Why Study Biology by the Sea?

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Why Have Biologists Studied at the Seashore? The Woods Hole Marine Biological Laboratory

JANE MAIENSCHEIN

In the summer of 1893, Bashford Dean presented a public lecture at the Marine Biological Laboratory (MBL) in Woods Hole. He spoke about the marine biological stations of Europe, noting that European biologists had long embraced the value of studying biology at the seashore. He pictured the biologist first learning about marine organisms at an inland European laboratory, studying material shipped from a coastal station. Then the student would visit one of those stations first to learn and then to carry out research. Dean pointed out that, with rich research materials, equipment, and libraries, "the station becomes, in short, a literal emporium, cosmopolitan, bringing together side by side the best workers of many universities, tending, moreover, to make their observations upon the best materials sharper by criticism, most fruitful in results." He continued: "It has often been remarked how large a proportion of recently published researches [sic] was dependent, directly or indirectly, upon marine laboratories." He noted that "general interest in the advancement of pure science" had become important in Europe in the previous decade but that the same was not true of

ONE

5

JANE MAIENSCHEIN

the United States. He sought to improve awareness among Americans, and he saw the MBL as a place to make the case for why biologists need marine stations (Dean 1894, 212).

This essay addresses the question of why biologists have studied at the seashore by looking briefly at previous answers such as Dean's. I first explore early studies at the seashore, then review Charles Kofoid's 1910 survey of marine stations. Historians extended Kofoid's story in a series of symposia and volumes around 1988, in connection with the MBL's centennial. This essay provides a summary of those studies and the resulting traditional picture of biology by the sea.

The essay then focuses on the MBL to show how Americans first embraced biology at the seashore. As the MBL's first director, Charles Otis Whitman, noted, the MBL offered a clear vision for an independent institution that brought together what he called *instruction and investigation*. From the beginning, the MBL leaders understood that students and researchers learn from each other and discover together and that they do so across the boundaries that normally separate biologists into different institutions and different disciplines with access to different tools and organisms. Having a building with running seawater, easy access to a wide diversity of research organisms, and a community of other curious biologists made the MBL and other marine institutions valuable. Coming together to carry out biology by the seashore has allowed new and otherwise unachievable biological advances for more than 130 years.

Despite this record of success, however, the viability of some marine institutions has recently come into question. In the United States, limited federal funding for biomedical research has made the traditional extended summer stays at marine laboratories a luxury that many scientists cannot afford. The positive aspects of year-round facilities by the sea are offset by the costs of maintaining them because many of the scientific and revenue-producing activities are in fact concentrated in the summer. In response to such challenges, institutions have hired full-time scientific staffs, hoping to support facilities with overhead charges on research grants, and have sought new conferences and courses to fill the off-season schedule. Fiercely independent institutions such as the MBL have found themselves responding to these sorts of pressures by affiliating with larger, deep-pocketed institutions (in MBL's case, the University of Chicago). While understandable, such changes have raised questions about how to preserve the unique, collaborative culture of marine stations that have relied on their independence.

6

These are not new problems; explorations of the history of selected institutions that have persisted over generations and the work done there help illuminate where we are today. Reflecting on these historical studies informs our understanding of why marine institutions have been and remain important.

Why Did Researchers Study at the Seashore?

As Dean showed clearly, by the end of the nineteenth century, discoveries at marine biological stations had contributed significantly to knowledge about the fundamental biology of organisms. Careful natural historical observations and experiments, typically during summer visits, continued to increase knowledge about such basic biological phenomena as fertilization, development, heredity, cells, regeneration, physiology, and the way in which external conditions influence biological processes. Technological developments in microscopy and imaging methods then enticed researchers to take their organisms from the beach indoors to the laboratory bench.

