the critical period concept.” *The early life history of fish*. Ed J.H.S. Blaxter (Berlin-Heidelberg: Springer, 1974), 3-19.

²⁴⁹ Just, *Basic Methods*, 11.

materials were once so abundant in the Woods Hole region that they became the de facto system for studying embryological development in invertebrates. They required a minimal amount of knowledge about the environment to collect because the species' reproductive cycle meant that ripe adults were always available during the research season. In addition, the eggs were hardy and consistently developed normally, and because of the ready supply of materials, researchers did not feel compelled to try to rear forms through their entire lifecycle in the lab. Researchers in the region took this availability for granted, and it was remarked that when the *Arabicia* resources declined due to overharvesting, little information could be offered regarding the natural habitat, reproductive cycle, or natural history of the species.²⁵⁰

Because of the difficulties associated with rearing and maintaining marine embryological specimens in the laboratory, their use declined around mid-century. Experimental embryologists turned to more easily accessed subjects, although they did continue to work and teach with sea urchin, smooth dogfish, and mummichogs when they were available at the seashore. However, fisheries researchers continued working with a wide range of embryological materials and the advancement of laboratory techniques in the second half of the twentieth century has seen a surge in interest in the field for experimental embryologists in genetics laboratories.²⁵¹

²⁵⁰ Erik Ellis, "What is Marine Biology?: Defining a science in the United States in the Mid-20th Century," *History and Philosophy of the Life Sciences* 29:4 (2007): 469-493.

²⁵¹ Wourms, "The rise of fish embryology"; for information on the link between marine stations and embryology in fisheries research, see Tim Smith, *Scaling Fisheries: the science of measuring the effects of fishing, 1855-1955*. (Cambridge: Cambridge University Press, 1994). On the importance of embryology to modern fisheries research, see Lee A. Fuiman and Robert G. Werner, *Fishery Science: The unique contributions of early life stages* (Malden, MA: Blackwell Science, 2002).

Conclusion

Early twentieth century embryological researchers struggled to find marine organisms that were plentiful, useful, and easily maintained in the laboratory.

Researchers interested in working with marine embryos needed to understand how the environment influenced spawning behavior, recognize the normal development of their collected specimens, and establish laboratory methods including fertilization and feeding techniques that facilitated that development in an artificial environment. This process was incredibly difficult and led to a limited number of embryological forms being regularly incorporated into investigations at marine stations. By far the most common species utilized for teaching and experimental work were echinoderms: they spawned throughout the summer season, had no specialized requirements in collection practices, and could be artificially fertilized in the laboratory. The less common and more problematic specimens to handle and maintain, such as Brooks' *Lucifer* and Fish's eels, provoked a host of new scientific questions and forced researchers to develop knowledge both inside and outside the laboratory while seeking answers.

Researchers interested in embryological work congregated at marine stations at the turn of the twentieth century in order to take advantage of available materials for surveys, fisheries and academic experimentation, and teaching. But the image of an easily accessed and maintained supply of embryological material is somewhat misleading. Embryology at marine stations linked researchers directly with their environment; they were forced to work within the confines of spawning hours and seasons, punctuated by changes in weather that could derail carefully laid research plans. If materials were effectively retrieved, fertilization in the laboratory required an understanding of the

organisms' normal development in their natural milieu and careful observation that bound the researcher to the specimen for hours and sometimes days in order to observe and facilitate growth of the embryo. Efforts to rear and maintain embryos into sexually mature forms lead to the development of special feeding methods and time sensitive feeding schedules. The difficulties encountered by researchers in these locations explains why access to an abundant amount of embryological material did not necessarily translate into the extended use of marine organisms in all embryological laboratories.

The precise choreography between field and laboratory required to collect, maintain, and rear these specimens in artificial environments suggests that embryological investigation had the ability to generate copious amounts of information about the general biology of the immediate marine environment. Contrary to our historical understanding of this field as exclusively bench- focused, we can see that embryology directly linked the laboratory and field environment and generated information about both of these faces of the marine station structure. It is important that historians understand that through the process of seeking to maintain organisms in captivity, researchers generated information that would serve as the basis for the growing field of marine biology.

Chapter 4

A Bundle of Nerves: Jellyfish and Neurophysiology at Marine Stations, 1850-1930

In 1850, Louis Agassiz outlined the reasons that naturalists and scientific investigators should pay close attention to *medusae*. Jellyfish had a “highly organized structure” about which the few investigators who worked with the creatures had conflicting opinions. According to Agassiz, “the structure deserves to fix the attention of the physiologists in the highest degree.”²⁵² Fifteen years later, his son Alexander Agassiz described medusae as “prophetic animals” that were “wonderful links which unite in one great whole the different members of the Animal Kingdom.”²⁵³ Both Louis and Alexander regarded the advanced physiological organization of these seemingly simple invertebrates as a core reason for scientific investigation.²⁵⁴

Curiosity about their place in the chain of being and, eventually, questions regarding their evolutionary history were not solely responsible for the use of these creatures in physiological experimentation at the turn of the twentieth century. Jellyfish were a common marine catch with a large seasonal availability and a distinctive reproductive process that provided researchers with consistent experimental material. Unlike crustaceans and fishes, many jellyfish species were available in complete

²⁵² Louis Agassiz, “Contributions to the natural history of the acalephae of North America, Part 1: on the naked-eyed medusae of the shores of Massachusetts, in their perfect state of development,” *Memoirs of the American Academy of Arts and Sciences* 4 (1850): 221–223.

²⁵³ Alexander Agassiz *North American Acalephae* (Cambridge, MA: Harvard University Press/Welch, Bigelow, & Co 1865), 11.

²⁵⁴ Louis Agassiz, was famously, not a Darwinist. His reasons for examining the jellyfish may seem evolutionary in retrospect, but his beliefs about its place in nature refer to a different form of taxonomy. For information on ideas about the great chain of being, see Arthur O. Lovejoy *The Great Chain of Being: A Study of the History of an Idea* (Cambridge, MA: Harvard University Press, 1936)

lifecycles in the same locations. The organisms appeared to suffer little stress from continuous and extensive tissue excision and electrification. They had simplistic structures easily extrapolated to human organ and nerve function. Finally, they were silent creatures that lacked noticeable features, allowing researchers to circumvent arguments about vivisection that often accompanied research on live mammals during this period.²⁵⁵ But these conveniences to physiological experimentation were offset by small, but important, inconveniences.

While medusae were abundant and accessible, they proved difficult to maintain in captivity. Jellyfish survived in laboratory aquaria for highly variable periods depending on their species, age, and health when placed in captivity. Robert T. Browne recorded that *Obelia nigra* lived 24 hours at most; *Phialidium bicophurum* (now known as *Clytia lamouroux*) survived 3 days.²⁵⁶ Jellies also proved difficult to cultivate through lifecycles. Although specimens deposited and fertilized eggs and even produced larvae and polyps in captivity, rarely did these polyps develop further. Juvenile jellies caught and placed in captivity rarely matured, suggesting that jellyfish could be maintained in stasis, but the aquarium environment was not conducive to studying development and the complete lifecycle in a single specimen.

Historians and sociologists have called attention to the variables that dictate organismal choice in scientific practice. Histories of model organisms and systems have

²⁵⁵ George Romanes believed that anti-vivisectionists could only have a problem with his jellyfish experiments if they also found eating raw oysters cruel. Though Romanes addressed the anti-vivisectionists in his 1885 *Jelly-fish, Star-fish and Sea Urchins*, it seems there was little concern about marine invertebrates from that corner. See Rob Boddice “Vivisecting Major: A Victorian Gentleman Scientist Defends Animal Experimentation, 1876-1885” *Isis* 102:2 (June 2011): 215-237.

²⁵⁶ Edward T. Browne. “On Keeping Medusae Alive in an Aquarium,” *Journal of the Marine Biological Association of the United Kingdom* 5 (1897-98), 179. Neither of these jellyfish have a common name. Throughout the chapter I will try to provide common as well as Latin names for the species referenced.

explored the coupling of tools and technologies to specific research questions.²⁵⁷ The use of organisms depends upon a variety of variables including availability, preparation and maintenance methods, research program and structure, and the investigators' place in "organizational contexts."²⁵⁸ Researchers responded to all of these variables when choosing organisms for physiological research.

Adele Clark highlights the importance of availability and ease of maintenance in choosing organisms for physiological experimentation. According to Clark, physiologists utilized "five major means of access": exotic specimens (materials foreign to local habitats, and/or rare to the experimental environment, or difficult to keep in captivity), mundane specimens (local/easily accessed/ easily kept in captivity), medically supplied (human cadavers/ovaries/ surgical waste), animals or specimens obtained from biological supply companies and onsite research colonies (such as primate groups).²⁵⁹

Clark's categories appear clear cut, but the use of jellyfish in physiology experiments fall into two of these categories. They were locally available and easily accessed at marine stations, suggesting that they were *mundane fresh specimens*; but they

²⁵⁷ Karen A. Rader. *Making mice: standardizing animals for American biomedical research, 1900- 1955*. (Princeton: Princeton University Press, 2004); Bonnie Tocher Claus, "The Wistar rat as a right choice: Establishing mammalian standards and the ideal of a standardized mammal," *Journal for the History of Biology* 26: 2 (1993): 329-49. Robert Kohler *Lords of the Fly: Drosophila Genetics and the Experimental Life* (Chicago: University of Chicago Press, 2004). Vassiliki Betty Smocovitis "The "Plant Drosophila": E.B. Babcock, the genus *crepis*, and the evolution of the genetics research program at Berkeley, 1915-1947," *Historical Studies in the Natural Sciences* 39: 3 (2009): 300-355. Michael Pettit "The Problem of Raccoon Intelligence in Behaviorist America," *British Journal of the History of Science* 43:3 (Sept. 2010): 391-421. Adele E. Clarke and Joan H. Fujimura (eds.) *The Right Tools for the Job: At work in Twentieth-Century Life Sciences* (Princeton, N.J.: Princeton University Press, 1992).

²⁵⁸ Joan H. Fujimura "The Molecular Biological Bandwagon in Cancer Research: Where Social Worlds Meet," *Social Problems* 35: 3 (June, 1988): 261-283. For an example of the historical arch of an experimental organism that went out of favor, see Gregg Mitman and Anne Fausto-Sterling "Whatever Happened to *Planaria*? C.M. Child and the Physiology of Inheritance," In Clark and Fujimura (eds.) *The Right Tools for the Job* (1992) 172-197 and Michael Pettit "The Problem of Raccoon Intelligence."

²⁵⁹ Adele Clark. "Research Materials and Reproductive Science in the United States, 1910-1940," in Gerald Geison (ed.) *Physiology in the American Context 1850-1940*. (Bethesda, MD: American Physiological Society, 1987), 323-50.

were difficult to keep alive for extended periods of time, placing them in a category of *exotic live specimens*. Following the Agassizs' work, debates about jellyfish nerve structure grew and the availability of these organisms at marine stations suggested that research programs would quickly grow around them, but subsequent difficulties arose in trying to maintain specimens in artificial environments. Attempts to utilize jellyfish in neurophysiological experimentation lead to the creation of new technologies and the adoption of certain species, but the use of these organisms was limited to specific locations and experimental programs.

This chapter examines the adoption of medusae for neurophysiological experimentation at marine stations between 1880 and 1940. Jellyfish could be found at nearly every station in the world, but they proved difficult to maintain under laboratory conditions. The most common species, including *Aurelia aurita* (moon jelly) and *Sarsia tubulosa* (clapper jelly), required specialized technology and feeding schedules to thrive in captivity. While the earliest research on the nerve structure of jellyfish utilized these species, their long-term upkeep required new technologies and advances in laboratory methods. Instead, heartier but highly localized species, such as *Gonionemus vertens* (clinging jelly) and *Cassiopea xamachana* (upside down jelly), were chosen for extended experimentation on pulsation and regeneration. Because the most widely distributed species were still inconsistently maintained in laboratories and the heartiest species were limited to specific locations, the organism was eventually discarded in favor of the giant squid axon after WWII.

Examination of the rise and fall of the jellyfish in neurophysiological research highlights the struggles that physiologists encountered while working in the newly

accessible environments of the marine station. Research on experimental organisms has focused on terrestrial species, but the use of marine species expanded along with the establishment of these new field locations. Researchers sought to experiment with locally abundant organisms, but those deemed useful remained delicate to work with or geographically bound. By examining the struggles to utilize these species, and the research programs that grew up around them, we can improve our understanding of organismal choice in early experimental life sciences, and also broaden our appreciation of where and how neurophysiologists worked during this period.²⁶⁰

Mundane Fresh Specimens

Medusae were plentiful near many marine stations; daily collecting provided both juvenile and adult forms throughout the most common research period (June-September). Stations listed available species in their publications of biological surveys. W.K. Brooks wrote three articles entitled “Notes on the Medusae of Beaufort, North Carolina.” Each article described the occurrence of jellyfish in the nearby waters, with special emphasis on the most abundant species. Similar surveys of local invertebrate populations were published by nearly every marine station in America.²⁶¹ Jellyfish have a distinctive

²⁶⁰ While some research has been done on physiology at marine laboratories, it has focused primarily on the work of Jacques Loeb and his work at Woods Hole, Mass. See Jane Maienschein. “Physiology, Biology and the Advent of Physiological Morphology,” in *Physiology in the American Context: 1850-1940*. Edited by Gerald Geison (1987) 177-194. See also Philip Pauly “General Physiology and the Discipline of Physiology, 1890-1935,” in *Physiology in the American Context: 1850-1940*. The history of neurophysiological experimentation has been underexplored. Research has focused on major research programs at Washington University in Saint Louis and the Rockefeller Foundation. See Robert L. Schoenfeld *Explorers of the Nervous System: With Electronics, an Institutional Base, A Network of Scientists* (Boca Raton, FL: Universal Publishers, 2006). The majority of other research has focused on the development of key concepts in the history of neuroscience with little attention to laboratory methods. Stanley Finger *Origins of Neuroscience: A History of Explorations into Brain Function* (Oxford: Oxford University Press, 2001); Mary A.B. Brazier *A History of Neuroscience in the Nineteenth Century* (New York: Raven Press, 1988); Edwin Clark and L.S. Jacyna *Nineteenth Century Origins of Neuroscientific Concepts* (Berkeley, CA : University of California Press, 1987)

²⁶¹ For examples see W.K. Brooks, “List of Meduse found at Beaufort, NC during the summers of 1880 and 1881,” *Studies from the Biological Laboratory The Johns Hopkins University Baltimore Vol. II* (N. Murray:

reproductive lifecycle (known as metagenetic): mature *medusae* produce eggs and sperm, the fertilized egg develops into free swimming *planulae*, and planulae develop into immobile *polyps*. Polyps can be solitary, or they can asexually multiply to resemble a coral community; the polyp form may only last days or can continue for months or years. Eventually they bud into new, free swimming, sexually immature *ephyrae*, which resemble the mature jellyfish within a few weeks.

During the research season, jellyfish commonly release sperm and eggs into the water every day, meaning that locations that contain adult forms commonly boast other developmental forms in the life cycle.²⁶² At Woods Hole, Charles and George Hargitt found that all forms of reproductive materials were consistently available. They collected throughout the day in various locations and found, for any given species, “embryos in all stages of growth.”²⁶³ Because of the continuous lifecycle available to collectors, they were not only able to collect enough material for their investigations, but were able to choose particular forms in the lifecycle. For example, T.H. Morgan specified in his work on regeneration that he used *Gonionemus* between 10 and 20mm diameter with somewhere between 40 and 60 tentacles.²⁶⁴ The high volume and continuous lifecycle of the specimens made this specificity possible and marked the jellyfish as a valuable experimental tool.

Baltimore, 1883): 135-146. Charles Hargitt, “Notes on a few Medusae New to Woods Holl,” *Biological Bulletin* 4:1 (1902): 13-23. While each laboratory had individual publications highlighting available jellyfishes for experimental work, by far the most popular and far reaching resource for determining available medusae was Alfred Goldsborough Mayer’s three part *Medusae of the World* published between 1910 (vol. 1 and 2 on hydromedusae) and 1923 (vol. 3 on scyphomedusae) (Carnegie Institution of Washington: Washington, D.C.).

²⁶² Charles W. and G.T. Hargitt “Studies in the Development of Scyphomedusae,” *Journal of Morphology* 21 (1910): 217-263.

²⁶³ *Ibid.*, 222.

²⁶⁴ T.H. Morgan “Regeneration in Hydromedusae, *Gonionemus vertens*” *The American Naturalist* 33:396 (Dec. 1900): 941.

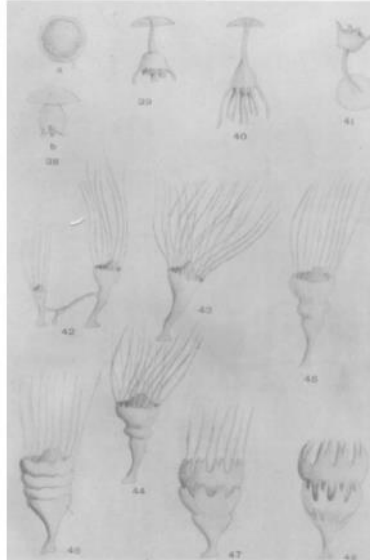


Figure 29 Charles and G.T. Hargitt illustrate the various forms from a lifecycle collected in the same location during one season. "Studies in the Development of Scyphomedusae" *Journal of Morphology* 21 (1910): Figures 38-48.

Depending on the location, various species in each lifecycle stage, including free floating reproductive material, were available for constant collection throughout the investigatory season. *Sarsia tubulosa* and *Aurelia aurita* were common jellies at northern stations, including Woods Hole, Massachusetts and Plymouth, England. Both species reliably occurred in great numbers in the littoral zone and could be collected continuously from early spring to late fall. Found in large groups, accessed close to land, and reliably available, these organisms showed up consistently in early experimentation with jellyfish. But the fact that certain organisms were accessible does not fully explain why they were utilized for research.

In the late nineteenth century, a debate raged between prominent naturalists from multiple disciplines regarding the existence and extent of the nervous system in jellyfish. In 1850, Louis Agassiz described nervous tissue in several species he found during dredging in Boston Bay, including the abundant *Sarsia* and *Bougainvillia*

supercilliaris.²⁶⁵ Reactions to Agassiz's findings were rife with denial. Many prominent naturalists-- including George Romanes-- questioned his findings; Agassiz himself came to doubt his own conclusions.²⁶⁶ Fifteen years later, Ernst Haeckel again described nerves in a hydromedusa, although he did not link his findings with Agassiz's original description. Many, including Thomas Huxley, continued to deny these findings. Haeckel's work was quickly followed by others asserting the existence of some type of nervous tissue in jellyfish; researchers in Germany, England, Italy, Russia and the United States were publishing on the existence of a nervous structure in medusa. However, Romanes' 1887 work eventually settled the matter.²⁶⁷

Georges Romanes' 1887 book *Jelly-fish, Star-fish, and Sea Urchins* brought the debate over the existence and structure of nervous tissue in medusae to a close.²⁶⁸ In the years before the publication of his book, both Romanes and Thomas Eimer published articles on the subject. These works utilized similar mutilation experiments to ascertain the extent of the nervous structure. Although these publications were cited by other researchers, they did not signal an end to the debate.²⁶⁹ The nervous structure of medusae was so contested that Romanes stated in *Jelly-fish* that his earliest experiments were merely "to obtain evidence of the very existence of nerve-tissue." He suggests that if jellyfish had nerve and muscle tissues, they were the lowest level on the "zoological

²⁶⁵ There is no common name on record for this species.-

²⁶⁶ Louis Agassiz. "Contributions to the Natural History of the *acalephae*," 221–316. George Romanes. "Preliminary observations on the locomotor system of medusa," *Philosophical Transaction of the Royal Society of London* 166(1867): 269–313. G.O. Mackie "The First Description of Nerves in a Cnidarian: Louis Agassiz's account of 1850." *Hydrobiologia* 530/531 (2004): 27-32.

²⁶⁷ Ernst Haeckel. *Die Familie der Riesselquallen (Geryonida)* (Leipzig:Engelmann 1865). For a list of publications proceeding Romanes' dealing with the nervous structure of jellyfish, see Romanes, *Jellyfish* (1885) 13-23.

²⁶⁸ George J. Romanes. "Preliminary observations on the locomotor system of medusa," 269–313; Thomas Eimer, *Zoologische Untersuchungen Mit Besonderer Berücksichtigung Der Biologie ... Separat-Abdruck Aus Den Verhandlungen Der Phys.-med.-Gesellschaft N.F.*(1874).

²⁶⁹ Romanes, *Jellyfish*, 13.

scale” with nervous systems and it was important “to ascertain whether or not the first occurrence of this tissue was to be met with in this class.”²⁷⁰ If, in fact, medusae contained muscle and nervous tissue, they might be utilized to study the evolution and function of higher systems.

Romanes’ experiments on nerve conduction rates had far reaching consequences for the use of jellyfish in physiological experiments. He utilized *Aurelia* to test the nerve conduction in excised sections of the jellyfish umbrella. Romanes excised the manubrium (the ‘handle’ of the umbrella that hangs underneath the umbrella) and seven of the eight marginal bodies.²⁷¹ The eighth marginal body was the source of “rhythmical discharges to the muscular sheet of the bell, the result being, at each discharge, two contraction waves, which start at the same instant, one on each side of the ganglion, and which then course with equal rapidity in opposite directions, and so meet at the point of the disc which is opposite to the ganglion.”²⁷² Romanes used the phenomenon of a single discharge creating contraction waves in opposite directions to test the rate of nerve conduction in jellyfish.