As with so many aspects of nature, the story of marine studies actually starts millennia earlier with Aristotle, who found marine life fascinating and informative for providing insights about living organisms. In his works focused on central phenomena of living systems, including *The Parts of Animals, The Generation of Animals, The History of Animals, The Movement of Animals,* and *The Progression of Animals,* he documented natural history, development, and distribution of marine as well as terrestrial organisms. Despite the obvious problems with these types of attribution, he is often referred to as the father of marine biology.¹

Although others also studied marine organisms, it was not until the nineteenth century that significant numbers of investigators began to undertake "nature study" at the beachside, often as a way of enlightening and educating a general population about life (Armitage 2009; Kohlstedt 2015). Others looked into the ocean depths for pragmatic reasons, such as the need to know about the ocean bottom when laying transatlantic cable in the 1850s (Thomson 1873; Anderson and Rice 2006). Though oceanography remains separate from marine biology as a discipline, discoveries of marine creatures in the ocean depths raised questions about the processes of living systems. Other drivers for the study of marine life have come from commercial interests in fisheries or from imperialistic motives to establish what lands could be conquered, what resources could be commanded, and what information could be controlled (see, e.g., Osborne 1994). In short, diverse interests have taken researchers to the seashore.

Exploring expeditions in the nineteenth century involved observing but also collecting and documenting, with the result that major exploring expeditions typically carried along at least one naturalist and an artist. Naturalists such as Thomas Henry Huxley and Charles Darwin, for example, found their lives and their ideas about nature significantly affected by long expeditions across oceans as they developed evolutionary explanations of the rich organic diversity they observed and recorded.

Huxley's study of relatively simple marine life-forms led him to ideas about protoplasm as a material basis for life and to reflection on ways that study of individual development through ontogeny relates to evolutionary development of species or phylogeny (Huxley 1913, vol. 1 [discussing the *Rattlesnake* voyage, especially during the years 1846– 50]). In Germany, Ernst Haeckel pursued similar questions about the connections of development and evolution through his biogenetic law, which held that ontogeny recapitulates phylogeny. His extensive study of marine organisms and his beautiful color drawings and paintings of marine life provided him the authority for his claims about both evolution and development (Richards 2008). Comparing development and morphology of different species suggested relationships among them. These studies took place at the sea but initially in the absence of marine stations or established institutions.

Aquariums provided another form of access to marine study, allowing observation of marine life without having to be actually at the seashore. Yet, until the late nineteenth century, there were only a few public aquariums, and only the wealthy could afford to keep the water sufficiently clean and aerated in their own aquariums at home (Barber 1984). Aquariums housed specimens for researchers as well as attracting public interest in marine studies, but they did not re-create nature, and they did not yet serve as laboratories (Nyhart 2009; de Bont 2015; Muka 2017). They were central to some—such as the Stazione Zoologica di Napoli (SZN)²—but not all marine stations.

A growing number of researchers began to move from the beach to comfortable rooms. They could study the natural history and environment outdoors, then move indoors to spread their collected specimens out on tables for further study while storing living organisms in seawater tanks. Researchers began to rent rooms where they could look closely with microscopes and other equipment that they could set up and use day after day and record their findings over longer periods of time than was convenient at the beach. They did not have to carry their specimens far and therefore could observe embryological development and physiological processes of the living organisms that would have been harder to study if the organisms had had to travel in jars for longer distances. Itinerant researchers—including notably Anton Dohrn and Ernst Haeckel, who rented rooms for research—soon began to long for even more permanent facilities where they could set up labs, leave their equipment, and return the next year to continue their research in reliable surroundings (Richards 2008; de Bont 2015).

By 1900, increasing numbers of researchers who aspired to become professional biologists had joined the migration to summer marine research sites and to a growing variety of institutions providing opportunities for seaside study. Small places for just one researcher and a handful of students existed alongside the magnificent building for the SZN founded by Dohrn in 1872 (Simon 1980; Groeben 1984; Benson 1988). Government facilities emerged as well, such as that at Plymouth, England (Southward and Roberts 1987). By 1893, so many places existed around the world with such different styles and purposes that Bashford Dean's MBL lecture may well have helped inspire the US government to commission a study to document and learn from what others were doing.

Kofoid's 1910 Survey of Marine Stations

The international development of marine stations caught the attention of the Bureau of Education in Washington, DC, which was then part of the Department of the Interior. The commissioner of education, Elmer Ellsworth Brown, requested a study of European stations with a published book to record the results. In his letter of transmittal for the resulting volume, he noted that both scientific research and traditional instruction are essential for educational programs. He explicitly intended the study to promote advancement of stations in America like those in Europe (Kofoid 1910, xi).

Charles Atwood Kofoid and his wife, Julia, took on the study, visiting European freshwater and saltwater marine stations through 1908 and 1909. Kofoid was born in 1865 in Illinois, graduated from Oberlin College in 1890, and received a PhD from Harvard University for research on cell lineage. With an appointment as assistant professor at the University of California, Berkeley, from 1903 until his retirement in 1936, he worked with William Emerson Ritter to develop the Marine Biological Association of San Diego, which later became the Scripps Institution of Oceanography. His biography in the National Academy of Sciences *Biographical Memoirs*, by the geneticist Richard Goldschmidt, explains his research commitments and his fascination with marine life, especially the plankton and protozoans (Goldschmidt 1951). It is also clear that the Kofoids enjoyed travel and discovering new places and new life-forms.

When he was asked to carry out the survey, Kofoid had already published the 1898 article "The Fresh-Water Biological Stations of America" in the *American Naturalist*. There he noted: "The fundamental purpose of all biological stations, both marine and fresh-water, is essentially the same. They serve to bring the student and the investigator into closer connection with nature, with living things in their native environment. They facilitate observation and multiply opportunities for inspiring contact with, and study of, the living world. They encourage in this day of microtome morphology the existence and development of the old natural history or, in modern terms, ecology, in the scheme of biological education" (Kofoid 1898, 391).

Kofoid went on to note that, while most marine stations were close to the sea, the United States had begun to offer some freshwater stations, especially in the Midwest. He pointed out that great potential for discovery lay in the mix of old-fashioned natural history description with experimental studies carried out by researchers and students working together.

For his larger study of stations in Europe and elsewhere, Kofoid visited each station for long enough to get a sense of its character. He documented the work being done, organisms studied, equipment used, and techniques developed. He also took photographs, included maps, and clearly paid close attention to the details of each station with the explicit intention that the European institutions could inspire development of more marine stations in the United States.

In the preface to the 1910 volume, Kofoid noted:

Special attention has been given to the economic or applied scientific phases of their activities in the firm belief that biological stations and their methods of attack upon biological problems are destined not only to add greatly, and, in a unique way, to the advance of knowledge but are also of prime economic importance. They are laying the foundations for a scientific aquiculture [*sic*] that will make possible the conservation of the aesthetic and economic resources of lakes and streams from threatened pollution and destruction, and that will facilitate the reaping even

tually of the annual harvest of the sea without destruction to its sources. (Kofoid 1910, xiii)

He then went on to describe nearly one hundred stations of various sorts, including the quite different, magnificent SZN, Plymouth Station in England, Station Biologique de Roscoff in France, and the then newly established station at Monaco.

Despite the differences in facilities and organisms studied, Kofoid identified key features of a successful station. It should be accessible, with available transportation, and near a city that can provide housing. A rich variety of flora and fauna, with pure water, are important for experimental study. Research stations benefit from the variety of organisms available in warmer waters, but that variety does not matter so much for teaching purposes. Aquariums to store organisms and a plumbing system to bring in local water both contribute to making research possible. When all these conditions are met, "the biological station is a unique agency in biological research, indispensable in the equipment of a nation for the upbuilding of leaders in biological teaching and in the development and expansion of the spirit of research" (Kofoid 1910, 6).

Kofoid's report made clear that the United States had opportunities to develop more marine stations, the message being that such development would benefit American biological research and education. Kofoid noted that over fifty Americans had visited facilities in Europe, which he felt demonstrated a demand for such research and facilities that was not being met in the United States. Americans could, and by implication should, establish more and diverse types of marine stations. In fact, a number of such stations soon appeared in the United States. While Kofoid's survey was certainly influential at the time, and many marine stations and programs did subsequently appear around the world (including the Misaki and Amoy Stations in Asia, on which see Luk, in this volume, and Ericson, in this volume), his arguments for the importance of marine stations and their research remain valid today.

Historical Studies of American Marine Stations

As the 1988 centennial of the MBL approached, historians began reflecting on the nature and role of marine stations in US biology. The MBL leadership collaborated with the SZN to hold a symposium in 1984 at the SZN's buildings on the nearby island of Ischia. The meeting brought together historians and experimental biologists to share reflections on a century of biology by the sea. Explorations of both research and teaching contributions provided insights into what was common between the two institutions and what differed and why. The discussions also raised questions about the future of marine institutions.