Each subsequent experiment required successive excisions of the umbrella, forcing the current to travel through a maze-like muscular structure created by the investigator. In each subsequent mutilation, Romanes found that stimulation of the nervous tissue eventually traveled throughout the entire structure, as long as the

²⁷⁰ Ibid., 11.

²⁷¹ According to both Romanes and Agassiz, the marginal bodies were structures integral to the function of the nervous system; they were contained within a tissue sack in covered-eye and were bare or sometimes absent in naked-eye medusa. The marginal bodies were located on the edges of the umbrella. Romanes. *Jellyfish*, Chapter II “Fundamental Experiments”

²⁷² Ibid., 67.

remaining section was linked to a marginal body.²⁷³ This lead Romanes to state that “it proves that the distinguishing function of nerve, where it first appears upon the scene of life, admits of being performed vicariously to almost any extent by all parts of the same tissue-mass.”²⁷⁴ He likened the nerve network of jellyfish to a sheet of muslin, in which nerve structures meet but never coalesce, allowing stimulus to pass throughout the whole organism without following a prescribed path; the system resembled a piece of loosely woven cloth more than a network of connecting tunnels or streets by which a stimulus *must* pass.²⁷⁵

Romanes’ fundamental experiments effectively settled the question of whether jellyfishes possessed nerve and muscle tissue. His work stimulated investigations into the nature of this structure and its importance to the general movement and function of the organism. In addition, it catapulted the jellyfish into ongoing laboratory analysis of neurophysiology, including questions of nerve rate conduction, the link between the nervous system and musculature, and the effect of a wide range of variables on the function of these systems.²⁷⁶

²⁷³ Both researchers utilized the term “mutilation” to describe the course of experiments they performed with *medusae*. It was used to describe experiments that required extensive vivisection of physical structures. The term is continuously used throughout the period highlighted in this paper and mimics the language of my historical actors, not a normative belief in the morality of these experiments.

²⁷⁴ *Ibid.*, 77.

²⁷⁵ *Ibid.*, 79.

²⁷⁶ Richard D. French, "Some Concepts of Nerve Structure and Function in Great Britain, 1875-1885: Background to Sir Charles Sherrington and the Synapse Concept," *Medical History* 14 (1970): 154-165; Richard D. French, "Darwin and the Physiologists, or the medusa and modern cardiology," *Journal of the History of Biology* 3:2 (Autumn, 1970): 253-274.

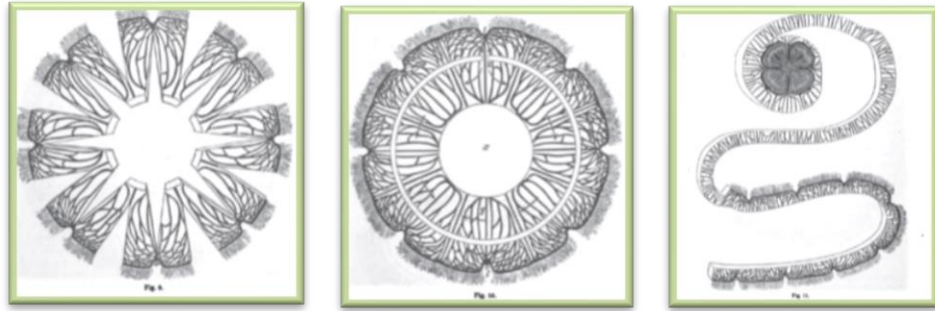


Figure 30 Three examples of umbrella excisions performed on jellyfish during mutilation experiments by George Romanes, *Jellyfish, Starfish, and Sea Urchins*, 67-70.

Jellyfish Use in Neurophysiological Experimentation

The acceptance of fundamental similarities in living organisms permeated physiological experimentation post 1900. Jellyfishes were commonly utilized in experiments on nerve function of higher organisms.²⁷⁷ George Howard Parker began his 1919 book *The Elementary Nervous System* by stating that

the dependence of human affairs upon the nervous system of man is so absolute that it was inevitable, as soon as this relation was understood, that the activities of the simpler animals should be interpreted as though these creatures were miniature human beings.²⁷⁸

In the work, Parker offered three organisms as examples of the elementary nervous structure: sponges, sea anemones and jellyfishes. He devoted 25 pages to sponges and another 25 to sea anemones, but 75 pages to jellyfishes. His review of the literature reinforced the Romanes/Eimer conception of the nerve-net and he reprinted many of Romanes' experiments. In addition, he highlighted the large amount of work done on nerve conduction rates in medusae.

Alfred Goldsborough Mayer performed the majority of experiments testing nerve conduction in jellyfishes at the Carnegie Institution of Washington's Dry Tortugas

²⁷⁷ Cheryl A. Logan, "Before There Were Standards: The Role of Test Animals in the Production of Empirical Generality in Physiology," *Journal of the History of Biology* 35:2 (Summer 2002): 329-363.

²⁷⁸ G.H. Parker. *The Elementary Nervous System* (Philadelphia and London: J.B. Lippincott Co., 1919), 7.

Laboratory. Initially known for his taxonomical work on medusae during his tenure as Alexander Agassiz's assistant, he became the leading experimentalist working with the organisms as the first director of the Tortugas Laboratory in 1903. His interest in the causation of rhythmical pulsation generated a robust research program in that location. Mayer attracted other experimentalists interested in the question of nerve conductivity and muscle response, including E. Newton Harvey. Both Mayer and Harvey replicated and expanded upon Romanes' work, changing water chemistry, depth of mutilations, and adjusting size and maturity of organisms to analyze the interactions between the nervous structure and muscle movement. A commonly cited outcome of these experiments comes from Harvey's research into new cuts: If the umbrella is mutilated so that there is no end point, nerve conduction of a single current will be sustained until the nervous/muscle matrix becomes too fatigued and the organism dies. Harvey's specimens survived for 11 continuous days of constant nerve conduction before expiring.²⁷⁹ These experiments created a baseline understanding of nerve conduction in jellyfish which other researchers quickly expanded upon.

Both Jacques Loeb and Alfred Goldsborough Mayer performed extensive experiments to ascertain the role of ion diffusion on the interactions between nerve and muscle. In 1900, Loeb published two papers on the influence of water ionization on rhythmical pulsations in jellyfish. The combination of experiments performed suggested to Loeb that while a pure NaCl solution was poisonous to marine creatures and killed them almost instantly, the addition of only a few more minerals facilitated normal pulsation, suggesting that "irritability depends upon the various ions, especially the

²⁷⁹ E. Newton Harvey. "The Question of Nerve Fatigue," *The Carnegie Institution Yearbook*, No. 10 (1912):130-131.

mineral ions (Na, Ca, K, and Mg) existing in definite proportions in the tissues.”²⁸⁰ Mayer utilized a kymograph²⁸¹ to record contractions that would indicate the “weak, exhausted, or pathological character of conducting tissue.”²⁸² He tested nerve conduction in untreated and distilled water and found that pulsation declined as conductivity declined, suggesting that nerve function depended on the electrical conductivity of the surrounding medium. Both Loeb and Mayer varied the mineral makeup of salt water in order to ascertain the effect on jellyfish pulsations. Much of Mayer’s work sought to produce abnormal pulsations in the jellyfish to ascertain the exact point when mineral imbalance caused musculature failure.²⁸³

Researchers acknowledged regeneration in lower invertebrates, but jellyfish contained the nerve/muscle net of somewhat higher organisms. The hypothesis that jellyfish could regenerate not just muscle tissue but the overlaid nerve network, spurred investigation. T.H. Morgan at the Marine Biological Laboratory (MBL) and Charles Stockard and Lewis Cary at Tortugas each published papers on the phenomenon. The majority of work on regeneration was done by G.T. Hargitt, who studied regeneration at Naples and the MBL. A major question in this research was the importance of the extent of injury to regeneration. Early theorists posited a positive correlation between size of injury and rate of regeneration; the larger the injury the faster the organism started

²⁸⁰ Jacques Loeb, “On the Different effects of ions on myogenic and neurogenic rhythmical contractions and upon embryonic and muscular tissue,” *American Journal of Physiology* 3:8 (March 1900): 383-396; Jacques Loeb, “On Ion-Proteid compounds and their role in the mechanics of life Phenomena-I. The Poisonous character of a pure NaCl solution,” *American Journal of Physiology* 3:7 (Feb. 1900): 327-338.

²⁸¹ A kymograph is a device that gives a graphical representation of spatial position over time. It consisted of revolving drum wrapped in paper; a stylus was attached to the phenomenon the researcher sought to capture. Mayer attached the stylus to a “disk” of a medusa and ran tests on the effects of various experimental variables on the muscular contractions.

²⁸² Alfred Goldsborough Mayer, “Nerve Conduction in *Cassiopea Xamachana*,” *Papers from the Tortugas Laboratory of the Carnegie Institution of Washington* Vol.6 (1917): 2-21.

²⁸³ Alfred Goldsborough Mayer, *Rhythmical Pulsation in Scyphomedusae* (Washington, D.C.: Carnegie Institution of Washington, 1906)

regenerating. Extensive experiments with jellyfish able to withstand multiple excisions over a long period of time found mixed results on this question.²⁸⁴

In addition to utilizing jellyfish to research basic neurophysiology, researchers extrapolated these results to more complex systems in vertebrates. Jacques Loeb considered jellyfish suitable for studying the function of the human heart because of the simple structure and the occurrence of rhythmical pulsations. According to Loeb,

the swimming bell of the Medusa may be divided into two regions, a marginal region containing the double nerve ring and its ganglia, and the central region which has no ganglia, but is said to possess scattered ganglion cells. The case is similar to that of the heart, which has ganglia in the auricles and sinus venosus, whose ventricle is however free from ganglia but contains scattered ganglion cells.²⁸⁵

Medical physiologists extrapolated both Loeb and Mayer's findings. Walter E. Garrey cited both in his work on fibrillary contractions in the human heart. S.J. Meltzer and J. Auer extrapolated jellyfish pulsation to the peristaltic movements of human intestines.²⁸⁶

In addition to the extrapolation to human organs, Alfred Goldsborough Mayer utilized jellyfish as a proxy for the human nervous system. During WWI, Mayer sought to contribute to the American war effort by shifting his experimental focus towards determining the root cause of shellshock. To ascertain if shellshock was primarily a condition related to the physical impairment of the nervous structure or a psychological

²⁸⁴ T.H. Morgan, "Regeneration in the Hydromedusae," 939-951; Charles R. Stockard "Studies on Tissue Growth: II. Functional Activity, Form Regulation, Level of the cut, and degree of injury in determining the rate of regeneration. The reaction of regenerating tissue on the body," *Journal of Experimental Zoology* 6:3 (May 1909): 433-469; G.T. Hargitt "Recent experiments on Regeneration," *Zoological Bulletin* 1:1 (Aug. 1897): 27-34; G.T. Hargitt "Notes on the Regeneration of *Gonionema*," *Biological Bulletin* 4:1 (Dec. 1902): 73-94. See also A.J. Goldfarb "Changes of Concentration of Sea Water and their influence on Regeneration," *Experimental Biology and Medicine* 10:3 (1913): 9-10.

²⁸⁵ Jacques Loeb. "On the different effects of ions," 383.

²⁸⁶ S.J. Meltzer and J. Auer "Peristaltic Rush," *American Journal of Physiology* 10:1 (Oct. 1907): 259-281; Walter E. Garrey. "The Nature of Fibrillary Contraction of the Heart- its relation to tissue mass and form," *American Journal of Physiology* 33:3 (March 1914): 397-414. Walter C. Alvarez *The Mechanics of the Digestive Tract* (New York: Paul B. Hoeber, 1922), 72.

condition specific to humans, he subjected jellyfish to repeated dynamite explosions and recorded those impacts on their behavior and ability to thrive. Because repeated exposures to blasts caused little long-term change in behavior or growth in his specimens (provided the jellyfish survived the initial explosion), Mayer concluded that shellshock was a psychological condition, but that it was “predominantly a psychic phenomenon, and being a hysteria it can be cured by hypnotic suggestion.”²⁸⁷

Because jellyfish were seen as the simplest form of muscle and nervous tissues, experiments on nerve regeneration and pulsation could be cited in articles on regeneration in higher vertebrates and even organ function in humans. The jellyfish exemplified a free floating human heart, intestines, and an advanced nervous system. But these *mundane fresh specimens* proved to be easier to catch than to work with; to perform the experiments highlighted above, investigators had to learn how to keep jellyfish alive in captivity. The rest of this chapter will examine this process.

Preservation Difficulties

The inability to keep specimens fresh impeded the earliest attempts to examine nerve structures but trying to preserve them for future studying was equally problematic. Salvatore Lo Bianco, the head collector at the Naples Zoological Station and one of the earliest experts on preparing and preserving marine specimens for shipping, dedicated a section of *The Methods Employed at the Naples Zoological Station for the Preservation of Marine Animals* to the attention required to preserve medusae.

²⁸⁷ Alfred Goldsborough Mayer, “On the Non-Existence of Shell Shock in Fish and Marine Invertebrates,” *Proceedings of the Academy of Natural Sciences* 3 (1917): 598.

The desired outcome when preserving a specimen was the retention of as many original characteristics of the organism as possible. Jellyfish contracted or partially dissolved during preservation. Bianco recommended narcotizing some specimens by either infusing their water with alcohol or tobacco. For other species, he suggested slowly boiling them and immediately transferring the specimens to cooled alcohol solutions. Regardless of the species, the method for preservation was involved, often extending over a period of several days. Pelagic (deep sea) specimens proved especially difficult to preserve; Bianco suggested that preservation of intact organisms (a rare occurrence after deep sea dredging) should begin immediately onboard ship.²⁸⁸

Closely following these methods of preservation still did not ensure natural looking specimens. No preservation technique allowed specimens to retain their natural coloring. Drawings and engravings made of medusae were almost always done from a living or extremely fresh specimen. Agassiz states in his 1850 work that while the copious engravings in his work may seem “rather superfluous,” illustrations from living *medusae* are required because

these animals are so perishable, that it will hardly ever be possible to preserve extensive series of them in our museums, or to procure of those capable of preservation a sufficient number to represent them in their different attitudes and under various circumstances, so as to fully illustrate all the details of their structure.²⁸⁹

In addition, even “successful” preservation could not retain all characteristics of the organism. Henry Bryant Bigelow stated that the preservation of jellyfish on board the *USBF Albatross* was “satisfactory both for gross anatomy and histology, its only

²⁸⁸ Salvatore Lo Bianco. *The Methods Employed at the Naples Zoological Station for the Preservation of Marine Animals*. Translated by Edmund Otis Hovey. (Washington, D.C.: Government Printing Office, 1899)

²⁸⁹ Agassiz, L. “Contributions” 222.

drawback being that otoliths are frequently dissolved.”²⁹⁰ By 1887, physiologists identified otoliths, structures located near the marginal bodies, as integral structures to the function of the nervous system. The inability to examine these delicate structures in a preserved specimen greatly reduced the utility of these specimens to physiologists interested in exploring questions surrounding the nervous structure.²⁹¹ Instead, investigators searched for ways to fashion laboratory tools and techniques to extend the delicate lifecycle of the organisms, and to find organisms hardy enough to thrive in laboratory conditions.

Exotic Live Specimens

One option for extending the experimental lifespan of medusae was to build a viable aquarium environment around the organism’s needs. Researchers noted the difficulties in maintaining jellyfish in aquaria, including questions about water quality, motion, and feeding habits. Early investigators interested in jellyfish succeeded in keeping individual specimens alive in captivity for varying periods, but these small successes did not translate into a systematic understanding of the process required to maintain them for extended periods. W.K. Brooks, interested in the development and lifecycle of the medusae, was able to rear several species of jellyfish in the aquaria at the Johns Hopkins Laboratory in Beaufort, North Carolina, but he failed to record his method for rearing and maintaining them, merely stating that he was able to rear some larvae and

²⁹⁰ Henry Bryant Bigelow XVI. *The Medusae: Reports on the Scientific Results of the expedition o the eastern tropical pacific, in the charge of Alexander Agassiz, by the US Fish Commission Steamer “Albatross” from Oct. 1904 to March 1905, Lieut. Commander L.M. Garrett, USN Commanding* (Cambridge, MA: Museum of Comparative Zoology, 1909),10.

²⁹¹ Louis Murbach, “The Static Function in *Gonionemus*” *American Journal of Physiology* 10:9 (Dec. 1, 1903): 202. Investigators did eventually figure out how to examine these structures in preserved specimens, but it required experimentation with preservation techniques. See L.J. Thomas “Morphology and Orientation of the Otocysts of *Gonionemus*” *Biological Bulletin* 40:6 (Jun. 1921): 287-296 + 298.

medusae in the home aquarium, although he struggled with several species.²⁹² In addition to Brooks, other investigators succeeded in rearing or maintaining some forms in captivity, but consistent methods were still required if physiologists wanted to perform extended experimentation. Figuring out the variables needed to create an aquarium that could sustain jellyfish life was a key problem for experimentalists.

Browne's Plunger Jar

Researchers seeking to maintain jellyfish alive for extended periods of time in captivity recorded similar phenomena. Adult forms collected and placed in the laboratory aquaria regained vigorous pulsations within a few minutes, but over the course of hours, days or weeks, the specimens slowly lost vitality, grew visibly ill or malformed, and eventually settled on the bottom of the tank to die. In 1902, Charles Hargitt called attention to a common phenomenon when working with captive jellyfish. According to Hargitt, larger specimens, used in regeneration experiments, failed to regenerate as quickly and were “more likely to deteriorate or utterly collapse.” Hargitt initially believed that these specimens had been weakened by the experimental mutilations performed, but after inspecting those on display in the attached public aquarium at the Naples Zoological Station, he suggested that the condition was linked to captivity and not experimentation. He described the condition as an

anomalous pathological phenomenon observed in large specimens both in the exhibition aquaria and in the small aquaria during the course of experimentation, namely, the appearance of whitish blotches, or patches of disintegrating tissues at various places on the exumbrella of the animal which sooner or later affected its health and general behavior.²⁹³

²⁹² W.K. Brooks, “List of Medusae at Beaufort, N.C., During the Summer of 1880-1881,” 137-148; W.K. Brooks, “Notes on the Medusae of Beaufort, N.C. Part II,” 467-478 in *Studies from the Biological Laboratory of the Johns Hopkins University* (Baltimore, MD: N. Murray, July 1883)

²⁹³ Charles Hargitt, “Regeneration of *Rhizostoma Pulmo*,” *Journal of Experimental Zoology* 1:1(May 1904): 75.

Hargitt was not the only investigator to report this problem. Jakob von Uexküll, the German biologist who theorized the *umwelt*, encountered these “whitish blotches” while working with jellyfish at Naples in 1900. Uexküll believed that the blotches produced a type of nervous stimulation, but Hargitt doubted this, suggesting that they were merely a symptom of pathology.²⁹⁴

In addition to Uexküll and Hargitt, Edward T. Browne, a researcher at the Marine Biological Association laboratory in Plymouth, England stated that he had limited success in maintaining jellyfish in captivity. According to Browne “when first placed into the aquarium it swims actively about” but quickly tired and settled onto the bottom of the tank; after several more attempts to swim, the jellyfish settled for the final time at the bottom of the tank and died. Hargitt and Uexküll merely mentioned their troubles as an experimental complication; Browne sought a technological fix.

In 1899, Edward T. Browne introduced his “plunger jar.” After the death of many jellyfish specimens in the laboratory, Browne concluded that the difference between the captive and natural environment was the tidal movement in the ocean that bore the jellyfish aloft on waves throughout their lifecycle.

When I have been watching medusae at the surface of the sea, I have noticed that they simply float along with the tide without often pulsating the umbrella. In my bell-jars the water was perfectly motionless, so that a medusa had to pulsate its umbrella in order to keep afloat, and as soon as the pulsations stopped it began to sink.²⁹⁵

Browne worked with objects found in the laboratory space, and consulted Edgar Johnson Allen, the director of the laboratory, to create an automatic system that mimicked marine

²⁹⁴ J.V. Uexküll, “Die Schwimmbewegungen von *Rhizostoma Pulmo*,” *Mittheilungen aus der Zoologischen Station zu Neapel Zugleich ein Repertorium für mittelmeerkunde*. F. Friedländer & Sohn: Berlin. (1901): 620-626.

²⁹⁵ Edward T. Browne, “On Keeping Medusae Alive,” 176.

motion. His “plunger jar” was a fairly simple apparatus consisting of a large ten-gallon bell jar, affixed with a glass plate raised and lowered by a simplistic pulley system to create a constant wave movement within the jar. Through the motion of filling and emptying, the bucket raised and lowered a wooden beam, creating a constant motion within the jar. Edgar Johnson Allen said in response to the successful creation of this automatic “plunger-jar” that he “was not a little pleased to have produced an efficient piece of apparatus from just ‘a treacle tin and a stick.’”²⁹⁶

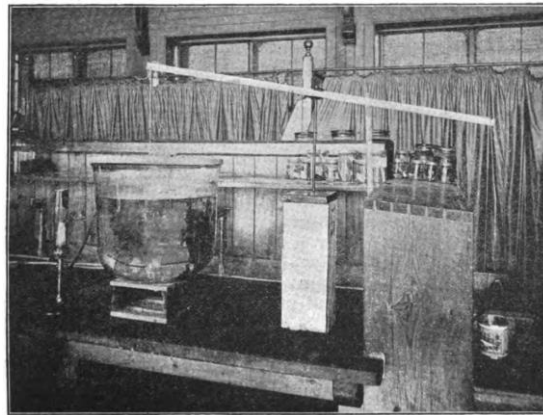


Figure 31 E.T. Browne's original plunger jar. You can see the repurposed treacle tin in this picture. E.T. Browne “On Keeping Medusae Alive,” 176.

Browne’s system proved extremely effective. Browne started the first plunger jar in the Plymouth laboratory on Sept. 4th, 1899. He reported that *Obelia* lived “very well” for about 10 days and then began to die off. This was a vast improvement; the species previously survived less than 24 hours in captivity. The plunger jar increased *Philalidium* survival time from 3 days to 6 weeks. In addition to boosting the time a specimen could survive in captivity, the plunger system allowed some species to thrive. Browne reported that many grew new tentacles. The jar’s water was not changed, but water was added when evaporation occurred and fresh copepods were added as a food source. He states

²⁹⁶ S. Kemp and A. V. Hill. "Edgar Johnson Allen. 1866-1942." Obituary Notices of Fellows of the Royal Society 4: 12 (1943): 361.

that “these experiments I think show that it is possible to keep medusae alive in confinement for several weeks without any change of water, and that they increase in size and develop more tentacles.”²⁹⁷

By combining observation and tinkering, Browne successfully simulated tidal movement into the laboratory. Some species lived longer than others, prompting Browne to wonder if a “slow revolving current” would be more suitable. He suggested adding a screw-propeller in the jar to achieve this effect. Continued observation of the needs of other organisms resulted in subsequent changes to the system. Researchers building upon his system suggested adding a filter so that that larva could be fed continuously but the water purity maintained. Eventually, experimentalists found that jellyfish required constantly circulating water, not only because of muscle exhaustion, but also because they produce copious amounts of mucous when they come into contact with other organisms, especially when they feed. The ‘Plunger Jar’ has gone through several updates to make it more efficient for the study of jellyfish and other marine invertebrates onboard research vessels.²⁹⁸ The plunger jar advanced the ability to maintain and rear medusa in the laboratory, but it was not a perfect device and others tried to pinpoint other variables that limited the captive lifespan of jellies.

²⁹⁷ Browne, “On Keeping Medusae Alive,” 179.

²⁹⁸ Ibid., 178.; F. G. Walton Smith “An Apparatus for Rearing Marine Organisms in the Laboratory,” *Nature* (Aug. 31, 1935): 345-346. See W. Greve. “The “Planktonkreisel” a New Device for Culturing Zooplankton,” *Marine Biology* 1:3 (1968): 201-203; W. Greve, “The Meteor “Planktonküvette”: A Device for the Maintenance of Macro Zooplankton Aboard Ships,” *Aquaculture* 6:1 (July 1975): 77-82; William W. Ward, “Aquarium Systems for the Maintenance of Ctenophors and Jellyfish and for the Hatching and Harvesting of Brine Shrimp (*Artemia Salina*) Larvae,” *Chesapeake Science* 15:2 (June 1974): 116-118; William Hamner, “Design Developments in the Planktonkreisel, a Plankton Aquarium for Ships at Sea,” *Journal of Plankton Research* 12:2 (1990): 397-402.

Jellyfish: The Slimers of the Sea

Many jellyfish species could survive without constantly moving water, but required a very specific diet; determining this diet was particularly difficult for investigators. Edward Browne's success with the plunger jar was achieved without concern for the specialized diet of the specimens. Two years after the publication of Browne's paper, Maude Delap, a naturalist and associate of Browne living on Valencia Island in County Kerry, Ireland, published the seminal work "Notes on the Rearing of *Chrysaora Isosceles* in an Aquarium" in *The Irish Naturalist*. Delap's paper, still cited as a source for information on keeping medusa in the lab, described her process of rearing a complete jellyfish lifecycle in her home aquarium.

In June 1899, Delap found a *Chrysaora isosceles* (compass jellyfish) on the shore of Valencia Harbor. She took it home and placed it in an aquarium for future study before preservation; when she looked in the aquarium the next day, she saw small swimming forms, which she believed to be the fertilized planulae. After two days, these forms had attached themselves to the side of the jar and tentacles began to develop, signaling the beginning of the polyp stage. Delap moved several planulae to jars and kept the polyps throughout the winter months. By April 1900, ephyrae budded from the polyps; by May they attained a mature form and developed their distinctive brown markings radiating from the center of their umbrellas (the reason for their common name). In June, the mature forms required larger vessels. By July, the jellyfish began to struggle and by August, they were so diminished in vigor Delap narcotized the specimens

for immediate preservation. She believed their deterioration was due to starvation, and the majority of her paper focused on the food provided throughout the lifecycle.²⁹⁹

Delap experimented with multiple food sources for each form. Her article assiduously recorded the food sources, including those sources that were rejected wholesale. During the polyp stage, she initially kept them supplied with copepods, “but the *Scyphistomae* [polyps], I found, preferred to feed upon small medusa, such as *Sarsia*, and little ctenophores-*Pleurobrachia*.”³⁰⁰ Keeping the growing ephyrae and full grown jellyfish supplied with food proved difficult in the later summer because of stormy weather and warm water conditions. As the supply of young medusae, especially *Sarsia*, declined, so did the health of the captive jellyfish. Their death from starvation prompted Delap to state definitively that “the chief trouble connected with rearing this medusae was to obtain a sufficient supply of food; its appetite was enormous.”³⁰¹ During the mature stage of the jelly, Delap reported that specimens were consuming two dozen medusae and ctenophores a day. The paper included a helpful list of what food was preferred, tolerated, or never consumed.

It had a great liking for small Anthomedusae and Leptomedusae, such as *Corymorpha*, *Margelis*, *Sarsia*, *Amphinema*, *Phialidium*, *Laodice*, *Euchilota*, &c.; also for the siphonophore *Agalmopsis*, and the ctenophores *Pleurobrachia* and *Bolina*. It had no objection to *Tonzoperis* and *Sagitta*. There were, however, two animals it would not touch, even after a few days' starvation-the anthomedusa *Tiara pileaa*, and the ctenophore *Beroe ovata*.³⁰²

Delap tried feeding the mature medusae fishes, but they only grasped the fish with their tentacles without consuming them. Her success did not stop at compass jellies. In the

²⁹⁹ Maude J. Delap “Notes on the Rearing of *Chrysoara Isosceles* in an Aquarium,” *The Irish Naturalist* 10:2 (Feb. 1901): 25-28; N.F. McMillan and W.J. Rees “Maude Jane Delap,” *The Irish Naturalists’ Journal* 12:9 (Jan. 1958): 221-222.

³⁰⁰ Delap “Notes” 25.

³⁰¹ *Ibid.*, 27.

³⁰² *Ibid.*, 27.

succeeding six years she published accounts of rearing *Aurelia*, *Pelagia perla* (mauve stinger jelly) and *Cyanea lamarcki* (bluefire jelly), providing detailed descriptions of food sources, life cycles, and water temperatures in each subsequent publication.³⁰³

Delap influenced other investigators interested in extending the life of captive jellyfish. Mary Lebour, a colleague of Browne at Plymouth, combined Delap's findings on food sources with Browne's plunger jar to ascertain if certain species actually did consume fishes. Lebour found that many jellyfish do eat fish, especially *Aurelia*, *Phialidium*, and *Obelia*. She found medusae in general to be "miscellaneous feeders" but that there is "generally some food more frequently taken than the rest," probably because of the abundance of the food sources in the natural environment.³⁰⁴ Like Delap, Lebour reported that medusae are voracious feeders. Because of the volume of food consumed, only one jelly was allowed to remain alive in each plunger jar. Lebour notes that one jellyfish consumed sixteen small fishes in the course of a half hour. Her work effectively combined the use of Browne's plunger jar to maintain captive jellies with Delap's focus on the importance of understanding the organism's diet in captive rearing. Lebour's specimens survived longer and were much healthier throughout their life cycle than Browne's initial specimens, suggesting that a combination of water movement and proper feeding could effectively rear and maintain certain species of jellyfish within the laboratory for extended periods.

³⁰³ Maude J. Delap. "Notes on the rearing, in an aquarium of *Cyanea lamarcki*, Peron et Lesueur," *Annual report of Fisheries, Ireland 1902-03. II* 1:2 (1905): 20-22; Maude J. Delap. "Notes on the rearing, in an aquarium, of *Aurelia aurita*, L. and *Pelagia perla* (Slabber)," *Report on the Sea and Inland Fisheries of Ireland for 1905, Part II. Scientific Investigations* (1907): 160-164 + 2 plates.

³⁰⁴ Marie V. Lebour, "The Food of Plankton Organisms. II," *Journal of the Marine Biological Association of the United Kingdom* 13 (1923): 75; See also Marie V. Lebour. "The Food of Plankton Organisms," *Journal of the Marine Biological Association of the United Kingdom* 12 (1922): 644-677; F. S. Russell. "Dr. Marie V. Lebour," *Journal of the Marine Biological Association of the United Kingdom* 52:03 (August 1972): 777-788.

Although investigators worked out the process of rearing and maintaining medusae in the laboratory, few if any sought to maintain specimens away from the shore. The need for specialized vessels and copious live food sources meant that investigators continued to utilize live specimens caught throughout the day at marine stations. Only one species, *Aurelia aurita*, was included in Frank E. Lutz et al's 1937 laboratory manual *Culture Methods for Invertebrate Animals*. The manual's main source of information on cultivation comes from Maude Delap's work between 1901 and 1907.³⁰⁵ But rearing organisms in the laboratory was not the only way to ensure long term survival and development in captivity. Other investigators sought jellyfish that seemed particularly suited to laboratory environments without onerous requirements of technological fixes and specialized food sources.

Hardy localized species

An alternative to developing new technologies or following a rigorous feeding schedule to sustain delicate medusae in the laboratory was to use species that proved more amenable to captivity. This section will highlight the two most commonly utilized medusae in experimental physiology investigations between 1895 and 1930:

Gonionemus murbachii (clinger jelly) and *Cassiopea xamachana* (upside down jelly).

Found in abundance in Woods Hole, MA and the Dry Tortugas (respectively), these species lived in an elastic natural environment that made them capable to survive in captivity without specialized technology or feeding schedules. Although they were

³⁰⁵ F. G. Gilchrist "Rearing the Scyphistoma of *Aurelia* in the Laboratory," edited by Frank E. Lutz, Paul L. Welch and Paul S. Galtsoff in *Culture Methods for Invertebrate Animals: A compendium prepared cooperatively by American zoologists under the direction of a committee from Section F of the American Association for the Advancement of Science* (New York: Dover Publications, 1937), 143.

hearty, they were not widely available, and demonstrate the link between location, organization, and scientific program in organismal choice.

***Gonionemus Murbachii* (hydrozoa)**

Gonionemus murbachii was first described by Louis Murbach at Woods Hole, Massachusetts during the summer of 1894. During that year, a number of small medusae were noticed in the inland structure known as the Eel Pond but it was not until the summer of 1895 that the mature jellyfish were so abundant that Louis Murbach stated that “over 200 were taken in one evening with a tow net.”³⁰⁶ Murbach initially described the specimen in 1895, identifying it as *Gonionemus vertens*, a species described by Alexander Agassiz in 1862 in the Gulf of Georgia in Washington State. In 1901, Alfred Goldsborough Mayer, working with Agassiz along the Atlantic Coast, identified the Woods Hole specimen as a separate species to *vertens*, renaming it *Gonionemus murbachii*. Regardless of name, the species quickly became popular with neurophysiologists. The first year the organism appeared in abundance near the MBL and the United States Fish Commission’s laboratory, Murbach remarked that “they were so much sought after as specimens that it is now difficult to find enough for completing the work.”³⁰⁷ The popularity of this medusa as an experimental organism was enhanced by several variables: availability, limited dietary requirements, and plasticity of captive habitat.

³⁰⁶ Louis Murbach. “Preliminary Notes on the Life History of *Gonionemus*,” *Journal of Morphology* 6:2 (1895): 494.

³⁰⁷ *Ibid.*

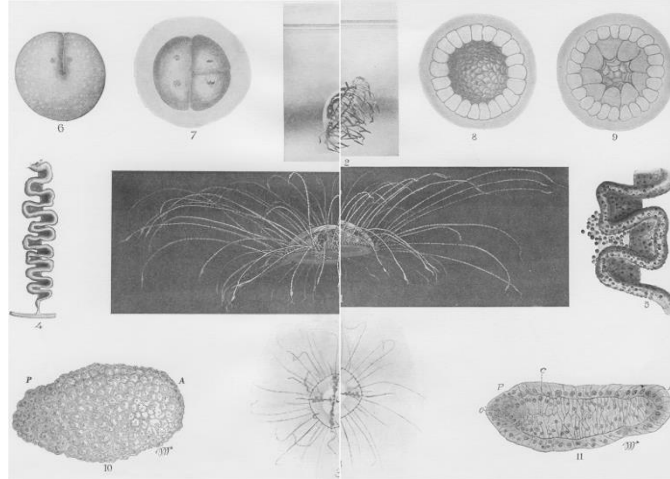


Figure 32 Perkins gave one of the robust descriptions of the Woods Hole *Gonionemus*, reviewing development from fertilization to adulthood. Henry Farnham Perkins "The Development of *Gonionema Murbachii*" *Proceedings of the Academy of Natural Sciences of Philadelphia* 54:3 (Sept.- Dec. 1902): Plate XXXI.

G. murbachii falls into Clarke's *mundane specimens* category. The species was locally abundant in the Eel Pond at Woods Hole, MA throughout the summer months.

Robert Yerkes described the simplicity of collecting viable live specimens:

Any disturbance in the water, such as stirring the grass with an oar or dip net, causes the animals to free themselves from the object to which they are attached, - either by the viscid bodies of the tentacles or by the lips of the manubrium, - and to swim to the surface. A convenient mode of capturing them is to disturb the water and then dip them up as they appear at the surface.³⁰⁸

Yerkes also noted that the jelly did not only migrate to the water's surface nocturnally; while many species required collecting at night, *g. murbachii* was equally available during the daylight hours. Though the adult specimen was abundantly available, planula and polyp forms were seldom collected from the Eel Pond, leading some investigators to speculate if perhaps these developmental stages took place in deeper waters out to

³⁰⁸ Robert Yerkes. "A Contribution to the Physiology of the Nervous System of the Medusae *Gonionemus Murbachii*. Part I. - The Sensory Reactions of *Gonionemus*," *American Journal of Physiology* 7:2 (1902): 436.

sea. Others believed that these stages were either too quickly cycled through, or the intermediate forms too minute, to be collected by dip netting.³⁰⁹

In addition to ease of collection, the species was relatively simple to maintain in captivity. Yerkes highlights the general diet of *G. murbachii*. The jellies consumed “small fishes, crustaceans, larvae of various kinds, and such dead organic material as comes within its reach.”³¹⁰ According to Yerkes, the Eel Pond received a large amount of “refuse” during the spring and summer, possibly explaining the large abundance of jellyfish in that location. The ability to survive on a wide range of food sources, and the initial habitat of a somewhat turbid water source with minimal water movement, allowed *Gonionemus* to adapt to its captive environment easily and made the species useful for neurophysiological experimentation.

Charles Hargitt initially rejected jellyfish for use in his regeneration experiments. “Owing to their peculiar delicacy and highly specialized character,” he dismissed their practicability as “doubtful.” But “the presence, however, of considerable numbers of *Gonionemus vertens*...the capacity of which to endure confinement in small aquaria was rather marked, revived the previous conception, and after reflection it was determined upon with some hesitation.”³¹¹ In his study, Hargitt kept his medusae in a small table aquarium and kept twenty individuals alive during successive regeneration experiments. Hargitt does not state if he fed his specimens; he merely notes water temperature as a cause of high mortality of his specimens.³¹²

³⁰⁹ Charles Hargitt “Notes on the Regeneration of *Gonionemus*,” 28.

³¹⁰ Yerkes “Contribution” 436.

³¹¹ Hargitt “Notes” 28.

³¹² *Ibid.*, 32-33.

Researchers published brief sketches of their experimental techniques for maintaining these jellies. Yerkes stated that he kept his experimental organisms in “shallow dishes” and “jars.”³¹³ Murbach retained his in an aquarium, although he did not specify if it was a small, table top aquarium with running water or a large jar (he used the terms aquarium and jar interchangeably in his publications).³¹⁴ T.H. Morgan, who was interested in testing Hargitt’s original assertions about the heartiness of *Gonionemus*, and especially their regenerative abilities, stated that he was able to keep his specimens alive, after the vivisection of the original medusae into four separate parts (each regenerated an incomplete but functioning medusae), for over two weeks in “excellent condition.”³¹⁵ Experimentalists listed jars, dishes, and tabletop aquaria as vessels in which the jellies thrived. The small size of *Gonionemus* allowed researchers to maintain large amounts of organisms in small spaces and the natural habitat of the jelly--stagnant, turbid water with little tidal movement-- helped it to adapt readily to a variety of glassware in the laboratory.

Ease of collecting, feeding, and caring for *G. murbachii* made it a popular experimental organism. By 1909, Murbach stopped adding *murbachii* to his methods section in publications, stating that “there would seem to be no need of stating that the Woods Hole species is the one under consideration.”³¹⁶ Physiologists working at Woods Hole utilized *Gonionemus* for physiological experiments, even though there were at least

³¹³ Robert Yerkes. “Contribution,” 434-449; Robert Yerkes, “A Study of the Reaction and Reaction-time of the Medusa *Gonionema murbachii* to Photic Stimuli,” *Amer. Jour. Physiol.*, 9, (1903): 279-307; Robert Yerkes, “The Reaction- Time of *Gonionemus Murbachii* to electric and photic stimuli,” *The Biological Bulletin* 6:2 (Jan. 1904): 84-95; Robert Yerkes, “Concerning the Behavior of *Gonionemus*,” *Journal of Comparative Neurological Psychology* 16 (1906): 457-463.

³¹⁴ Louis Murbach, “Some Light Reactions of the Medusa *Gonionemus*” *Biological Bulletin* 17:5 (Oct. 1909): 354-368; Murbach, “The Static Function in *Gonionemus*,” 201-109; Louis Murbach, “On the light receptive function of the marginal papillae of *Gonionemus*.” *The Biological Bulletin* 14, no. 1 (1907): 1-8.

³¹⁵ Morgan. “Regeneration in the Hydromedusa,” 943.

³¹⁶ Murbach, “Some Light Reactions,” 354 (first footnote)

two other species commonly available. Both *Aurelia* and *Bougainvillea* could be maintained in a plunger jar after 1899 but they were rarely utilized in neurophysiological experimentation after the discovery of the clapper jelly in the area.³¹⁷ Because it required little upkeep in the laboratory and was easy to collect, *Gonionemus* became the organism of choice for neurophysiologists at Woods Hole.

***Cassiopea Xamachana* (scyphozoan)**

In 1892, W.K. Brooks reported the summer work of the Marine Zoological Laboratory of Johns Hopkins at Port Henderson, Jamaica to the president of the university. Brooks identified a new jellyfish species found near the station, which he named *Cassiopea xamachana* (referred to by locals as the Guinea Corn Blubber). The species, now known as the “upside down jelly,” was found sitting umbrella-side down in the semi-stagnant, brackish waters of mangrove swamps and lagoons. Brooks found that it not only survived, but also reproduced in the temporary aquaria of the new station. Unfortunately, any work planned on the upside down jelly of Jamaica eventually stalled after Johns Hopkins relocated their laboratory to another portion of the island due to a yellow fever epidemic. However, Alfred Goldsborough Mayer reported the presence of the same species in the large “moat” bordering the Carnegie Institution of Washington’s Tortugas Laboratory near the Florida Keys. Physiologists at the laboratory quickly took advantage of this hardy specimen for live experimentation.³¹⁸ Similar to *Gonionemus*, *Cassiopea xamachana* was easy to collect, had a simple diet, and could survive in a wide range of laboratory environments.

³¹⁷ For an overview of the jellyfish available during the season at Woods Hole, see Box F Folder 2 Merkel Jacob Collection. Marine Biological Laboratory Archives: Woods Hole, MA.

³¹⁸ W.K. Brooks “Johns Hopkins Marine Laboratory” *Science* 19: 465 (Jan. 1892): 10-11



FIG. 4. WHERE *Cassiopea* LIVES. Lagoon of Bahia Honda Cay, Florida Coral Reef.

Figure 33 The "moat" from shore. The photographed is captioned by Mayer as "where *Cassiopea* lives." Mayer, "The Cause of Pulsation," 486.

Collecting *Cassiopea* was an easy process. The species thrived in the shallow waters surrounding the main island of the Dry Tortugas. Unlike *Gonionemus*, individual upside down jellies were visible from the surface of the water. Cary states that "the medusae can be procured in great numbers from the moat at Fort Jefferson at Dry Tortugas, Florida, so that specimens of any desired size can be selected for experimentation."³¹⁹ Collectors need only choose their desired specimens, and then utilize a dip net to gently pick them out of the water for transport to the laboratory. Upside down jellies were so plentifully available and easily captured that Alfred Goldborough Mayer eventually skipped the process of transferring the organisms to the laboratory. During his experiments on shellshock, Mayer built lath cages in the moat to hold developing jellies. He recorded growth in these specimens, and eventually utilized them for his research on dynamite and nerve structure. *Cassiopea* were reliably available in all sizes in the moat, meaning that investigators had direct access to the organism and could collect with specificity.³²⁰

³¹⁹ Cary, "Regeneration," 3.