SZN director Antonio Miralto sounded an optimistic note about the important role marine stations could play as he asked, "What laboratories for what science?" He wrote: "I believe that science should fit within a broad, non-restrictive, non-deterministic cultural frame-work. Indeed, science should become the focal point of a process of cultural renewal; a point of reference for future generations; and a driving force in all fields, scientific and non." He argued that we must beware of creating isolated institutions and instead should encourage broad international exchange of ideas. Scientific laboratories need culture, he urged, including through visual arts and music: "As in the past, science can determine many aspects of the future of humanity. Men of science must look beyond the limits of their own research activities, and, by their culture and enlightenment, become intellectual leaders" (Miralto 1985, 203-4). Such a beautiful Italian sentiment had also appealed to the more practically minded Americans in establishing the MBL to promote cooperation, learning together, and sharing the culture of science.

The papers from this meeting of historians and scientists appeared in a special supplemental issue of the MBL's journal, the *Biological Bulletin* (see "The Naples Zoological Station and the Marine Biological Laboratory" 1985). In addition, soon thereafter the *Bulletin* reprinted a historical volume by Frank Lillie, the second MBL director (see Lillie 1944).

In 1986, the American Society for Zoology organized a session on the topic of "American marine biology and institutions" at its annual meeting. In his introduction to the session, Ralph Dexter noted the origins of US marine study and the growth to more than fifty marine institutions (Dexter 1980). My talk asked, "Why do research at the seashore?" and pointed to changes in questions asked and methods used over the decades of the MBL in particular. I noted the dual interests in working at the seashore both because that is where the marine organisms live and because it is pleasant for researchers to live there as well. Even as it became possible to ship more living organisms to, say, Kansas for research or teaching, researchers and students still chose to visit the seaside institutions (see Maienschein 1988). Discussion at the symposium made clear that a large percentage of the audience had themselves made the trip to study by the seashore at some point as students or researchers. Everyone who commented enthused about the experience, regretted not being able to make the trip more often, and expressed hope that marine stations would have a solid future continuing to attract future generations. The MBL stood as a favorite place that evoked nostalgic longings to return and reports of the impact time spent there had made on so many different people's biological research and teaching.

The MBL: Why Woods Hole?

The history of early US marine stations began with schools focused on natural history. Notably, Louis Agassiz and his son Alexander set up the Anderson School on the island of Penikese in a string of islands off the southern tip of Cape Cod. The school lasted only two seasons, and students and faculty noted a number of limitations of the remote location. Yet the group was enthusiastic about study at the seashore, and many of the Penikese students and assistants went on to play leadership roles in other institutions. Agassiz's student and assistant Burt G. Wilder provided an excellent sense of both what Agassiz hoped to accomplish and what happened there, who attended, and what Agassiz meant by the call he posted, "Study Nature, Not Books" (Wilder 1898). Among the students at Penikese were Charles Otis Whitman and Cornelia Clapp, who was the first person to arrive the first year at the MBL and who became the first librarian, the first female trustee, and an excellent scientist and teacher.

In 1880, Agassiz's student Alpheus Hyatt established a similarly shortlived summer laboratory at his home in Annisquam on Cape Ann, on the shore north of Boston. He attracted support from the Boston Society of Natural History and the Woman's Education Association of Boston, both of which later supported the MBL. As with the Anderson school, Hyatt's seaside lab offered instruction in natural history with a focus on the diversity of organisms. It attracted such students as Thomas Hunt Morgan, between his undergraduate studies and his graduate studies at Johns Hopkins. In addition, it was intended to offer research facilities and opportunities for advanced biology students and researchers (Maienschein 1985a). Although neither the Penikese or the Annisquam school lasted long, both clearly indicated that the Boston area had a number of supporters with a lively interest in the sea for practical as well as research interests.

Another Agassiz student, William Keith Brooks, had served as an assistant both to Louis's son Alexander and to Hyatt at the Boston Society. In 1876, he moved to the new Johns Hopkins University, where he became professor of zoology and established research labs in Jamaica and then the Chesapeake Zoological Laboratory. Yet those remained small facilities for small groups of Johns Hopkins students and defined projects.