³²⁰ Had the Tortugas Laboratory not shut down after the death of Mayer, an "on-site colony" argument might be made for these jellyfish. Mayer was well on his way to studying the group *in situ*. Series 4 Box 9.

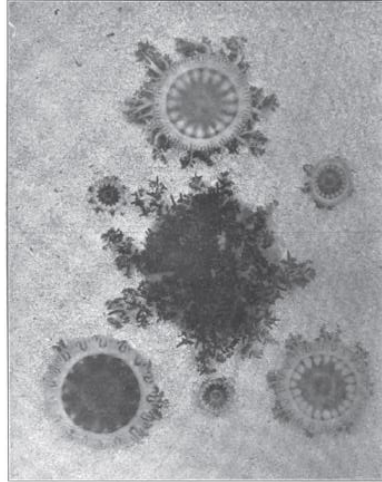


Figure 34 A photograph of *Cassiopea xamachana* umbrella side up (edges) and manubrium side up (center). These jellyfish are photographed in a tank with a sandy bottom and appear similar to the way they might look to the collector from the boat. Mayer “The Cause of Pulsation,” *The Popular Science Monthly* (Dec. 1908): 482.

In addition to ease in collecting, *Cassiopea*'s diet was well suited to captivity. When researchers took them into the laboratory, they discovered that the jellies could survive for long periods without any apparent food source. After working with the species for over 10 years, Mayer wrote a to-do list of experiments in his daily research notebook: “Starve *Cassiopea* in artificial seawater made from cistern water at Tortugas and compare the rate with filtered natural seawater. Also, try to feed *Cassiopea* and see what it actually does eat!”³²¹ It appears that most researchers took for granted that *Cassiopea* thrived without an apparent food source; it was not until much later that researchers found that the species hosts zooxanthelle in its subumbrella structure. The jelly exposes its subumbrella to the sunlight, allowing the zooxanthelle to photosynthesize, providing a constant food source for the jellyfish. Cary, Mayer, Stockard, and Hargitt mention weight loss in their experimental organisms but did not

Alfred Goldsborough Mayer Papers. Syracuse University: Syracuse, NY; Alfred Goldsborough Mayer “On the Non-Existence of Shell Shock,” 597-98.

³²¹ Series 4 Box 9. Alfred Goldsborough Mayer Papers. Syracuse University: Syracuse, NY.

have to deal with a loss of vitality or the byproducts of feeding such as excess of mucous or detritus in the laboratory aquarium.³²²

Similar to *Gonionemus*, *Cassiopea* thrived in a wide range of captive environments. The species' original habitat of stagnant water meant that constantly moving water was not required for maintenance. Cary and Stockard both found that *Cassiopea* did not require daily changes of water. Cary states that a

daily change of water was more than offset by the harmful effects of the agitation attendant upon the changing of the disks from one jar to another. Since my experiments necessitated the daily measuring of the regenerated tissue which could be done only by removing the disks from the jars and placing them upon a background of colored glass, the water was changed daily.³²³

In addition to not needing water changes, Mayer felt that *Cassiopea* was the best organism on which to study temperature and mineral interactions with nerve conduction. Unlike *Aurelia*, a jelly found throughout temperate and tropical oceans, *Cassiopea* had a smaller window of optimal temperature survivability. It only lived in water within a 15 degree range of the highest and lowest temperature the organism could survive. Mayer reported it was actually more sensitive to temperature, ceasing its motions and becoming completely paralyzed at around 9 degrees in either direction. The combination of an easily maintained organism with the ability to narrow the parameters at which nerve conduction functioned helped Mayer narrow the variables regarding temperature in his experiments.³²⁴ With no need to feed the organisms, no reason to change the water consistently, and the ability to narrow variables about temperature requirements,

³²² Alan E. Verde and L. R. McCloskey. "Production, Respiration, and Photophysiology of the mangrove jellyfish *Cassiopea xamachana* symbiotic with zooxanthellae: effect of jellyfish size and season." *Marine Ecology Progress Series* 168 (1998): 147-162.

³²³ Cary, "Regeneration," 4.

³²⁴ Alfred Goldsborough Mayer. "The effects of temperature upon tropical marine animals," *Papers from the Tortugas Laboratory* 6, no. 1 (1914): 1-24. Series 4 Box 9. Alfred Goldsborough Mayer Papers. Syracuse University: Syracuse, NY.

Cassiopea became a useful species for physiologists who braved the long journey to the Dry Tortugas.

In addition to their ability to survive in captivity, both *Gonionemus* and *Cassiopea* shared another important trait: They quickly recovered and regenerated vigorously throughout multiple mutilation experiments. Both clinger and upside down jellies could survive and thrive after multiple mutilation experiments. Loeb and Morgan both performed experiments on *Gonionemus* cut into four parts, Morgan keeping those mutilated sections for up to three weeks in captivity.³²⁵ Hargitt states that he knows of no other organism

which affords so good a type for this sort of observation and experimentation. It was not unusual to have specimens under direct observation in the ordinary aquaria of the laboratory rooms for from four to six weeks and without apparent deterioration, even in some cases under the severe tax of extensive mutilation made necessary by the experiments to which they were subjected.³²⁶

Cassiopea was equally capable of surviving extensive excisions. Mayer found that complete removal of the manubrium, sub umbrella, and part of the umbrella left a completely functioning “disk” of muscle and nerve tissue that could survive for months. Extensive experiments were performed on these free swimming “disks” and results were extrapolated to organ, and especially, heart function in higher vertebrates.³²⁷ In addition to skipping feedings and water changes, investigators could quite literally excise unneeded parts of the organism, effectively creating a free swimming, responsive disk of muscle and nerve tissue.

³²⁵ Morgan, “Regeneration,” 943.

³²⁶ Charles Hargitt “Regeneration of *Rhizostoma Pulmo*,” 74.

³²⁷ Mayer, *Scyphomedusae*, 25.

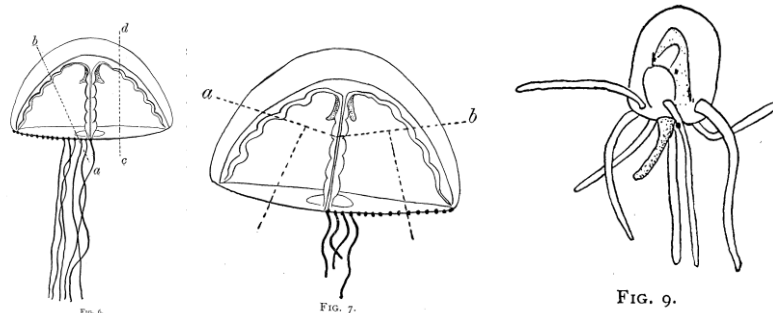


Figure 35 These three figures appear in T.H. Morgan's paper on regeneration in *Gonionemus*. The first two images show the cuts made by Morgan, and the third is a drawing of the "regenerated" organism from 1/4 of the original specimen. Its tentacles were malformed, but the organism continued to pulsate normally for almost 1 month. Morgan, "Regeneration," 944-945.

Major research programs grew up around these two organisms at their respective marine laboratories. Neurophysiological experimentation at Woods Hole revolved around *Gonionemus* and its regenerative abilities. The MBL table system meant that those interested in jellyfish had to apply for research space, but the Tortugas Laboratory worked by invitation. Mayer courted young physiologists interested in nerve research. Mayer made a yearly list of researchers to invite to the laboratory; he actively recruited physiologists Lewis Cary from Princeton in 1913 and C.R. Stockard from the Cornell Medical School in 1914, both of whom did substantial work on pulsation and regeneration with *Cassiopea*.³²⁸ He also sought to bring medusae experts such as E. T. Browne from Plymouth to work with *Cassiopea*. The MBL and the Carnegie Institution Tortugas Laboratory became centers of neurophysiological research centered around the jellyfish species available in those locations.

However, the inability to transfer these species from the seashore to the university laboratory limited their overall usefulness to physiologists during this period. By the end of WWII, jellyfish had almost disappeared as research organisms in neurophysiology.

³²⁸ Field Notebook (starting 1912) Series 4 Box 9 Alfred Goldsborough Mayer Papers. Syracuse University Library Manuscript Collections; Syracuse, NY.

Two factors lead to this decline: the uptake of the squid giant axon throughout the marine station network and the closure of the Tortugas station.

In the mid-1930s, experimentalists interested in nerve structure at the MBL turned to the newly discovered squid giant axon. Work on *Gonionemus* fell precipitously after Howard J. Curtis and Kenneth S. Cole started their research in Woods Hole. The maintenance of squid in the laboratory proved equally difficult to that of jellyfish, but the eventual success of laboratory methods for rearing squid and extracting usable axons lead to the uptake of the experimental system in neurophysiological experiments. Post WWII, other laboratories learned how to maintain and rear squid in the laboratory and the use of the squid giant axon spread throughout the marine station network, displacing jellyfish in neurophysiology experiments at the water's edge.³²⁹

Research with jellyfish also suffered from the loss of the Tortugas marine station and easy access to *Cassiopea*. In 1922, Alfred Goldsborough Mayer died at the Tortugas station from complications of tuberculosis. Mayer was the driving force behind the placement of the laboratory and especially of the neurophysiology research program that developed around *Cassiopea*. Each year, he sought out researchers interested in nerve studies to invite to the stations. Without Mayer, work on *Cassiopea* faltered and support for the station in the Carnegie Institution and the larger biological community waned. While the laboratory remained open throughout the 1930s for, it was closed in 1939.³³⁰

³²⁹ Little has been written on the uptake and spread of the squid giant axon as an experimental system. For information on the early use of axons at MIT see Chapter 4 of Nicholas Rasmussen *Picture Control: The Electron Microscope and the Transformation of Biology in America, 1940-1960* (Stanford: Stanford University Press, 1997). For information on the early experiments at Woods Hole and the subsequent Nobel-prize winning work done with squid axons at Plymouth, see Alan Hodgkin's autobiography *Chance and Design: Reminiscences of Science in Peace and War* (Cambridge: Press Syndicate of the University of Cambridge, 1992).

³³⁰ James D. Ebert, "Carnegie Institution of Washington and Marine Biology: Naples, Woods Hole, and Tortugas." *Biological Bulletin* (1985): 172-182.

After WWII, the majority of neurophysiological research at marine stations was being performed with squid giant axons and jellyfish had largely disappeared from the literature on nerve function.

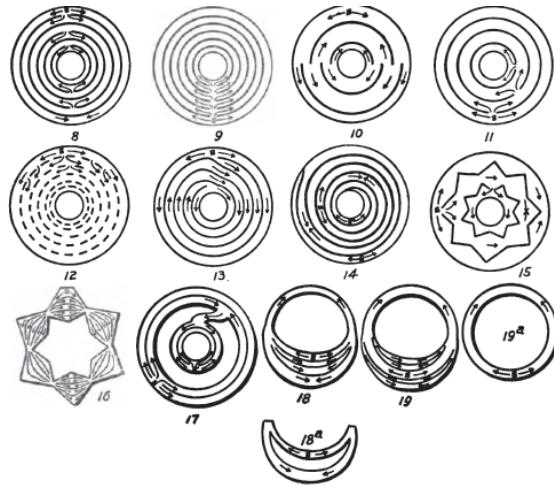


Figure 36 These are only some of the disks Mayer excised from the umbrellas of the *Cassiopea*. The arrows indicate the direction of nerve conduction through the tissue. Mayer, "Rhythmical Pulsation of the Scyphomedusae," 25.

Conclusion

Through the efforts of neurophysiologists at marine laboratories, several species of jellyfish became truly mundane organisms for experimental work in the early years of the twentieth century. Widely available species such as *Aurelia aurita* were maintained in captivity with proper feeding schedules and simple technological fixes to basic glassware. Highly localized species such as *Gonionemus vertens* and *Cassiopea xamachana* allowed scientists to create generalizable experimental tools out of these highly malleable organisms. For a quarter of a century, jellyfish were consistently utilized experimental organisms in neurophysiology research at marine stations.

Permanent marine stations, and the basic technologies contained therein, allowed researchers from multiple disciplines to adapt abundant local specimens for specific

research purposes. Scientists expressed an interest in the neurophysiology of jellyfish by the mid 19th century, but their position as a mundane fresh specimen belied their difficulty to maintain in captivity. The expansion of marine stations resulted in the adaptation of certain species to laboratory conditions and helped researchers transition these exotic live specimens into truly mundane materials.

Chapter 5

Illuminating Animal Behavior: The impact of malleable marine stations on tropism research

On October 20, 1930, a representative of General Electric's educational sales division sent a letter to Winterton C. Curtis at the Marine Biological Laboratory in Woods Hole, Massachusetts inquiring after two sunlamps sent to the laboratory several months before. "I have been asked by the Sunlamp Sales Division" wrote A.C. Stevens "whether or not these have yet been put into service. If so, we should like very much to know in what way they will be used and something of the results obtained or expected."³³¹ It is clear from the letter that Stevens has no understanding of the possible uses of a sun lamp at a marine station, stating merely that the lamps were sent on the recommendation of Dr. W.R. Whitney, the director of the research laboratory of General Electric. But, then, why would Whitney believe that a marine station required, or at least could find *some* use for, a set of sun lamps?

Marine stations, located at water's edge, might seem like a counterintuitive place to send artificial sunlight, but beginning in the late 19th century, the rise of tropism studies on aquatic invertebrates brought new lighting technologies and spaces into aquatic laboratory spaces. Identification of UV in sunlight, and the link between UV and medical properties (including disinfectant and overall health), made sunlamps and their artificial lighting precursors prominent in physiology laboratories.³³² But these instruments were also being utilized in animal behavior studies. Animal behavior

³³¹ A.C. Stevens to W.C. Curtis Oct. 20, 1930 "1930 No Order" Mekel Jacob Collection. Marine Biological Laboratory Archives: Woods Hole, MA.

³³² Philip E. Hockberger, "A History of Ultraviolet photobiology for humans, animals and microorganisms." *Photochemistry and Photobiology* 76:6 (2002): 561-579.

researchers brought gas burners, carbon arc-lamps, incandescent bulbs and Nernst glowers into marine laboratories in a bid to create a controlled research environment for the study of phototropism behavior (animal reaction to light stimuli). Tropism research combined available invertebrates, new lighting technologies, specially crafted glass enclosures, and specialized dark rooms to study tropism behavior in these spaces.

In Philip Pauly's 1987 biography of Jacques Loeb, he dedicates an entire chapter to the tropism debate in animal behavior between Loeb and Herbert Spencer Jennings. Loeb advanced research in the mechanistic reactions of animals to light and sought to establish a mathematical law to predict and therefore manipulate these tropisms. Jennings disagreed with Pauly's mechanistic and highly quantified thesis of tropic behaviors, and theorized that organisms followed a "trial and error" form of movement based on "fright" response in light reactions. According to Jennings, each individual reacted differently depending on their internal physiology at the moment of stimulus.³³³

As shorthand, the Loeb-Jennings debate nicely encompasses many of the ideological issues in phototropism studies during this period. Loeb and Jennings each give voice to opposing theories about phototropic behavior.³³⁴ While historians have focused on the ideological differences between the two- Loeb was uninterested in theoretical concepts such as the evolution of thought, behavior, or consciousness while Jennings sought to link his studies with those exploring these larger concepts- I believe a

³³³ Pauly, *Controlling Life*; Philip Pauly, "The Loeb-Jennings Debate and the science of animal behavior" *Journal of the history of behavioral sciences* 17:4 (Nov. 1981): 504-515; Arnold E. S. Gussin, "Jacques Loeb: The man and his tropism theory of animal conduct" *Journal of the History of Medicine and Allied Sciences* 18:4 (1963): 321-336. For information on Jennings' career, see Sharon Kingsland "A Man out of Place: Herbert Spencer Jennings at Johns Hopkins, 1906-1938" *American Zoologist* 27:3 (1987):807-817.

³³⁴ E.D. Congdon presents Loeb and Jennings as the leaders of opposing theories of phototropism: trial [and error] and phototaxia and places Jennings and Loeb as the head of these two groups. His paper provides a fantastic primer for those who wish to see the alignment of researchers under these two banners. E.D. Congdon, "Recent studies upon the locomotor responses of animals to white light." *Journal of Comparative Neurology and Psychology* 18:3 (June 1908): 309-328.

more fruitful approach to examining this debate, and its impact on the field of tropism studies in animal behavior , and animal behavior studies in general, is by identifying the changes in the experimental process enacted by these opposing theoretical beliefs. In conjunction with their theoretical differences, Loeb and Jennings focused on separate experimental variables and thereby developed different experimental methods.

Loeb and Jennings each concentrated on experimental variables that mirrored their theoretical convictions. Loeb favored a highly quantified approach, focusing on experimental variables such as light intensity and technological readings while paying little attention to individual specimen behavior and less attention to alternate forms of experimental organisms or species. Jennings published highly qualified work that examined individual test subjects' tropic reactions, paying close attention to physiological understandings of the organisms and their natural behavior patterns.

Although Pauly suggests that the “fitful and inconclusive” debate ended when Jennings prevailed and interest in invertebrate behavior waned, researchers retained interest in the subject of tropisms and examinations of phototropic behavior expanded into general animal behavior studies.³³⁵ Disciples of each man continued to test their respective mentors' theories and refine their experimental techniques.³³⁶ These methods, including advanced lighting technologies, advanced glassware, animal prep techniques, and the process of reporting findings, developed throughout the Loeb-Jennings debate and researchers integrated them into the study of tropisms.

³³⁵Pauly, *Controlling Life*, 119.

³³⁶In fact, Loeb published his largest work on tropisms *Forced Movements, Tropisms, and Animal Conduct* (Philadelphia and London: J.B. Lippincott and Co., 1918). At this time, he was still debating Jennings (even though Jennings had indeed moved on from animal behavior into genetics work). Loeb carried a major grudge against Jennings personally as well as professionally. Sharon Kingsland remarks on the relatively amazing fact that Jennings career was unscathed by his brush with Loeb. Kingsland, “A Man out of Place,” 807-8.

This paper will examine the impact of the Loeb-Jennings debate on laboratory-based experimental practice. First, I will look at the development of the tropism debate, tracing the roots of the debate and the movement of tropism studies from botanical to animal physiology laboratories. Next, I will look at the evolution of experimental practice throughout the Loeb-Jennings debate, concentrating on changes in organism choice, technologies, and spaces. Finally, I will analyze the impacts of these changes for tropism studies post-debate. Investigators interested in tropism studies after 1915 integrated experimental processes forwarded by both scientists into their research, establishing a method acceptable for proponents of both quantitative and qualitative studies of animal behavior.

It is not a coincidence that this debate took place at marine stations. The malleability of the spaces combined with the accessibility of a wide range of living organisms meant that two researchers examining the same behavior could potentially develop conflicting experimental designs working next to each other. The marine station design placed little constraint on experimental procedure, but instead facilitated multiple approaches to the same questions. This debate played out in marine stations precisely because the plastic environment allowed two researchers interested in the same questions to create a system that examined a wide range of variables.

The Origins of Tropism Research

S.O. Mast's 1911 book *Light and the Behavior of Lower Organisms* traces the history of tropism studies and explores the introduction of the term "tropism" into theories of animal behavior. Mast's historical tracing of the term begins with Augustin

Pyramus de Candolle. De Candolle recorded observations of plant movement (opening and closing of petals and leaves) based on the time of day. In 1835, he coined the term “heliotropism” to describe what he perceived as plant movement in reaction to lighting changes. In 1863, Wilhelm Hofmeister added to the theory by introducing the concept of *negative* and *positive* heliotropism to describe behavior of turning toward or away from a light source. Mast explains that Hofmeister’s addition meant “the term tropism then gradually came to signify not merely turning, but turning due to the direct effect of the stimulating agent on the tissue producing the movement, and this signification it has retained to some extent to the present time.”³³⁷ In the twenty years after Hofmeister, two experimental groups, Julius von Sachs in Germany and the Darwins in England, would advance and complicated theories of tropism, and set the stage for tropism studies in animals.³³⁸

Debates regarding the proper experimental process of studying tropism emerged between Julius von Sachs and the Darwins. In 1880, Charles and Francis Darwin published a co-written book *The Power of Movement in Plants*, an addition and experimental follow-up to Charles Darwin’s 1875 *The Movement and Habits of Climbing Plants*. *The Power* advanced several theories, including the concept that specific areas of a plant were sensitive to stimulus, the root tips were sensitive to gravity and coleoptile (the protective tip of emerging seedlings) were positively heliotropic.³³⁹ Francis Darwin greatly influenced *The Power* (the third son and seventh child of Emma and Charles).

Francis, who spoke German, spent time in Julius von Sach’s physiology laboratory in

³³⁷ Samuel Ottmar Mast. *Light and the Behavior of Lower Organisms* (New York: John Wiley & Sons: 1911), 11.

³³⁸ In the rest of this paper, I will be using the term “animals” as a form of differentiation from plants- not as a technical term.

³³⁹ Peter Ayers. *The Aliveness of Plants: The Darwins at the Dawn of Plant Science* (London: Pickering & Chatto, 2008), 109-110.

Germany before becoming his father's secretary and research companion. Von Sachs, an established botanist whose 1868 *Lehrbuch der Botanik* cemented his place as the preeminent plant physiologist in the world, pioneered methods in water culture as well as the role of starch in plant physiology. More importantly for this discussion, he studied the effects of light and temperature on germination, flower opening, and transpiration and invented laboratory apparatuses, the klinostat and the auxanometer, to study these phenomena.³⁴⁰

Although *The Power* contained up-to-date references to recent experimental work on tropic behavior and outlined the Darwins' experimental process, von Sachs found it lacking in experimental finesse and used his disagreement with the Darwin's experimental procedures to deny their conclusions. Von Sachs disagreed with the Darwin's conclusion that root tips sense gravity instead of the entire root. In addition, he denied the Darwin's conclusions that coleoptiles (seedling tips) sensed light, and that light intensity, in addition to directionality, played a role in plant curvature and movement.³⁴¹ The form of his objections is interesting considering that similar research on root tips and geotropism had been proposed by Thodor Ciesielski only ten years before. Von Sachs denied Ciesielski's theory of geotropism, but praised his experimental method. In contrast, von Sachs denied the Darwins' theory of geotropism and also called their experimental procedure into question. In reaction to the Darwins' root tip theory, von Sachs harshly stated

³⁴⁰ The klinostat (or clinostat) reduces the gravitational pull on developing plants. The auxanometer measures the rate of growth in plants. *Ibid.*, 101. Soraya de Chadarevian, "Laboratory science versus country-house experiments. The controversy between Julius Sachs and Charles Darwin," *British Journal of the History of Science* 29 (1996): 34-35.

³⁴¹ *Ibid.*, 111

In such experiments with roots not only is great precaution necessary, but also the experience of years and extensive knowledge of vegetable physiology, to avoid falling into errors, as did Charles Darwin and his son Francis, who, on the basis of experiments which were unskillfully made and improperly explained, came to the conclusion, as wonderful as it was sensational, that the growing point of the root, like the brain of an animal, dominated the various movements of the root.³⁴²

According to von Sachs, the Darwins' work was unreliable because it was performed, not in a laboratory, but in the Darwin family country home. The lack of experimental finesse, including a distinct lack of technology to perform intense quantifiable research, pushed von Sachs to deny, not only *The Power's* conclusions, but also the entire method of experimentation. In contrast to von Sachs' highly technologized work, the Darwins' access to advanced instrumentation was limited.³⁴³ Von Sachs' reputation in plant physiology meant that fellow experimentalists agreed with him and rejected the Darwins' conclusions. But, this debate was only the first of many revolving around the study of tropisms, and the next battle would be fought in marine laboratories over the behavior of aquatic organisms.

The expansion of tropism research from plants to animals came as a result of new mechanical and evolutionary understandings of life. Judy Johns Schloegel and Henning Schmidgen outline the importance of cell theory and the impact of Darwinism in establishing a ““general physiology” that sought to discern properties of life common to all living beings.”³⁴⁴ Instead of focusing on vertebrates such as frogs, rabbits, and dogs, investigators focused on the cell as the most elemental form of life. Protozoa became popular experimental organisms in psychophysiological laboratories, and were

³⁴² Julius von Sachs, *Vorlesungen uber Pflanzenphysiologie*, trans. by H.M. (Oxford: Ward Carendon Press, 1887), 689. Quoted in Ayers *Aliveness of Plants* (2008), 106.

³⁴³For a full examination of the argument between von Sachs and the Darwins, see Soraya de Chadarevian “Laboratory science versus country-house experiments,” 17-41.

³⁴⁴ Judy Johns Schloegel and Henning Schmidgen, “General Physiology, Experimental Psychology, and Evolutionism: Unicellular Organisms as Objects of Psychophysiological Research, 1877-1918” *Isis* 93:4 (Dec. 2000): 616.

particularly popular in tropism studies because of their obvious reactions to light, their ease in handling, and their accessibility. Jacques Loeb, after studying with von Sachs, took up the study of tropisms in protozoa, particularly algae. Both von Sachs and Loeb relied heavily on a mechanical understanding of organismal behavior, suggesting that homologous parts equaled homologous behaviors. Because both plants and animals were made up of cells, their orientation to light was similar to Loeb: phototropism in both groups was a reaction of light on the protoplasm of the cell.³⁴⁵

Herbert Spencer Jennings approached tropism studies with protozoa from a different angle. He studied in Jena with Max Verworn, a Haeckelian seeking to develop a physiology of both individual and species behavioral development (a theory of recapitulation for behavior). Verworn succeeded in interesting Jennings in behavior as a problem, and Jennings started research on protozoa to ascertain the evolution of behavior at its lowest level. The combination of the cell theory and the theory of evolution suggested to Jennings that studying lower organismal behavior would shed light on the evolution of behavior. Especially interesting to Jennings was his belief that, because of their quick life cycles and generally simple structure, the experimentalist would be able to view the evolution of animal behavior in succeeding generations of single celled organisms.³⁴⁶

The study of tropisms continuously linked plant and animal behavioral studies. In Charles Davenport's 1896 work on chemical and physical variables on protoplasm (including a hefty section on the effect of light on behavior), he states that his scientific interest is in the response of "living organisms" and "accordingly, no distinction should

³⁴⁵ Pauly, "The Loeb-Jennings Debate," 505-507.

³⁴⁶ *Ibid.*, 508.

be made between animals and plants.”³⁴⁷ E.B. Wilson compares hydroid reactions to those of green plants.³⁴⁸ Jacques Loeb continued to analyze plants and animal behavior together in his 1918 *Forced Movements* stating, “The writer was able to show that sessile animals behave toward light exactly as do sessile plants; and motile animals like motile plants” and S.O. Mast included several sections to testing previous theories of plant behavior in his 1911 work *Light and the Behavior of Organisms*.³⁴⁹ Other investigators took notes from plant physiologists: Elizabeth Towle (working with T.H. Morgan at Bryn Mawr) reproduced F. Oltmann’s 1892 experiment with *Volvox* (green algae) during her experiments with *Cypridopsis vidua obesa* and *Daphnia*.³⁵⁰

As behaviorists transferred concepts regarding heliotropism from plants to protozoa and lower metazoa, the terminology shifted and expanded. Investigators commonly applied the term *phototaxis* when speaking about animals that both orient towards light and move towards that light. *Phototropic* referred to those organisms that orient towards light but do not move towards that source and *photopathic* referred to organisms that neither orient nor move toward light, but have some reaction to changes in light intensity.³⁵¹ However, the simple uses of positive and negative phototropism remained in use throughout the first half of the twentieth century. Arnold E.S. Gussin has stated that “the word [tropism] was originally reserved for plant movement; it should

³⁴⁷ Charles Davenport, *Experimental Morphology: Effect of Physical and Chemical Agents on Protoplasm* (New York and London: The Macmillan Company, 1897), iv.

³⁴⁸ E. B. Wilson, “The heliotropism of hydroids,” *The American Naturalist* 25:293 (May 1891): 417.

³⁴⁹ See also S.O. Mast, “Reactions to light in the larvae of the Ascidians, *Amaroucium constellatum* and *Amaroucium pellucidum* with special reference to photic orientation,” *Journal of Experimental Zoology* 34:2 (Oct. 1921): 182.

Jacques Loeb, *Forced Movements*, 15.

³⁵⁰ Elizabeth Towle, “A study of heliotropism in cypridopsis,” *American Journal of Physiology* 3:8 (March 1, 1900): 360. During these experiments, T.H. Morgan wrote to Charles Davenport for information for advice on a method to create “colored light.” Morgan to Davenport, March 6, 1898. Box 72 Folder 1 “1893-1905” Charles Benedict Davenport Papers. American Philosophical Society: Philadelphia, PA.

³⁵¹ Mast, *Light and the Behavior of Lower Organisms*, 153-166.

never have been applied to animal, even less to human, behavior,” but this analysis of the word usage is shortsighted.³⁵² Physiologists and behaviorists in a post Darwin, post-cell-theory scientific community applied tropism to animal behavior as they continuously redrew or, in some sense, erased the plant/animal boundary. But the arguments regarding the optimum experimental process for studying behavior between von Sachs and the Darwins would not disappear, but become entrenched during the Loeb-Jennings debate.

Organisms

Animal behaviorists utilized a wide range of organisms at the turn of the twentieth century. American-based behavioral studies most commonly used rats and pigeons during this period, but experimentalists often stepped outside of this diptych for examinations of specific behavioral questions.³⁵³ One such group of questions involved tropism studies. Tropism researchers commonly worked with single celled aquatic organisms, such as the planktonic crustacean *Euglena*. However, a large portion of the Loeb-Jennings debate revolved around the variety of species chosen and the condition of the individual organism at the time of experimentation. This section will highlight the portion of the Loeb-Jennings debate concerning organismal choice and use, the reason that aquatic organisms took a prominent place in these studies, and the changes made regarding experimentation with and reporting about organisms utilized.

Herbert Spencer Jennings and Jacques Loeb had differing views on the importance of the experimental organism in tropism studies. Loeb believed that tropist behavior could be quantitatively analyzed and predicted; the key to the quantitative

³⁵² Gussin, “Jacques Loeb,” 335.

³⁵³ Michael Petit “The problem of raccoon intelligence in behaviorist America” *British Journal for the History of Science* 43:3 (Sept. 2010): 391-421; Donald A. Dewsbury “A brief history of the study of animal behavior in North America” *Perspectives in Ethology* 8 (1989): 85-122.

approach was symmetry- radial symmetry in the case of plants and cnidaria and lateral symmetry in the case of higher organisms such as mammals. Loeb believed his emphasis on symmetry provided a key to understanding most tropic phenomena: that most organisms contained this symmetry meant that any conclusions Loeb drew from experimentation from a single group of organisms should hold true for others with matching symmetry.³⁵⁴ His research focused on data drawn from group reactions to light. He based his conclusions regarding the Bunsen-Roscoe Law from “the average of from 40 to 60 individual observations, each being the average of the path of many thousands of animals.”³⁵⁵ This focus on the aggregate allowed Loeb to draw sweeping conclusions from his data, and to statistically fit thousands of individual reactions into what he believed to be universal numbers attached to behavior. Though Loeb sought a universal theory of tropic behaviors, he did not see the need to greatly vary his experimental organisms. To test the Bunsen-Roscoe Law³⁵⁶ on organisms, Loeb and Northrop chose to work with barnacle larvae, an organism Loeb had previously worked with and found particularly reactive to light.³⁵⁷ Arnold Gussin states that Loeb had an “uncanny knack for choosing organisms that would “fit” his hypothesis.” Regardless of his “uncanny knack,” Loeb placed less emphasis on organismal choice, individual actions, and internal conditions than Herbert Spencer Jennings.

³⁵⁴ Loeb, *Forced Movements*, 15.

³⁵⁵ *Ibid.*, 543.

³⁵⁶ Loeb and Wateney described the Bunsen-Roscoe Law thus: “the time to required to bring about the heliotropic curvature of plants changes inversely with the intensity of illumination.” Jacques Loeb and Hardolph Wateney, “On the identity of heliotropism in animals and plants” *Proceedings of the National Academy of Science* (1915): 45.

³⁵⁷ Jacques Loeb and John H. Northrup, “Heliotropic animals as photometers on the basis of the validity of the Bunsen-Roscoe Law for tropic reactions.” *Proceedings of the National Academy of Sciences* 3:9 (Sept. 15, 1917): 541.

In direct opposition to Loeb, Herbert Spencer Jennings believed that the way to understand tropic behavior was to more thoroughly understand your experimental organisms. In the first pages of Jennings' work on the behavior of starfish, he states that

It is of the utmost importance, if we are to understand the behavior of organisms, that we think of them as dynamic — as processes, rather than as structures. The animal is something happening. In connection with these internal processes, we find that most organisms have a system of movements, of the body as a whole or of its external parts. This system of movements we call behavior. It is closely bound up with the internal processes; indeed, the two sets of activities are really one, and we shall be led far astray if we try to think of the behavior separately from the internal processes.³⁵⁸

In a more succinct definition of his stance on the next page, he asserts that “The general problem of physiology is: How are the bodily processes kept going? The general problem of behavior is: How are the bodily processes kept going by the aid of movements?”³⁵⁹

This focus on the internal condition of the organism influencing behavior led Jennings to report that behavior was variable based on the amount of time a specimen had lived in captivity, their feeding schedule, and sometimes, their natural disposition.³⁶⁰ Researchers needed to pay close attention to these variables when recording behaviors. In addition to calling for greater attention paid to the condition of experimental organisms, Jennings felt that an individual's behavior could tell the experimenter more about tropic reactions than could group aggregation. Where Loeb sought universal laws with aggregate data from large groups, Jennings focused on individual paramecium (*stentor*), positing a theory that light reactions were largely “trial and error” in organisms.³⁶¹ This focus on the individual reaction, as opposed to watching the reaction of thousands of minute organisms as a

³⁵⁸ Herbert Spencer Jennings, “Behavior of the Starfish, *Asterias Forreri* De Lorient,” *Contributions from the Laboratory of the Marine Biological Association of San Diego* 4:2 (Nov. 26, 1907): 56.

³⁵⁹ *Ibid.*, 57.

³⁶⁰ At one point, Jennings describes reactions of mild tempered versus exceedingly ill-tempered starfish. *Ibid.*, 70.

³⁶¹ Herbert Spencer Jennings, *The Behavior of Lower Organisms* (New York: Columbia University Press, 1907), 22; Mast, *Light and the Behavior*, 44.

single group, opened the door to a wider species for research, as well as more extensive experiments with individual specimens.

The choice of experimental organisms is made based on multiple variables, including the experimental model, accessibility of organisms, ease of working with a given species in the laboratory, and a scientific understanding of that organism (physiology, morphology, taxonomy and general behavior) before the work begins.³⁶²

Tropism experiments were performed on a wide range of animals including insects, protozoa, and lower (invertebrate) forms of metazoa.³⁶³ The largest group experimented upon were aquatic organisms, ranging from large numbers of protozoa to starfish, jellyfish, crabs and hydra.³⁶⁴ Researchers chose aquatic organisms for multiple reasons including the availability of large quantities of a single species, the availability of multiple categories of organisms in a given location, and the relatively easy handling of certain groups. Marine stations became the epicenters of tropism research, and work performed at these locations highlights a larger shift in experimental procedure in the behavioral sciences.

Investigators performing tropism work congregated at marine stations³⁶⁵ to work with protozoa or invertebrate metazoa. Protozoa and infusoria are prevalent in water

³⁶² Adele E. Clark and Joan H. Fujimura, *The Right Tools for the Job* (Princeton, N.J.: Princeton University Press, 1992); Robert Kohler, *Lords of the Fly: Drosophila Genetics and the Experimental Life* (Chicago: University of Chicago Press, 1994); See also Adele E. Clarke, "Embryology and the rise of American reproductive sciences, circa 1910-1940" in *The expansion of American biology* eds. Keith Benson et al (New Jersey: Rutgers University Press, 1991), 107-132.

³⁶³ Samuel J. Holmes, "The reactions of *Ranatra* to light," *Journal of Comparative Neurology and Psychology* 15.4 (1905): 305-349. George Howard Parker, "The phototropism of the mourning-cloak butterfly, *Vanessa antiopa* Linn." *The Mark Anniversary Volume* ed. G.H. Park (New York: Henry Holt and Company: 1903)453-470.

³⁶⁴ For a list of organisms utilized for tropism experimentation between 1900 and 1907, see Congdon, "Recent Studies," 318-321.

³⁶⁵ While this dissertation deals mainly with marine laboratories, the rise of lacustrine laboratories follows a similar trajectory to that of marine laboratories outlined in chapter 1. For a list of lacustrine laboratories in Europe at the turn of the 20th century, see Charles Atwood Kofoid *The Biological Stations of Europe*

environments; thousands of experimental organisms can be collected.³⁶⁶ They were generally easy to maintain in the laboratory due to their elastic diet and the plasticity of the environment in which they flourished. In the “material and apparatus” section of Mast’s work with the fresh water protozoa *stentor coeruleus*, he states that “the animals used in the following experiments were obtained by letting aquatic plants collected in a pond known to contain *Stentor*, decay in battery jars nearly filled with water.”³⁶⁷ In addition to the ease of collecting and maintaining protozoa, researchers also used “higher” organisms. Lower metazoa, including echinoderma, anthropoda, and cnidaria, were easily accessed in the littoral zone close to shore. Although many of these organisms proved more difficult to maintain in the laboratory (see Chapter 3), they still proved popular.

Researchers selected organisms for tropic experiments based on experimental goals. Jacques Loeb and experimentalists interested in studying aggregate movements of specimens often chose colony dwellers that could be analyzed as a unit. Loeb was particularly fond of both protozoa and hydroids. His work on the hydroid *Eudendrium* displays his typical process. In a paper seeking to establish the efficiency of different lights spectrums on curvature production in hydroids, Loeb and Hardolph Wasteneys exposed *Eudendrium* “with a number of newly regenerated polyps” in a glass container to

(Washington, D.C.: Government Printing Office, 1910). The most popular fresh water laboratories in the US between 1890 and 1930 were the USBF laboratories at Put in Bay, Ohio and Fairport, Iowa. University of Wisconsin, The University of Minnesota and The University of Michigan. See Michael J. Lannoo *The Iowa Lakeside Laboratory: A Century of Discovering the Nature of Nature* (Iowa City: University of Iowa Press: Iowa City, 2012); Ernst John Dornfeld, “The Allis Lake Laboratory, 1886-1893.” *The Marquette Medical Review* 21:3 (1956): 113-142.

³⁶⁶ Yerkes collected these organisms from rainwater ponds on Harvard’s campus, but the same holds true of collecting plankton and bacteria in marine and lake areas. Robert Mearns Yerkes, “Reactions of Entomostraca to stimulation by light. II. Reactions of *Daphnia* and *Cypris*.” *American Journal of Physiology* 4:8 (Dec. 1900)405-422.

³⁶⁷ Mast, “Light Reactions in Lower Organisms,” 360.

a light spectrum. Little beyond the newly regenerated form of the organisms is mentioned, although the authors highlight the difficulty of working with young hydroids due to their delicate forms.³⁶⁸ Three separate experiments were performed on the same group of hydroids by varying the color spectrum to which they were exposed. Wasteneys and Loeb concluded that the spectrum required for curvature production in *Eudendrium* is similar to those of *Avena Sativa* (wheat).

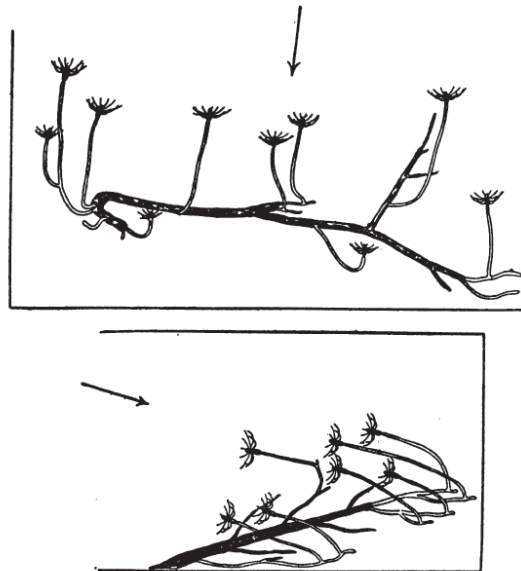


FIG. 26.—Polyps of *Eudendrium*, all growing toward source of light. The arrow indicates the direction of the rays of light, which in one case fall in from above, in the other from the left side.

Figure 37 Jacques Loeb illustrates his work with hydroids, an organism Loeb utilized for aggregate data about tropic responses. *Forced Movements*, 66.

While Loeb's experimental structure and particularly his choice of colonial organisms was taken up by other tropism researchers, including Charles Davenport. Others more sympathetic towards Jennings' theory chose very different organisms upon which to experiment.³⁶⁹

³⁶⁸ Loeb and Wasteneys, "On the identity of heliotropism in animals and plants," 45.

³⁶⁹ C.B. Davenport and W.B. Cannon, "On the Determination of the direction and rate of movement of organisms by light." *The Journal of Physiology* 21:1 (March, 1897): 22-32; C.B. Davenport and F. T. Lewis, "Phototaxis of *Daphnia*" *Science* 9:219 (Mar. 10, 1899):368.

Herbert Spencer Jennings' emphasis on the internal basis of behavior, and the importance of comparative studies and examining the movements of individual specimens, resulted in a varied set of organisms employed in tropism studies. In *Behavior of Lower Organisms*, Jennings dedicated over half of his work to protozoa, but unlike Loeb, concentrated on the movements of individuals as opposed to the group. Jennings uses the same species of protozoa as Loeb to analyze individual courses of movement. In his 1904 *Contributions to the Study of the Behavior of Lower Organisms*, Jennings states that, "The light reaction is thus somewhat inconstant, and varies among different individuals. It varies considerably with *Stentors* of different cultures; from some cultures almost all the individuals show it, while from others it is barely noticeable. This variability and inconstancy run through all manifestations of the light reaction in *Stentor*."³⁷⁰

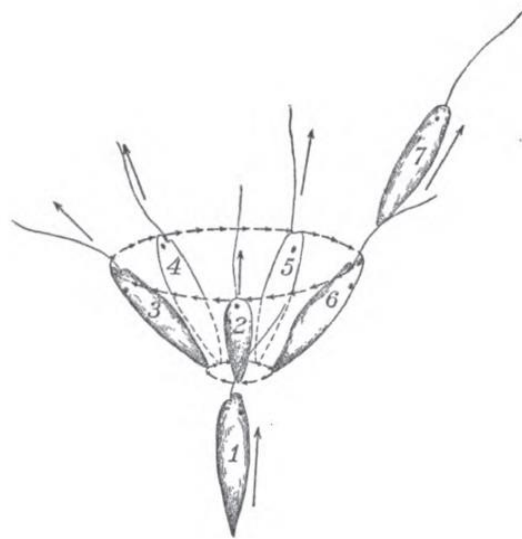


FIG. 21.*

Figure 38 The original caption reads: "Diagram to illustrate the reactions of *Euglena* when illumination is decreased." Most of Jennings' illustrations highlighted individual actions of organisms. *Contributions*, 53.