Woods Hole—at the southern tip of Cape Cod—became the home for permanent biological research in America. Woods Hole already housed the US Fish Commission (USFC), with a solid building and an active fisheries-oriented program. Despite his own smaller marine expeditions to other places, Brooks also sent his graduate students to the USFC station, established by Spencer Fullerton Baird in 1885 (Benson 1979). While the USFC focus remained on practical matters related to fisheries, Baird welcomed researchers working on a range of topics to use the lab. He pointed to the rich diversity of life at this location, where the warm waters of the Gulf Stream and the colder waters of the Newfoundland Current come together. In his centennial reflective essay, W. D. Russell-Hunter wrote about the considerable advantages of Woods Hole for reasons of biodiversity (as we call it today), water quality, and other ecological considerations (Conklin 1944; Russell-Hunter 1985).

At the USFC, Baird strongly supported the idea to develop an independent marine laboratory as a complementary, independent institution for both research and instruction just across the street from the USFC in Woods Hole. He looked forward to expanding the local biological community. In his history, Lillie recalled how the MBL had started when a group of Boston Society of Natural History members, along with the Woman's Education Association of Boston, decided in 1886 that the time had come to establish a marine biological laboratory dedicated to education and research. With Baird's support, they decided on Woods Hole. Their permanent and independent institution became the MBL (Lillie 1944). The MBL opened its doors in 1888 and began to grow in size and activity. The zoologist Winter Conway Curtis, who later testified in the Scopes trial, reported on the good times at the early MBL and USFC and the significant ways in which the two institutions reinforced each other (Curtis 1955; Galtsoff 1962).



FIGURE 1.1. Map of the Woods Hole and Penikese Island area, Cape Cod, Massachusetts, 1892. Map courtesy of the University of Chicago Library (Map G3701.P5 svar.U4 no. 112 1892 MapCI).

From its opening in 1888 until 2013, the MBL remained ferociously independent, with Whitman writing strong letters insisting that it should never become affiliated with any one university.³ When the University of Chicago opened in 1892, Whitman became the first chair of the Biology Department while also continuing in his unpaid position as MBL director. Despite several efforts starting in the 1890s to affiliate the two institutions, Whitman worried that the MBL needed national support rather than affiliation with just one group or one university. Ironically, and also perhaps quite appropriately, a century and a quarter later, in 2013, when the MBL Corporation addressed the question whether to become formally affiliated with the University of Chicago, the vote was overwhelmingly in favor (Maienschein 2014).

At the end of a railway line, Woods Hole provided a welcoming place for families to travel for the summer and enjoy the seaside research life together (Pauly 1988). Lillie met his future wife during the embryology course, and a number of other researchers pointed to the importance of their family connections with Woods Hole, with wives and children



FIGURE 1.2. Marine Biological Laboratory, Woods Hole, Mass., 1890s. Photograph by Howard Stidham Brode (1890–1958). https://history.archives.mbl.edu/archives/items/marine -biological-laboratorywoods-holl-mass.



FIGURE 1.3. Thomas Hunt Morgan, Edmund Beecher Wilson, Ross Granville Harrison, and Morgan's family apparently picnicking on the beach near Woods Hole, n.d. Photograph by Alfred Francis Huettner (b. 1884). https://history.archives.mbl.edu/search?search_fulltext= thomas+hunt+morgan%2C+E.B.+Wilson+andothers+having+a+picnic.

lobbying to return summer after summer. Thomas Hunt Morgan dedicated his 1901 *Regeneration* to his mother, thanking her for spending summers in Woods Hole and helping care for her grandchildren so that both he and his wife, Lilian Vaughan Morgan, could spend time doing research. A photograph shows Morgan (center rear), his mother, Ross Granville Harrison (left), Edmund Beecher Wilson (right, with teacup), and other family members enjoying one of many picnics at the beach. The life of the lab and life on the beach merged in many ways. Many MBL scientists report meeting collaborators on the beach or through their children who had become friends.