³⁷⁰ Herbert Spencer Jennings. *Contributions to the Study of the Behavior of Lower Organisms* (Washington, D.C.: Carnegie Institution of Washington, 1904), 32.

The second section of *Behavior* is dedicated to invertebrate metazoa. In this section, Jennings compared the behavior of hydra, jellyfish, sea cucumbers, and starfish. Tropism research was only one aspect of Jennings' work and it becomes clear that Jennings believed that the study of reactions to light was only part of a larger study of the general behavior of an organism. A researcher could not merely study light reactions without also understanding general behaviors in terms of reproduction, feeding, and fear responses. Jennings, and researchers interested in a wide comparative analysis of behavior, chose to research trophic behavior on a wide variety of organisms. Raymond Pearl and Leon J. Cole compared light reactions of a diverse group of lower organisms including crustaceans, leeches, nemertean, and snails in the same paper.³⁷¹ In one of the most diverse experiments performed, Victor Shelford compared light behaviors in a large group of organisms collected from the same niches (rapids and pool areas in Lake Michigan).³⁷² Others chose to only slightly vary their organismal use by choosing different subspecies. E.B. Wilson compared two subspecies of hydra: *h. Fusca* and *h. viridis*.³⁷³ S.O. Mast also chose to vary his subspecies, comparing light reactions in the larvae of the ascidians *Amaroucium Constellatum* and *Amaroucium Pellucidum*.³⁷⁴

One important variable for choosing tropism test organisms was the ability to closely follow their movements. The size and speed of organisms influenced investigators use of certain species. In S.J. Holmes' work on *Ranatra* (water stick-insects), he explained his choice of stick-insects by comparing difficulties found working with a

³⁷¹ Raymond Pearl and Leon J. Cole, "The Effect of very intense light on organisms" *Report of the Michigan Academy of Science* (1902):77-78.

³⁷² Victor E. Shelford, "An Experimental study of the behavior agreement among the animals of an animal community" *Biological Bulletin* 26 (1914): 294-315.

³⁷³ E.B. Wilson, "The Heliotropism of *hydra*" *The American Naturalist* 25:293 (May 1891): 413-433.

³⁷⁴ S.O. Mast, "Reactions to light in the larvae of the ascidians, *Amaroucium constellatum* and *Amaroucium pellucidum* with special reference to photic orientation" *Journal of Experimental Zoology* 34:2 (Oct. 1921): 148-187.

variety of other organisms. “Animals vary greatly as regards both the definiteness of their reactions to light and the ease with which their movements can be followed.” According to Holmes, copepods, cladocera, and ostrapoda react noticeably to light, but are difficult to follow individually while larger invertebrates are easier to follow but have sometimes indefinite reactions to lighting changes making it difficult to draw robust conclusions.³⁷⁵ Concerns about the difficulty of following individual ostrapoda were circumvented by Elizabeth Towle by choosing a subspecies that was both more sensitive to light and large enough to isolate and examine individual courses of movement.³⁷⁶ W.J. Crozier and Leslie B. Arey chose to work with *chiton* (a mollusk) because the “behavior of very slowly moving animals in an illuminated field” proved easy to follow and map for clearer results. The authors bemoan the inability to utilize multiple organisms at the same time because of their large size, but state that the ability to follow a slow moving organism over a superimposed grid drawn onto the aquarium far outweighed these concerns. E.B. Wilson also expressed his delight at working with a slow organism: hydras were easy to follow and record “on account of their slowness.”³⁷⁷

Experimentalists seeking to test previous findings regarding tropism behavior greatly expanded the organisms preferred for tropism research. S.J. Holmes tested body axis orientation conclusions in Loeb’s tropism theory by experimenting with fiddler crabs, which orients “sidewise.”³⁷⁸ W.J. Crozier, when testing Loeb and Wasteneys’ conclusions regarding the Bunsen-Roscoe theory, utilized available organisms while teaching at the Bermuda Biological Station for Research (Harvard and NYU’s marine

³⁷⁵ Holmes, “Renatra,” 305-306.

³⁷⁶ Towle, “Heliotropism in *Cypridopsis*,” 347.

³⁷⁷ W.J. Crozier and Leslie B. Arey, “On the significance of the reaction to shading in *Chiton*,” *American Journal of Physiology* 46:5 (Aug. 1918): 488; E.B. Wilson “The heliotropism of hydra” 413.

³⁷⁸ S.J. Holmes, “Phototaxis in fiddler crabs and its relation to theories of orientation” *Journal of Comparative Neurology and Psychology* 18:5 (Nov. 1908): 493-497.

station). He looked at light reactions in *Balanoglossus* (sea worms) and *Chiton* (marine molluscs).³⁷⁹ The number of organisms employed in tropism research continued to expand due to reactions to the Loeb-Jennings debate. Philip B. Hadley included a paper on heliotropic reactions in the American lobster larvae within his other larger work on the species' behavior.³⁸⁰ Louis Murbach's extensive research on the behavior of *Gonionemus* also included research on phototactic responses. Crozier's general research on nudibranch behavior included a section on phototropic responses.³⁸¹ The Loeb-Jennings debate did not merely influence the choice of organisms, but also influenced the variables researchers recorded regarding the handling and maintenance of the organisms in the laboratory.

Researchers testing the theory that behavior stemmed from internal conditions paid close attention to, and in turn reported in official papers, a multitude of variables, including age, time in captivity, and time of rest before experimentation that they theorized influenced the behavior of individual organisms. One of the most common variables to report was that of age. Both Loeb and Jennings came to the conclusion that the age of the organism mattered when studying phototropism. Young or newly hatched specimens commonly proved to be positively phototropic, whereas the mature form was negatively phototropic. Crozier and Arey found that young *chitons* are the opposite: the young are negatively phototropic. Analyzing the age difference in tropic responses

³⁷⁹ W. J. Crozier, "The Photic sensitivity of *Balanoglossus*," *Journal of Experimental Zoology* 24:2 (Nov. 1917): 211-217; Crozier and Arey, "On the significance of the reaction to shading in *Chiton*," 487-492.

³⁸⁰ Philip B. Hadley, "The behavior of the larval and adolescent stages of the American Lobster (*Homarus Americanus*)" *The Journal of Comparative Neurology and Psychology* 18:3 (June 1908): 199-301. This paper on phototaxis was the fourth and final paper on the behavior of the larval lobster. The first three were on rheotaxis, galvanotaxis, and the reaction of blind lobsters to light.

³⁸¹ Louis Murbach, "Some light reactions of the Medusa *Gonionemus*" *Biological Bulletin* 17:5 (Oct. 1909): 354-368.; W.J. Crozier and Leslie B. Arey "Sensory Reactions to *Chromodoris Zebra*" *Journal of Experimental Zoology* 29:2 (Oct. 1919): 261-310.

required researchers to include information about the collection and maintenance of these organisms in the laboratory. The experimentalists often utilized two specimens collected in separate locations to compare light reactions.³⁸² In addition, Jennings and other researchers made observations that certain organisms were only positively phototropic if they were underfed. If they had been fed sufficiently, they were continuously negatively phototropic, suggesting that light reactions might be tied to feeding reactions. Testing these hypotheses involved the recording of maintenance procedures in the laboratory. In Wilson's research on the tropic responses of hydra, he starved the organisms and then recorded their tropic responses. Wilson came to the conclusion that hydra become positively phototropic (or more so than "normally") to place themselves "in the position of maximum food supply." Wilson notes that the common food sources of the hydra are all positively tropic, therefore the organism may have evolved a response mechanism of positive tropism.³⁸³

Researchers also included handling details to explain the organisms' condition at the beginning of an experiment. Depending on organismal choice, researchers interested in the impact of internal conditions on behavior tweaked variables such as feeding, illumination, water temperature, and even the amount of organisms placed in the experimental system at a given moment. Experimentalists studying animal behavior often noticed a marked shift in behavior after animals "recovered from handling." Cora Reeves emphasizes the need to maintain "natural" and "normal" conditions for the fishes "otherwise response is often inhibited by unnatural conditions of by manipulations that induce fright." Proper maintenance involved water temperature, food, illumination until

³⁸² Crozier and Arey, "On the significance of the reaction to shading in *Chiton*," 489.

³⁸³ Wilson, "Heliotropism of Hydra," 417.

experimentation, and little handling.³⁸⁴ In addition, Crozier noted differences in light sensitivity between *balanoglossus* in “bad condition” from handling and those “in physiologically good condition.”³⁸⁵ Working with protozoa was often simpler, but experimentalists still recorded the amount of time that organisms were allowed to “rest” after being transferred from the general aquarium to the experimental apparatus. William Tower allowed his organisms 12 to 18 hours of rest after transfer from the main aquarium to the experimental aquarium. Wilson experimented on hydras that were maintained in the aquarium for two months before the experiment began. The time allotment for settling ranged from thirty minutes for protozoa to hours or days for organisms such as medusa and echinoderma.³⁸⁶

Close attention to organismal choice, and an emphasis on the condition of experimental subjects, was an important experimental process for researchers seeking to expand on the hypothesis commonly associated with Jennings that individual behavior was as, or more, important than group behavior. But Jennings’ emphasis on organismal variables does not mean that Loeb was not interested in controlling aspects of the experimental process. Loeb’s thesis, that phototropic reactions were universal and quantifiable, pushed him to make his experimental procedure as universally applicable as possible. His answer was a reliance on technology and the newest research coming out of photochemistry and photobiology.

³⁸⁴ Cora Daisy Reeves, “Discrimination of light of different wave-lengths by fish” *Behavior Monographs* 4:3 (1919): 3.

³⁸⁵ Crozier, “The photic sensitivity of *Balanoglossus*,” 242. C. F. Phipps performs certain experiments on newly collected specimens, but only utilizes those specimens kept in the laboratory for “some weeks” for research on the effect of different chemicals on light reception. C.F. Phipps, “An experimental study of the behavior of amphipods with respect to light intensity, direction of rays and metabolism” *Biological Bulletin* 28:4 (April 1915): 216.

³⁸⁶ Wilson, “Heliotropism of Hydra,” 424.; William Tower, “Loss of the ectoderm of *hydra viridis* in the light of a projection microscope” *The American Naturalist* 33:390 (June 1899): 505. C.F. Phipps “An experimental study of the behavior of amphipods” 211.

Technology

In a 1904 report submitted by Herbert Spencer Jennings to the Carnegie Institution following his stay at the Stazione Zoologique in Naples on a Carnegie Research Grant (No. 83), he outlined the future of his animal behavior research.

According to Jennings

This line of work does not primarily require extensive or novel apparatus, nor great laboratories. While new apparatus may be needed from time to time as the work develops, ordinary well-equipped laboratories, such as are found in the zoological and physiological departments of many of our universities, amply suffice for most of the work.³⁸⁷

Instead of technological requirements, Jennings highlights time requirements—animals must be watched extensively and this watching takes uninterrupted stretches of time.

Jennings' report makes animal behavior studies appear non-technologically bound but this is a shallow reading. Jennings states that little *new* technology was needed for animal behavior studies, but he does say that an “ordinary well-equipped laboratory” at a university would suffice.

Jacques Loeb frequently stated that he wanted to replace a heavily anthropomorphized method of animal behavior research with the objective and quantitative methods of the chemist and physicist. Loeb sought to do this by stringently controlling and reporting the exact stimuli to which his subjects reacted. In parallel to Jennings' arguments for a more diverse experimental specimen roster, Loeb advanced cutting edge artificial lighting technologies with experimental instrumentation to specify and quantify his experimental process and results. In his earliest experiments, Loeb

³⁸⁷ Herbert Spencer Jennings to Carnegie Institution of Washington, March 25, 1904, Carnegie Institution of Washington Folder, Herbert Spencer Jennings Papers *American Philosophical Society*: Philadelphia, PA.

employed a very simplistic experimental set-up: protozoa were placed in a beaker and exposed to sunlight through a window in the laboratory.

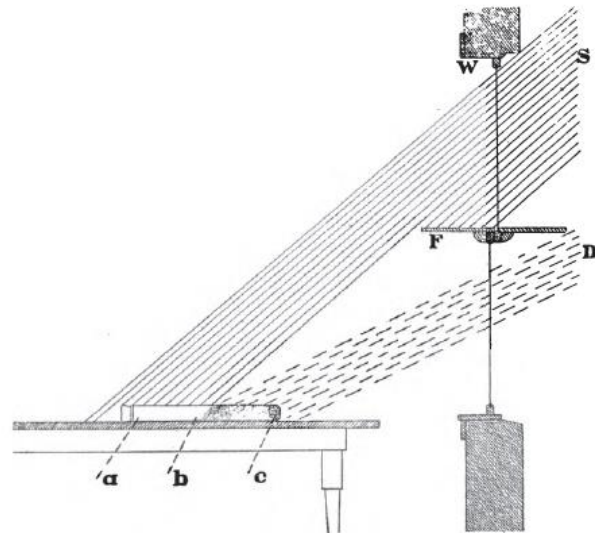


FIG. 10.—Showing that positively heliotropic animals will move from sunlight into shade if in so doing the illumination of the two eyes remains the same.

Figure 49 This relatively simplistic experimental set-up uses a beaker full of organisms and direct and shaded sunlight. Loeb, *Forced Movements*, 50.

Each successive experiment brought more technological interventions, including multiple lighting sources, enclosures built to test reactions to differing colors of light and to minimize reflection, and heat reduction solutions. The introduction of these technologies allowed researchers to quantify the stimuli in tropism experiments, but also raised questions about the quality and applicability of the data. This section will highlight the technology increasingly utilized by Loeb and other researchers interested in controlling the external stimuli in tropism studies. For simplicity, we will first examine specialty enclosures and move to lighting technology. It should become apparent that both specialty enclosures and lighting technologies were utilized in tandem to create a controlled experimental process.

Enclosures

In addition to the abundance of organisms, another draw for tropism researchers to work with aquatic species was the ability to view behavior three dimensionally. Behaviorists working with aquatic species could view the organism from a multitude of angles and easily introduce stimuli from multiple directions. Marine stations contained hundreds of glass containers that could be utilized for tropism experiments (see Chapter 1), but tropism researchers eventually settled on several prominent variations on the glass-sided aquarium for experimentation. A prominent technology, a slide or stage-aquarium, helped researchers interested in following the movements of protozoa under the microscope. In addition to this invention, researchers built or modified traditional aquariums with paint, colored glass, and fabric to control stimuli without continuously shifting organisms to new containers. These aquarium variations were created *de novo* with found materials in the laboratory setting. Often included in publications were the schematics or directions for creation of the apparatus so the result could properly be retested.

Researchers studying the impact of light stimuli on small aquatic protozoa often built an aquarium that fit onto the stage of their microscope: the stage or slide aquarium. In 1893, C.J. Cori first described a modification to the microscopic slide that would allow researchers to view minute organisms in a liquid solution. He called this modification a “stage aquarium.” The original design included a glass aquarium made from a strip of glass bent in a U formation to serve as the side and bottom of the structure. The object holder (5 x 10cm) formed the back wall and a small cover (30 x 40mm) formed the front. While easy to construct in the laboratory, this design allowed limited visibility and was

difficult to load. In 1894, he modified his invention to increase the visibility of the organism within the enclosure, and to allow the removal of the enclosure from the microscope stage.³⁸⁸

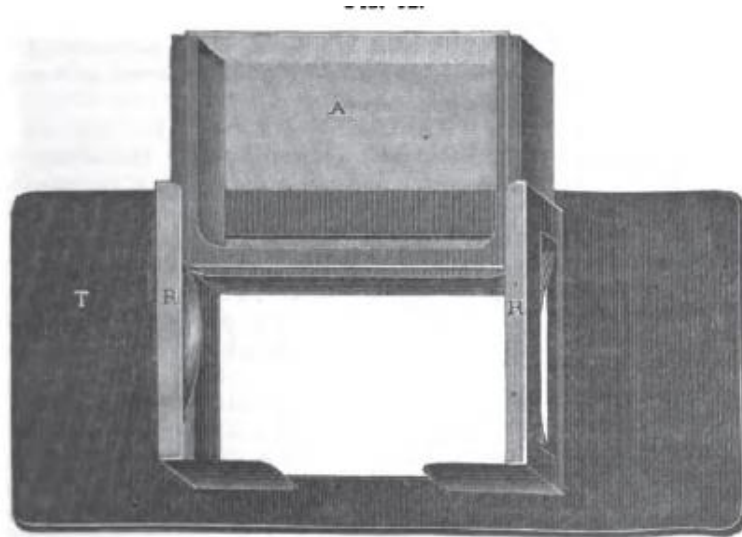


Figure 50 C.J. Cori's modified stage aquarium. The aquarium had a glass front and back and was removable from the stage. This apparatus would eventually become indispensable to tropism research. *Journal of the Microscopical Society*, 121.

William Tower first mentioned the stage aquarium in tropism studies in his treatise on *hydra viridis* (freshwater green hydra). Tower placed the hydra in a stage aquarium for 12 to 16 hours, and then “carefully placed [the aquarium] upon the stage of the projection microscope.”³⁸⁹ S.O. Mast recorded the use of a “slide aquarium,” so named because he made his out of microscope slides glued together with balsam boiled in linseed oil.³⁹⁰ He employed the slide aquarium when analyzing the movements of amoeba, but the set up would have worked for any organism that could fit in the relatively small enclosure.³⁹¹

³⁸⁸ C.J. Cori, *Journal of the Royal Microscopical Society* (London: Williams and Norgate, 1894), 121-122.

³⁸⁹ Tower, “Loss of Ectoderm,” 505.

³⁹⁰ Mast, *Light and the Behavior of Lower Organisms*, 93,104.

³⁹¹ Mast, *Light and the Behavior of Lower Organisms*, 152.

Pearl and Cole also placed their specimens in slide aquaria.³⁹² The combination of a stage aquarium and a projection microscope allowed researchers interested in the individual movements of specific specimens to use a wide variety of species, not merely those large enough to be tracked easily by the human eye.

Although early tropism studies were performed in a variety of glassware,³⁹³ most experimentalists employed similar apparatuses for their research. Tropism researchers were interested in reactions to both light and dark, and their experimental equipment required strict control over these variables. Experimental setups mandated an enclosure that permitted light to be systematically introduced to subjects and minimized unwanted light or shadow.³⁹⁴ The structure settled upon was rectangular in shape to reduce the possibility of light distortion, commonly in the form of a traditional aquarium (all glass) or a specially built tin trough. The experimental tin trough (the bottom and sides were tin and the ends were glass) was utilized in experiments that looked at movement toward or away from a light source. The inside of the trough was painted black and organisms received photo stimuli from only two directions. Robert Yerkes set up a tin trough for his study on *Daphnia* and Elizabeth Towle used a similar set-up for her work with *Cypridopsis*.

³⁹² The other alternative to using a stage aquarium was placing a small amount of water on the slide surrounded by Vaseline. Mast often used this method, but found that some organisms could get caught in the Vaseline and it would impede their movement. Mast, *Light and Behavior*, 329; Pearl and Cole, "The effect of intense light," 77.

³⁹³ The earliest mention of tropism studies, particularly those by Trembley, mention mason jars as experimental implements. Mast, *Light and the Behavior of Organisms*, 149, 237.

³⁹⁴ Mast highlights the counterintuitive results obtained in tropism studies with oddly shaped containers and highlights the impact of light refraction in these instances. The results are not counterintuitive, the light directionality is opposite of that originally believed.

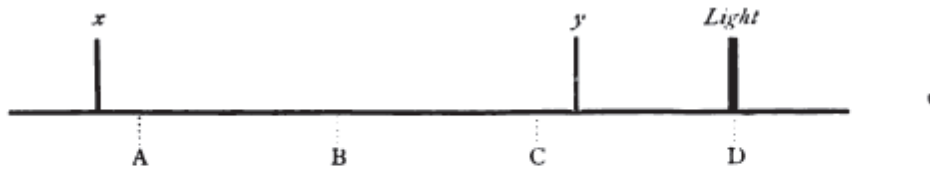


FIGURE 4. — x , y , ends of trough; A, point at which animal started; C, point at which trip was finished; distance A C = 50 cm.; distance A B and B C each 25 cm.; distance of light from starting point (A D) 75 cm.

Figure 41 Robert Yerkes included this diagram of his tin trough in his 1900. Many investigators imitated this experimental set-up. Yerkes, "Reaction of Entomostraca," 408.

Other researchers modified readily available glass aquaria. Davenport and Cannon built a glass enclosure painted "dead black" inside and out for their 1897 study.³⁹⁵ Jacques Loeb also fashioned a glass enclosure, but instead of painting the aquarium completely black, he surrounded it with black paper.³⁹⁶

The common modification of using black paper or fabric to reduce reflection allowed researchers to continually modify the aquarium throughout the study. This proved important when studying reaction to light directionality; light could be directed into the enclosure through a given set of openings, and then a new set could be cut into the paper. In addition, organismal reaction to specific colors of light was a major research agenda during this period. If researchers utilized an all-glass aquarium, they could easily replace the dark paper with a plate of colored glass. This ability to change multiple areas of the aquarium easily by removing paper is beautifully evidenced in Paul Bert's experiments with colored light reactions in multicellular organisms. Bert initially exposed subjects to a prism of light through a small vertical cut in the opaque screen. The subjects were exposed to different colors of light separately through the cut. Then, Bert

³⁹⁵ Davenport and Cannon, "On the Determination of the Direction," 25.

³⁹⁶ Loeb, *Forced Movements*, 107.

removed the opaque screen on one side of the aquarium, exposing the organisms to the whole spectrum at once.³⁹⁷ E.B. Wilson utilized the aquarium to test hydra light sensitivity. He covered one side with yellow, opaque, and blue glass and left the fourth area uncovered (white light); the top and other three sides of the aquarium were covered with black paper.³⁹⁸ The use of opaque screens with a traditional aquarium allowed experimenters to modify their enclosure easily, maintaining a consistent environment while changing lighting variables. The stage aquarium, tin trough, and modified aquarium were the most common apparatuses used in tropism research. These enclosures became the standard equipment for tropism studies. Simple but effective enclosures were important for controlling research conditions, but by far the most closely monitored, and most frequently shifting experimental technology was the light source utilized to produce experimental stimuli.

Lighting Technology

The use of artificial lighting technologies expanded rapidly in the first decade of the twentieth century. Researchers incorporated new lighting technologies that allowed them to vary light intensity, more tightly control lighting conditions, and to research any time of day (or night). A wide variety of artificial lighting caused many investigators to worry that light sources were not being reported correctly and that experiments could not be repeated with similar results. But new tools that measured UV spectrums, heat, and light intensity allowed experimentalists to quantify lighting for standardization and experimental replication. With the introduction of new lighting technologies, researchers were also forced to question the “natural” reactions of their subjects under experimental

³⁹⁷ Mast, *Light and the Behavior*, 336-337.

³⁹⁸ Wilson, “Heliotropism of Hydra,” 421-422.

conditions which they would not commonly encounter in their initial aquatic environments. Concerns about calibrating stimuli for experimental purposes and the “naturalness” of technologically became built into the experimental process.

Tropism researchers most commonly experimented with gas burners, carbon-arc lamps, and Nernst glowers. The gas burner, specifically the Welsbach burner, was one of the first artificial lighting technologies used in tropism studies. Baron Carl von Auer Welsbach invented the Welsbach burner in 1885 and slowly perfected the design to emit brighter, whiter light over the course of the next four years.³⁹⁹ The Franklin Institute praised Baron Welsbach and the Welsbach Light Company for “putting a thoroughly practicable mantle on the market.”⁴⁰⁰ Davenport and Cannon, Yerkes, and Towle all worked with Welsbach burners. Yerkes explained that different intensities of light could be obtained by either reducing the gas or moving the instrument (he chose to move the burner).⁴⁰¹ The Welsbach was a convenient light source, but it did not produce a high intensity light, nor was it particularly similar to sunlight. While the burner consistently produced light and was easily operated, by 1905 tropism researchers had decidedly turned away from them in favor of carbon- arc lamps and Nernst glowers.

The carbon arc-lamp was a popular choice for researchers investigating the effect of intense light on behavior. While the carbon arc-lamp was invented long before the Welsbach burner, it was not until 1890 that a more efficient and cost-effective design was produced in the United States. They produced light through the application of an electric arc between two carbon electrodes. Arc-lamps produced a large amount of UV light,

³⁹⁹ “The Welsbach Light” *Science* 12:312 (Dec. 21, 1900): 951-956.

⁴⁰⁰ *Ibid.*, 956.

⁴⁰¹ Davenport and Cannon, “On the determination of direction,” 25.; Towle, “A study of heliotropism in *cypridopsis*” 347.; Yerkes, “Reaction of *Entomostraca*,” 408.

especially useful for the study of spectrum differences in phototropism. Loeb and Wasteneys used them to test the effects of different spectrums on *Eudendrium*.⁴⁰² Pearl and Cole studied the effects of intense light on phototropic responses in a multitude of organisms with arc-lamps.⁴⁰³ But these lighting sources also had drawbacks- they were so bright that they could cause eye problems in people operating them, and extremely intense arc lamps could give users sun burns.⁴⁰⁴ In addition, they proved costly because of a short life span (8-16 hours). Another light source, the Nernst glower, had more power than the Welsbach burner and a longer lifespan than the arc lamp; it was to this lighting source that many researchers eventually turned.

Nernst glowers came upon the American research community later than burners and arc lamps; they were not introduced to the United States until 1898 and production stabilized in 1901. The light source worked similarly to an arc lamp or incandescent bulb, but it did not require a vacuum to produce light. Instead, electricity was conducted through a ceramic mixture of zirconium oxide heated to incandescence. The light produced was softer than the arc-lamp and was thought to be closer to natural sunlight. Loeb chose Nernst glowers for several experiments and S.O. Mast stated that of all artificial light sources, he found that “The Nernst single glower lamp was the... most satisfactory source of light for all experiments, both quantitative and qualitative, providing the intensity required was not great.”⁴⁰⁵ The ceramic glower was long lasting and provided softer light, but it had a downside: it required a separate heating filament to

⁴⁰² Loeb and Wasteneys, “On the identity of heliotropism,” 45.

⁴⁰³ Pearl and Cole, “The effect of intense light,” 77.

⁴⁰⁴ Hockberger “A History of Ultraviolet Photobiology,” 564.

⁴⁰⁵ Mast, *Light and the Behavior*, 362.

prepare the ceramic to conduct electricity on its own. Even with this downside, the Nernst glower became very popular in tropism studies.

Artificial lighting technologies did not immediately produce lighting conditions perfect for studying tropic behaviors; they often required additional technological fixes to focus and temper their rays. The most common of these technologies was a maze of mirrors meant to fix the point of the light toward a specific location.

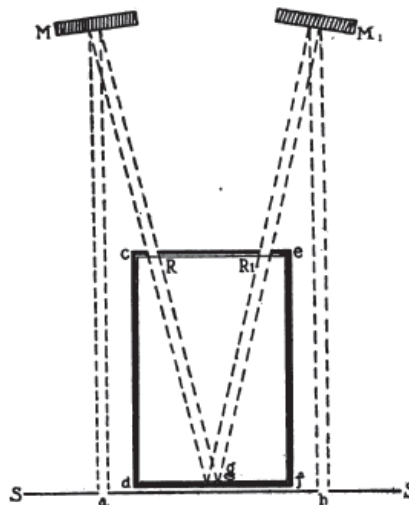


FIG. 34.—Method of determining the relative heliotropic efficiency of two different parts of the spectrum. (After Loeb and Wastenays.)

Figure 42 Jacques Loeb's diagram of his experimental aquarium. A and B represent the initial light, M represent mirrors and R and R1 represent the openings in black paper through which the light is directed. *Forced Movements*, 107.

In addition to mirrors, researchers tried to lessen the impact of the heat given off by artificial lights. When using artificial light (and especially the intense carbon-arc lamps), experimenters placed a thin aquarium filled with alum between the light source and the experimental enclosure to absorb electrical heat. In many experiments, researchers sought to ascertain behavioral differences to multiple light intensities, but attaining and maintaining consistently graded light intensities, both in a single experiment and through

the course of multiple studies, proved difficult. For this purpose, Robert Yerkes built his “light grader.”

Yerkes first described his light grader, built to provide researchers with “a band of light regularly graded,” in his 1902 work on light and heat reactions of *Daphnia pulex*. The grader was comprised of two light sources passed through alum aquariums, contained by black fabric, and reflected by mirrors, to produce a graded light band focused directly onto the experimental enclosure, usually located on a stage in a stage aquarium.

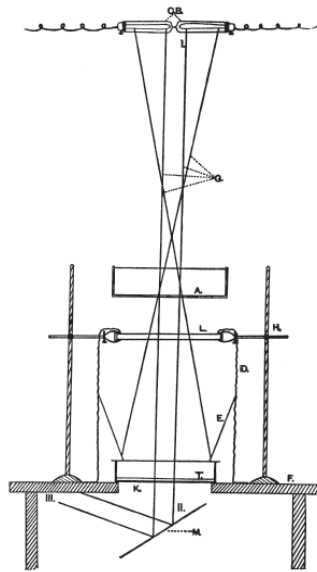


FIGURE A.—Apparatus for Giving a Band of Light Regularly Graded in Intensity.
C, B., two 16-candle-power electric lamps; *G*, rays of light; *I, II, III*, course of rays; *A*, a dish containing solution of alum 10 cm. deep; *H*, frame for lens; *L*, *B*, screens to cut off light from ends of glass box; *T*, *D*, cloth curtains to exclude light; *F*, table for apparatus; *K*, slit in table for passage of rays; *M*, mirror. Scale 1/2.

Figure 43 Yerkes’ original light grader. The two light sources are at the top of the diagram. You can see all of the implements utilized to alter artificial light, including mirrors (m), alum (a), and black cloth (d). *The Mark Anniversary Volume*, 363.

S.O. Mast utilized a light grader modified to suit the conditions of the experiments” in his experiment with plants in 1911.⁴⁰⁶ Victor Shelford and C.F. Phipps created self-built light

⁴⁰⁶ Ibid., 60

graders for their work, both pointing to Yerkes and Mast's designs as inspiration and blueprint.

Jacques Loeb's insistence on a heavily quantified study of behavior led to his uptake of artificial lighting technologies. Although Loeb performed his earliest and seemingly rudest experiments with direct and diffused sunlight, he quickly switched to technologically produced stimuli from multiple sources, including gas burners, carbon arc lamps, and Nernst glowers. Loeb led the way in quantifying light intensity in the experimental process. He did this by bringing in photometers to measure the intensity of his lighting sources, utilizing thermopiles to measure the heat given off by them, and spectrosopes to measure wavelengths and therefore the exact "color" of glass being utilized in preference experiments. In Mast's *Light and Lower Organisms* he highlights the importance of quantifying stimuli because "in experiments on the effect of colored light on organisms it is therefore essential to know what sort of light is being used as a stimulating agent; many results are unreliable because this was not known, or at least is not recorded."⁴⁰⁷

As Loeb and other researchers focused on external stimuli analysis increasingly relied on testing technologies to quantify stimuli, their results took a similar turn. Loeb's results pages became increasingly graph based. [Figure 7] Large tables outlined light intensity, water temperature, chemical makeup of the water, and duration of stimulus exposure. His results became increasingly numerical in nature; researchers seeking to replicate his work could duplicate the experimental variables via these tables. Regardless of the experimental organism, the exact experimental set-up could be reproduced with the quantified information in Loeb's results tables. While Jennings focused on the internal

⁴⁰⁷ Ibid., 313.

workings of individual specimens, Loeb's work reflected his reliance on aggregate data and quantifying external stimuli. Loeb's uptake of lighting technologies helped him realize his ultimate goal of quantifying the study of animal behavior.

Architecture

The use of natural sunlight in tropism research initially declined with the introduction of artificial lighting technologies. Researchers quantifying stimuli found it difficult to work with direct sunlight for more than a few hours a day. The shifting angles of the sun's rays, the inability to work on overcast days, and the possibility that other factors were creating uncontrollable variables made natural sunlight an unreliable light source. Davenport and Cannon criticized J. Oltmann's conclusions because he failed to properly record the angle of the sun. Davenport and Cannon claimed that Oltmann's findings were insufficient because, "so far as the data go, there might well have been, in this case, a movement in the direction of the sun's rays."⁴⁰⁸ After Loeb began experimenting with artificial light sources in the laboratory, he rarely used sunlight again in his research, instead choosing to work with quantifiable and universally reproducible light sources. But the introduction of artificial lighting in the laboratory did not make natural light obsolete. In fact, natural sunlight became a sort of control for testing animal behavior in the laboratory.

The use of artificial lighting technologies to study animal behavior caused some researchers to question the results as artificial and the behavior as merely laboratory based. In 1918, W.J. Crozier, Loeb's student and a researcher at the Bermuda Biological Station, enumerated arguments against Loeb's universal understanding of tropisms. Crozier states that one argument against Loeb was that his results were "laboratory

⁴⁰⁸ Davenport and Cannon, "On the determination of direction," 24.

product[s].” Crozier immediately counters this argument by stating it is “quite beside the point.”⁴⁰⁹ It is true that to Loeb, this criticism was “beside the point”; Loeb was interested in understanding and controlling the tropic responses of organisms, but he was not invested in the finding the deep seated causes of these reactions. But other researchers, including Crozier, might have taken this argument seriously. Although some might see Crozier’s “beside the point” comment as indicating his disinterest in pursuing questions of laboratory production of behavior, his process of testing Loeb’s findings suggests something different. Unlike other researchers that tested results by closely following the original experimental procedure, Crozier changed one thing about Loeb’s research: he tested them with direct and diffused sunlight.⁴¹⁰

After the introduction of artificial lighting technologies, researchers mostly used natural sunlight in tropism studies in a comparative capacity. Crozier was not the only researcher to turn to natural sunlight when testing tropic results. S.O. Mast often exposed organisms to multiple sources of light, including sunlight. In his research on the paramecium *stentor*, he worked with a gas burner, incandescent bulbs, a carbon arc lamp, sunlight (direct and diffused), and a Nernst glower.⁴¹¹ Elizabeth Towle compared reactions of organisms to light from a Welsbach burner and both diffused and direct sunlight. Crozier placed organisms in “diffused light from a north window” at the

⁴⁰⁹ Crozier and Arey, “On the Significance of the reaction,” 487.

⁴¹⁰ The exception is his use of natural light is his challenge of the Bunsen-Roscoe law while studying *holothurians* (sea cucumbers). The experiment requires two beams of varying intensities. For this experiment, Crozier utilized incandescent bulbs. W. J. Crozier, “The behavior of holothurians in balanced illumination” *American Journal of Physiology* 43:4 (July 1917): 512. In another experiment with holothurians, Crozier utilizes both sunlight and a tungsten bulb. He only utilized low-intensity bulbs with sea cucumbers because they are incredibly sensitive to illumination and quickly expire is overly exposed to light. W.J. Crozier, “The illumination of a *holothurian* by light” *American Journal of Physiology* 36:1 (Dec. 1914): 8-21.

⁴¹¹ Mast, “Light reactions in lower organisms,” 362. Mast utilized direct and diffused sunlight in many studies. See Mast, “Reactions of the light of larval *ascidians*,” 154; Mast, *Light and the Behavior of Organisms*, 150.

Bermuda Biological Station.⁴¹² Mast, Crozier, and Towle all included sunlight in their experiments without sacrificing quantitative methods; instead, they fit the use of natural sunlight into the growing technologized field with architectural and technological changes.

As tropism studies became consistently technologized, most researchers moved their studies to dark rooms. Researchers that sought to control and quantify external stimuli sought, not only to quantify their light sources, but to eliminate ambient light contamination during the experimental process. Some researchers placed one layer of black paper around their enclosures, and another layer of black fabric around the entire experimental system to block ambient light, but this process was time, energy, and material consuming with mixed results. The more popular option was the movement of tropism studies from the open lab rooms to dark rooms. Photographic darkrooms allowed researchers to diminish ambient light, while using mirrors and minimal black fabric scrimms to direct light stimuli. Crozier utilized dark rooms in his research with sea cucumbers, an organism with such intense light responses that he kept them in the dark - room to prevent ill effects from low level ambient light. Crozier exposed the cucumbers to light “by admitting sunlight, or light from a 40 c.p. tungsten filament, through a diaphragm into a blackened box containing the holothurians in a flat-sided glass aquarium.”⁴¹³ Researchers did not have to give up the use of sunlight if they moved into dark rooms. Many dark rooms were set up with heliostats to direct sunlight into the room. The heliostat could go unused until needed. If a researcher chose to work with sunlight in

⁴¹²Crozier and Arey, “On the significance of the reaction,” 489.

⁴¹³ Crozier, “The orientation of a *holothurian* by light” 10.

a comparative study, they could easily direct the light into the required area without losing effectiveness because of light saturation.

Marine stations expanded dark rooms in the first decades of the twentieth century. Photographic use of these rooms rose during these decades, as well as tropic and bioluminescent experimentation. Between 1917 and 1929, The Hopkins Marine Laboratory at Stanford University expanded to include six specialty darkrooms: a photographic darkroom, three for spectroscopy, one reserved for polarimetry and photometry, and one darkroom with a heliostat that drew its light directly from the roof of the building.⁴¹⁴ Most aquatic invertebrates exhibit *some* tropic behavior, either during the first moments of their life or as an evolved feeding response. The focus on these behaviors at marine stations meant a physical change to the laboratory structure: as behaviorists began to routinely test tropic responses and animal behavior became more established at these laboratories, more dark rooms were required.

The Loeb-Jennings Legacy

The Loeb-Jennings debate was as much about experimental procedure as theoretical beliefs regarding tropic animal behavior. Jacques Loeb and Herbert Spencer Jennings each approached the study of animal behavior with a particular theoretical agenda. Loeb ascribed to the mechanical understanding of animal behavior and scorned what he believed were anthropomorphized descriptions of tropism; Jennings approached it from an evolutionary belief in behavior, placing particular emphasis on an individual organism's adaptive mechanisms in a given situation, of which light exposure was only one of many at any given moment. Yet these two seemingly conflicting theoretical

⁴¹⁴ W.K. Fisher, "The Hopkins Marine Station of Stanford University" *The Scientific Monthly* Vol. 29 No. 4 (Oct. 1929): 301.

outlooks need not have created the enmity between Loeb and Jennings that was evinced as late as 1917 in Loeb's writings. In describing Jennings' view on "trial and error,"

Loeb states

Jennings has maintained that all reactions of unicellular organisms are due to "fright" or "avoiding reactions" and it seems as if at one time he even intended to deny the existence of tropisms and to maintain that all animals were influenced only by rapidly changing intensities of light. It is needless to discuss such an idea (which he probably no longer holds) in view of the contents of the preceding chapters. He seems, however, to cling to it as far as asymmetrical unicellular organisms are concerned.

Loeb's language in discussing Jennings' theories is that of dismissal. The use of the term "cling" in the final sentence portrays Jennings as childishly stubborn and highlights Loeb's annoyance at this continued argument. In a footnote, Loeb explains that the use of "fright reaction" by "an anthropomorphic biologist" is "a term that not only assumes the existence of sensations without any adequate proof, but removes the problem from the field of quantitative experimentation."⁴¹⁵ But Loeb does not disagree with Jennings only because of his "anthropomorphic" theories; instead, theoretical concerns were mirrored by different experimental procedures. It was this that fed the "debate" between Loeb and Jennings.

In Loeb's *Forced Movements*, he discredits Jennings' results based on flawed experimental process. Jennings' "trial and error" theory of animal behavior is accepted by Loeb in respect to *paramecium*, which Loeb admits have asymmetrical cilia and therefore may not fit his theory. But, Loeb states that when Jennings sought to expand this theory to *Euglena* he "goes too far." Loeb's tropism theory had been tested on *Euglena* and he sought to find the reason that Jennings' results disagree strongly with his own. He decried

⁴¹⁵ Loeb, *Forced Movements*, 96.

Jennings' lighting set up when testing phototropic reactions in *Euglena*.⁴¹⁶ Loeb denied Jennings and Mast's previous work on the relative efficiency of the spectrum on causing phototropic responses. He credited Mast with remedying their mistakes with a more effective experimental procedure and states that "Mast's results with this [new] method" coincide with Loeb and Wasterney's and therefore may be taken as support for the applicability of the Bunsen-Roscoe law to tropism behavior.⁴¹⁷

More interesting than his disagreement with Jennings' results is when he actually agrees with them. One might be tempted to think that Loeb's dismissal of Jennings as "anthropomorphic" would allow him to dismiss all of his scientific claims on principal, but this was not the case. Loeb occasionally found Jennings' research acceptable (although never in direct opposition to his own findings). In the case of chemical exposure changing phototropic responses, Loeb sides with Jennings' finding against Pfeffer after Lillie, saying pronounced that Jennings' process gave "incomparably more delicate results than Pfeffer's."⁴¹⁸ Loeb also utilized Jennings' findings on paramecium and geotropism.⁴¹⁹ So, what are we to make of the debate between Loeb and Jennings? How and why did Loeb so vehemently disagree with Jennings on some findings but not others?

The different experimental systems of Loeb and Jennings allowed Loeb to disagree with Jennings on the basis of experimental procedure. In her discussion of the von Sachs-Darwin debate, Soraya de Chadarevian states that, "arguments about the quality of experiments and the skill of experimenters are characteristic of scientific

⁴¹⁶ Ibid.

⁴¹⁷ Ibid., 97.

⁴¹⁸ Ibid., 149.

⁴¹⁹ Ibid., 155.

controversies.”⁴²⁰ In the case of the Loeb-Jennings debate, separate theoretical beliefs about animal behavior lead to differing emphases on experimental variables; these different experimental variables made it easy to attack each result and sustain a “debate.” Jennings concentrated on internal conditions of the experimental organism. When he bothered to record the external stimuli he utilized in his experiments, he referred to them as basic components, stating he used “incandescent bulbs” with no indications of candle power or type of bulb. Loeb increasingly quantified his external stimuli, highlighting different sources of light and intensities. He was less concerned with the internal conditions of his experimental subjects, rarely explaining where they were collected, their age, or their condition after collection. The differences in experimental procedure allowed Loeb to openly, and vehemently disagree with Jennings’ conclusions. Differing theoretical theories regarding tropism findings lasted long after Jennings left the field to take up the study of protozoan genetics, but the open debate between these two theoretical sides did not continue.

The next generation of tropism studies were performed by a group of researchers with similar theoretical convictions as their mentors, but who melded experimental procedures in a bid to form a more cohesive experimental process for the field. The two most prominent tropism researchers after Loeb and Jennings were W.J. Crozier and S.O. Mast. W.J. Crozier studied under Loeb and is credited as a “devoted follower” of Loeb. Historians have called attention to Crozier’s role in carrying Loeb’s mechanical understandings of psychological phenomenon to his most famous student, B.F.

⁴²⁰ De Chadarevian, “Laboratory Science versus Country House Experiments,” 30.

Skinner.⁴²¹ S.O. Mast was Jennings' student and his earliest tropism experiments were performed in tandem with Jennings. In Mast's 1911 work *Light and the Behavior of Lower Organisms*, Mast clearly uses Jennings research as a starting point for investigating tropic behavior, and challenges research that disagrees with those results. In most instances, Mast finds that his "observations confirm the conclusions of Jennings."⁴²² Both Mast and Crozier continued the tropism research of their mentors, but did not continue the debate named for them.

Unlike their mentors, Crozier and Mast utilized a similar experimental set-up that combined both quantitative and qualitative methods in the study of animal behavior. Mast recorded the internal conditions of his subjects, comparing multiple species and highlighting handling and maintenance conditions in his research. In addition to this, he adopted artificial lighting technologies and the technological additions required for highly quantifiable work. Crozier remained concerned with the quantifiable external stimuli his mentor considered important, but paid extensive attention to varying experimental specimens, reporting capture and maintenance information, and varying lighting sources. Both men found reasons to agree with their mentors' results, but they also sought to add nuance to their experiments and sometimes challenged the results of those researchers. Mast's later research challenged previous work performed with Jennings, and Crozier reported tropism reactions in sea cucumbers that added nuance to Loeb's most pet theory: the application of the Bunsen-Roscoe law of tropism responses.⁴²³ Interestingly, Loeb finds little fault with Mast and barely mentions Crozier in his 1917 *Forced Movements*.

⁴²¹ Timothy D. Hackenberg, "Jacques Loeb, B.F. Skinner and the Legacy of Prediction and Control," *The Behavior Analyst* 18:2 (1995): 225-236. See also Pauly *Controlling Life* Chapter 8 "The Loebian Influence in American Biology"

⁴²² Mast, *Light and the Behavior of Organisms*, 132.

⁴²³ W.J. Crozier, "The Behavior of *Holothurians* in balanced illumination" *American Journal of Physiology* 43:4 (July 1917): 510-513.

Loeb only questions Mast's previous work with Jennings, work that was decidedly less quantitative. Instead, Loeb was still attacking Jennings' earlier research but finding little fault with those continuing his research with new experimental tools.

The research methods utilized by Crozier and Mast, with attention to both internal conditions and external stimuli, were widespread by 1917. While it did not erase the theoretical differences in those studying tropism behaviors, it did minimize the type of easy dismissal of results inherent in the Loeb-Jennings debate. Tropism experiments, like the one set up by Cora Reeves to analyze wave length discrimination in fish in 1919, demonstrate the multiple experimental variables tropism researchers considered important following the Loeb-Jennings debate. Reeves outlined six requirements for the optimum experimental set-up for a study of light reactions: 1. An experimental aquarium that the fish could continuously live in so they would not have to be moved and risk mishandling or fear response 2. An experimental procedure that wouldn't arouse fear 3. Two large stimulus patches of mixed light intensity of "restricted and known wave-length." 4. Patches for offering stimuli 5. Constant conditions for the aqueous environment of the fishes and 6. An experimental procedure that could allow for equation of light to behavior.⁴²⁴ Reeves' final experimental system is a perfect example of the combination of the experimental concerns put forward by both Loeb and Jennings.

⁴²⁴ Reeves, "Discrimination of light of different wave-lengths by Fish" 4.

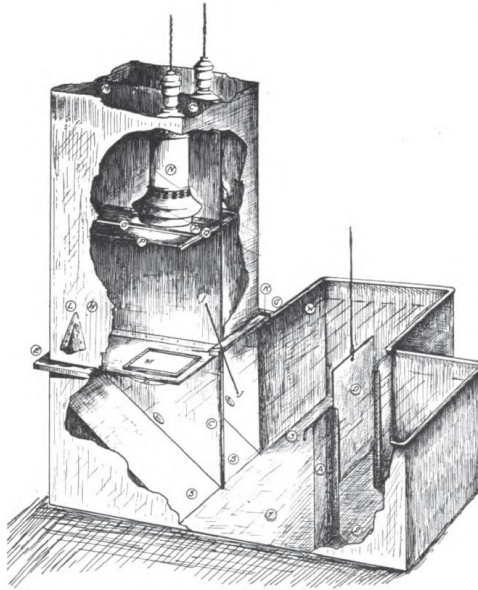


FIG. 2

Perspective View of Aquarium and lamphouse with part of each cut away, to show interior.

- Aquarium and food release.*
 1. Stimulus compartment: "r" recess for stimulus plate.
 2. Discrimination Compartment.
 3. Retention Compartment.
 A, movable partition between 1 and 2 (the partition between 1 and 3 not in place).
 C, fixed partition.
 D, sliding door in A.
 EG, parts of the frame which surround the base of the lamphouse.
 I, J, slender food-bar in position for feeding the fish.
 K, position of electro magnet by which the food-bar may be held in horizontal position.
- Light Apparatus.*
 L, H, lamphouse. Below L, H, hooded air-inlet.
 M, C, partition through lamphouse, an upward extension of C.
 N, Nernst lamp in one half of lamphouse, one in the other half partially shown.
 The glowers of these lamps are across the compartments and thus parallel with the long axes of the cylindrical lenses shown at SL. They are at the principal foci of these lenses:
 O, slit opening of variable width.
 P, sliding metal plates which form the slit.
 Q, frame which supports metal plates PP and in which they slide.
 RF, ray filter in its kit.
 SL, cylindrical lens.
 S, S, stimulus plates.
 W, indicates water level.

Figure 44 Cora Reeves' experimental aquarium combined concerns about internal conditions and external stimuli in one system. Reeves, "Discrimination of Light," 6.

Reeves was part of a larger generation of animal behavior researchers that combined Loeb and Jennings' concerns to create a basic experimental structure for tropism studies that took both internal conditions and external stimuli into account.

We can see a parallel between the von Sachs-Darwin and Loeb-Jennings debates. Variations in the experimental process fueled theoretical debates. But unlike the von Sachs-Darwin debate, which ended when laboratory work overcame that of country house experimentation in scientific credibility, the Loeb-Jennings debate did not end with a clear winner. Philip Pauly suggests that Jennings "won" the debate regarding tropism

research, but that interest in invertebrate behavior dropped off after 1915, and therefore it was an empty victory. Skinner, in turn, revitalized Loeb's mechanistic theories for behavior later in the century.⁴²⁵ Pauly's tracing of outcomes is technically correct, but fails to highlight the lasting effects of the debate on biology and work at marine stations. Reductionist studies of invertebrate animal behavior did decrease in the second quarter of the twentieth century, but this does not mean that the experimental process honed during the Loeb- Jennings debate was forgotten. While tropic reactions in invertebrates no longer stood at the center of a large debate regarding the nature of *all* animal behavior, all research on invertebrates did not cease. Detailing a newly identified organism's behavioral responses to light became routine. The post-cell theory, post-Darwin biology community that easily transferred tropism theory from plants to invertebrates did the same to vertebrates. Cora Reeves and Gertrude Marean White cited research on plants and protozoa in their studies on light reactions in fishes.⁴²⁶ Investigators continued to pay attention to phototropic reactions in aquatic organisms (both vertebrate and invertebrate), and the experimental systems developed during the Loeb-Jennings debate remained an integral part of phototropism studies.

Researchers at marine stations utilized multiple artificial lighting technologies by 1930, when the Marine Biological Laboratory received complimentary sun lamps from General Electric. Tropism researchers consistently brought new light technologies into the laboratory. The new sun lamp was merely the most recent in a long line of artificial lighting technologies investigators deemed useful for physiology and behavior studies. The experimental process that emerged from the Loeb-Jennings debate was both

⁴²⁵ Pauly, *Controlling Life*, 119.

⁴²⁶ Gertrude Marean White, "Association and Color Discrimination in Mudminnows and Sticklebacks" *Journal of Experimental Zoology* 27:4 (Feb. 1919): 443-498.

technologically dependent and equally technologically malleable. As long as an investigator utilized supplemental technology, such as photometers, black paper, mirrors, and light graders, and reported handling and maintenance procedures for experimental organisms, they could assure a scientific conversation regardless of theoretical leanings.

Marine stations were the optimal environment for the Loeb-Jennings debate to play out. Researchers were not confined by rigid architecture and organismal availability—the wide range of organisms and the malleability of the spaces allowed the debate to flourish. Unlike the original Von Sachs- Darwin debate, the argument did not center on the difference between modern laboratory versus home experimentation, but instead on experimental design. Loeb and Jennings worked in the same laboratory spaces, but developed significantly different procedures for testing trophic reactions.

Conclusion

On July 16, 1927 at 2pm, Charles Benedict Davenport and Thomas Hunt Morgan met at Penn Station in New York City to board a train. At 3:20pm they boarded the train that would take them down the Eastern seaboard to Key West, where they would board the *Anton Dorhn* to be ferried to Loggerhead Key in the Dry Tortugas. On the way, these two well-known figures in American biology shared meals, a sleeping car, and conversations. Davenport and Morgan spent 10 days collecting, observing, and researching at the Carnegie Institution of Washington's Tortugas marine station and returned to Key West on July 30th to make the long trip back to New York.⁴²⁷ In total, they spent nearly three weeks together and after the excursion, Davenport made plans to go to Woods Hole to do research and to stay with Morgan and his family for a night on the way.⁴²⁸

At the time, both Davenport and Morgan were well-established keystones of the American biological community and had a long history with marine stations. Charles Davenport studied with E.L. Mark at Harvard University and visited marine stations to do research throughout his graduate work (see Chapter 5). After he earned his doctorate, he established his own research station, The Cold Spring Harbor Laboratory in New York. Davenport's station is perhaps best-known during this period for its emphasis on eugenics, but it facilitated a wide-range of life science research.⁴²⁹ T.H. Morgan, who studied with W.K. Brooks at Johns Hopkins, also did research at marine stations

⁴²⁷ Charles B. Davenport to T.H. Morgan. July 5, 1927. Box 72. Folder 7 "1925-1927" Charles Davenport Papers American Philosophical Society: Philadelphia, PA.

⁴²⁸ T.H. Morgan to Charles B. Davenport. August 6, 1927. Box 72. Folder 7 "1925-1927" Charles Davenport Papers American Philosophical Society: Philadelphia, PA.

⁴²⁹ Jan Witkowski. *Illuminating Life: Selected Papers from the Cold Spring Harbor Laboratory, 1903-1969*. (Cold Spring Harbor New York: Cold Spring Harbor Press, 2000); E. Carleton MacDowell "Charles Benedict Davenport, 1866-1944" 17:1 (March, 1946): 2-50.

throughout his graduate and professional career (See Chapters 3, 4, and 5). In addition to working there himself, as a professor of biology, first at Bryn Mawr and then at Columbia, Morgan brought his students to study at these institutions as well (See Elizabeth Towle's work in Chapter 5).⁴³⁰ Both Davenport and Morgan weighed in during the debate about the placement of the Tortugas laboratory; Davenport wanted a laboratory that gave access to a fuller picture of the American Atlantic and organismal migration along the coast- Morgan wanted a station that facilitated teaching and the easy movement of both teachers and students.

Davenport and Morgan's visit to the Tortugas station highlights the strength and importance of the liquid laboratory network to both American and marine biology at the turn of the twentieth century. While there were certainly overlaps in their work, by 1927, Davenport and Morgan were interested in different areas of the life sciences. Davenport often provided Morgan with research materials from Cold Spring Harbor, but they were colleagues and not collaborators.⁴³¹ As stated above, they also believed that marine stations were important for different reasons. However, liquid laboratories functioned as nodes that brought together biologists from diverse areas of the life sciences. Traveling to the Tortugas allowed these colleagues to interact over a substantial period of time both in and out of the laboratory. The ability to perform individual experimentation and observation in a collective environment allowed researchers with dissimilar goals to interact and exchange information. These interactions strengthened the identity of American biology and centered that identity in these marine locations.

⁴³⁰ Garland E. Allen. *Thomas Hunt Morgan: The man and his science* (Princeton, NJ: Princeton University Press, 1978).

⁴³¹ Davenport apparently sent Morgan a box of crabs upon which to experiment. Morgan then requested 100 smaller crabs that would better serve his purposes. Morgan to Davenport, May 11, 1922. Box 72 Folder 6 "1921-1924" Charles Benedict Davenport Papers. American Philosophical Society: Philadelphia, PA.

The journey to the Tortugas station was an important episode in American biology, but it also represents a turning point in the history of marine stations. Alfred Goldsborough Mayer died in 1922, and by 1927 the Carnegie Institution was questioning the importance of maintaining the Tortugas station. The Institution provided funding for researchers interested in visiting any station in the United States or Europe, and they maintained the Cold Spring Harbor laboratory as well. Within the guiding hand of Mayer, and his vision of the station, it foundered. Carnegie asked major figures in American biology to visit the station and report on its importance to the biological community.⁴³² While no invitation or response survives from Morgan or Davenport, it is possible that this was the impetus for their trip.

By the late 20s and early 1930s, the marine station network was changing. These changes can be traced to two sources: WWI and the growth of biochemistry. During the First World War, all marine stations turned their attention to producing information that would support the American war effort. The American navy conscripted the boats from each station and researchers worked for the war effort on land. Alfred Goldsborough Mayer sought to contribute by finding the cause of shell shock;⁴³³ the Puget Sound Biological Laboratory in Washington began studying and harvesting sphagnum moss, which the Red Cross used for bandages throughout the war.⁴³⁴ The change to private and university stations during the war was marked, but there was a larger shift at fisheries stations that lasted long after the war concluded.

⁴³² Ebert, James. "Carnegie Institution of Washington and Marine Biology: Naples, Woods Hole, and Tortugas." *Biological Bulletin* 168 (June, 1985) 172-182.

⁴³³ Mayer, "On the non-existence of shell shock in fish and marine invertebrates." *Proceedings of the Academy of Natural Sciences* 3 (1917): 597-598.

⁴³⁴ Natalie N. Riegler. "Sphagnum moss in World War I: The Making of Surgical Dressings by Volunteers in Toronto, Canada, 1917-1918" *Canadian Bulletin of Medical History* 6 (1989): 27-43; J. W. Hotson, "Sphagnum From Bog to Bandage," *Puget Sound Biological Station Publication*, 2 (1919):211-247.

During the war, the government began to slowly shift the research at their marine stations from the general life sciences to a more distinct focus on experimenting on fish stocks and gathering statistical information on them. In 1917, Hugh Smith, the Commissioner of Fishes, stated in his yearly report that

In biological work the year has been marked by substantial readjustments. These have arisen partially from enlarged responsibilities and opportunities coming from an increase in personnel, partly from the fact that some of the investigations have progressed to a stage justifying or requiring a rearrangement of plans, and partly from the conditions of national exigency. On the whole, the changes and the new undertakings have the effect of concentrating the efforts of the Bureau upon problems of most immediate practical importance.⁴³⁵

Woods Hole began to focus on rearing and stocking lobster throughout the Northeast and Beaufort turned its attention more fully to farming black terrapin and understanding wood-boring marine worms in order to protect American ships from destruction. No longer did they send open invitations to universities and researchers, but instead started to train their own researchers in specific fisheries methods. In 1926, the Bureau of Fisheries announced that, “A review of the progress made in fishery investigations during recent years indicates that a distinct branch of scientific study that may be termed “fishery science” has been developed.” The Fish Commissioner described it as a hybrid science, combining zoology, geography, ichthyology, marine ecology, and oceanography with the methods of biometrics and vital statistics.⁴³⁶ The Bureau of Fisheries diverted much of its funding to this new scientific discipline and closed its laboratories to researchers not performing specific work on fisheries concerns, effectively breaking ties with much of the rest of the network.

⁴³⁵ Hugh Smith. *Report of the U.S. Commissioner of Fishes* (Washington, D.C.: Government Printing Office, 1918), 79.

⁴³⁶ Henry O'Malley. *Report of the U.S. Commissioner of Fishes* (Washington, D.C.: Government Printing Office, 1927), xxxii.

In addition to the impact of WWI, the growth of new life science disciplines, especially chemistry, also changed the structure of liquid laboratories. Around 1920, chemists began to flock to marine stations for the same reasons that other life scientists had done so before them. But unlike the previous group, chemists required built in laboratory equipment to keep themselves, and other researchers, safe. Fume hoods and shake-resistant tables, and emergency showers and sinks were common in chemistry laboratories, and these were required at marine stations if chemists became regular visitors.⁴³⁷ Laboratories with the budget and space to make these changes restructured their spaces; specialty chemistry laboratories were added at stations from Hopkins Marine Station to the Marine Biological Laboratory. The open, non-specific laboratory space that had made these stations so versatile gave way to more specialized structures. While each laboratory continued to cater to a wide variety of researchers, they shared research space only with others interested in the same scientific questions; interdisciplinary interactions only occurred in shared spaces such as dining halls and dorms. The Tortugas station had the most open architectural structure of any marine station and was still located in difficult location. Unable to make the shift to this more modern type of marine station, the Carnegie Institution decided to close it in 1932 and use its resources to support research at other locations.⁴³⁸

The network of liquid laboratories changed significantly in the 1930s; research at stations became highly specific and centered around disciplinary studies. Marine stations are no longer at the center of American biology. Most scientists now build their research programs around model organisms that are easily reared and maintained in terrestrial

⁴³⁷ For a history of the growth of chemistry in America, see Robert E. Kohler. *From Medical Chemistry to Biochemistry: The making of a biomedical discipline* (Cambridge, UK: Cambridge University Press, 1982).

⁴³⁸ Ebert, "Carnegie," 182.

laboratories; the majority of biological researchers are no longer expected to visit marine stations yearly to work with available specimens. Some marine species have continued to be useful to mainstream biological investigation. The zebrafish and platyfish are both used in cancer research; dogfish, sea urchin, and mummichogs are still considered integral to studying embryological development.⁴³⁹ Other species, such as jellyfish, have been replaced by systems that have proved easier to rear and maintain in the laboratory. Neurophysiological experimentation with the squid giant axon has overtaken that with jellyfish, not because it is easier to keep squid alive in captivity (it is actually as difficult or harder), but because squid are plentiful in many locations and the axon can be excised and kept fresh for shipping, meaning that researchers need not worry about building an artificial environment in which to keep their subjects.⁴⁴⁰

However, marine stations have become integral to the identity of marine biology. In the 1950s, scientists sought to clearly define marine biology to capitalize on the large influx of research money from the government. Instead of focusing on consistent methodologies, the field became defined by “a geographic space and one that explicitly espoused a pluralistic methodological approach that could satisfy the diverse group of scientists that found their identity through the study of marine life.”⁴⁴¹ Marine stations allow multiple disciplines to perform research on a variety of marine environments;

⁴³⁹Prince Masahito, Takatoshi Ishikawa, and Haruo Sugano. “Fish tumors and their importance in cancer research” *Japanese Journal of Cancer Research* 79 (May 1988): 545-555.; Manfred Scharl. “Platyfish and swordtails: a genetic system for the analysis of molecular mechanisms in tumor formation” *Trends in Genetics* 11:5 (May 1995): 185-189.; Stephane Berghmans et al. “Making waves in cancer research: new models in the zebrafish” *BioTechniques* 39 (August 2005): 227-237.

⁴⁴⁰ James W. Atz “Fundulus Heteroclitus in the Laboratory: A history” *American Zoologist* Volume 26 Issue 1 (1986): 111-120 and Jane Oppenheimer “Fifty Years of Fundulus” *The Quarterly Review of Biology* Volume 54 Issue 1 (Dec. 1979): 385-395; A.R. Foltz et. Al. “Echinoderm eggs and embryos: procurement and culture” *Methods in Cell Biology* 74 (2004): 39-74.

⁴⁴¹ Ellis, “What is Marine Biology?” 471.

together with ship-based activities they make up the core of marine biological research today.⁴⁴²

More research into marine stations can shed light on the transition from general life sciences to the rise of marine biology at these stations from the 1930s to the present. While the nature of the network changed throughout this period, marine stations still continue to operate as a large information-sharing network. There are over 120 laboratories in the National Association of Marine Laboratories. Organized in the 1980s, the Association strives to promote research, conservation, public outreach, and “the efficient exchange of information, constructive cooperation, and productive coordination among NAML member institutions and across regional associations.”⁴⁴³ The NAML continues the long tradition of linking the marine network through open information sharing. Working at the water’s edge continues to be important to the process of biological research and to the growth of our scientific and cultural construction of the marine environment.

⁴⁴² For information on post-WWII oceanography and marine science, see Naomi Oreskes. “A Context of Motivation: US Navy Oceanographic Research and the Discovery of Sea-Floor Hydrothermal Vents” *Social Studies of Science* 33 (Oct. 2003): 697-742. Helen Rozwadowski. *Fathoming the Ocean: Human Enterprise and the Opening of the Deep Sea* (Cambridge, MA: Harvard University Press, 2005); Helen Rozwadowski. *The Sea Knows No Boundaries: A Century of Marine Science Under ICES*. (Seattle and London: University of Washington Press and International Council for the Exploration of the Sea, 2002).

⁴⁴³ National Association of Marine Laboratories Website [available at <http://www.naml.org/about/>] accessed 3.11.14

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