Marine Studies at the MBL

Having a permanent lab with buildings in which to store materials and equipment along with laboratory benches and meeting rooms made the MBL attractive for multiple purposes. In its early years, summer participants arrived with a mix of goals and needs. They got their feet wet watching the abundant life-forms in the intertidal zones, and they scooped and transported specimens to observe them in the lab. Often that meant putting on clumsy waders and carrying buckets, glass jars, and smaller tubes to collect specimens and take them away. Having shared teaching facilities near the labs for independent researchers helped inspire everyone to work and learn together. Observing the different organisms over time yielded a great deal of new information about marine invertebrates and small fish that then allowed researchers and students to compare what they found. The coexistence of investigation and instruction provided a strong foundation for the young MBL.

In his history, Lillie discussed the importance of the courses for bringing young people to learn about biological research alongside the more established teachers and independent researchers to create a mix of generations. Lillie noted: "There is a large body of students in this country enthusiastic about biology and eager to make a firsthand acquaintance with marine life; on the other hand, there are their instructors, many of whom are anxious to carry on their investigations in the summer under conditions furnished by the Laboratory but who are often without means to do so. The Laboratory brings them together in Woods Hole" (Lillie 1944, 86). This was true in 1888, and it remains true now.

The long-term courses included invertebrate zoology (which ran from 1888 to 1988 in various evolving forms), marine botany (which became marine biology from 1963 to 1967 and experimental marine botany between 1968 and 1979), physiology (from 1892 to the present), and embryology (from 1893 to the present) (for a more detailed discussion, see MacCord, in this volume). Lillie explained how the courses work, noting: "Naturally, the courses have been kept abreast of advancements in their fields and have been modified somewhat by successive instructors, but in their essential conceptions they have remained the same" (Lille 1944, 87). This is still true, with the addition of new, highly technical courses such as gene regulatory networks or computational approaches, special topics courses including the history of biology, and new secondary education courses.

Students and researchers could collect their own materials, but they also relied on the Supply Department for additional organisms. Under the guidance of Director George Gray, the growing department provided a boat and captain as well as a catalog of what was found and preserved specimens of many organisms. Since 1994, the George M. Gray Museum collection has been housed at Yale University and has

WHY HAVE BIOLOGISTS STUDIED AT THE SEASHORE?



FIGURE 1.4. MBL botany class collecting specimens, 1895. Photograph by Baldwin Coolidge (1845–1928). https://history.archives.mbl.edu/archives/items/botany-course-photograph -1895-collecting-specimens.

added more specimens, photographs, and other materials to provide a rich record of New England marine biodiversity (Peabody 2018).⁴

Study of individual organisms focused especially on physiology, heredity, and development at first, then later also on neurobiology. These fields benefited from the ready availability of living material collected fresh from the sea. The wide diversity of organisms also allowed comparative studies. For several early summers, for example, Whitman assigned students and colleagues to study cell lineage of different organisms using similar methods so that they could map out and compare consistent and distinctive details of cell lineage in development. What were the exact patterns of cell division for each, and how did those patterns compare? Such research informed understanding of individual embryological development. It also allowed examination of evolutionary relationships, with the assumption that greater similarities and homologies of form or patterns reflected evolutionary closeness. And this approach brought the individual researchers into a community, comparing details, learning from each other, and raising new questions as they found reassuring similarities or surprising differences (Maienschein 1978).

The Woods Hole summer involved a lot of time observing outdoors and also embracing the new experimental ethos of biological discovery of the 1890s. For example, at the MBL in 1894, William Morton Wheeler presented a translation of Wilhelm Roux's introduction to his new *Archiv für Entwickelungsmechanik* on "developmental mechanics" with its call to carry out manipulative experimental research at the bench (Roux 1895). At the MBL, young scientists who became luminaries in biology took up this call, including Thomas Hunt Morgan, Jacques Loeb, Edmund Beecher Wilson, and many others who thrived under the laboratory's welcoming leadership of Charles Otis Whitman and then Frank Rattray Lillie.

As historians have argued vigorously, this experimental turn was not a matter of what the historian Garland E. Allen has called a "revolt from morphology." There was no rejection of descriptive methods or morphological studies but rather a combining of these approaches with study of physiology, embryology, evolution, and other aspects of what was being labeled *biology* (Allen [1975] 1978; Maienschein, Rainger, and Benson 1981; Caron 1988).

This is not the place to provide extensive details about all the research carried out at the MBL over its over 130 years and how it has changed over time. Some examples suffice to show the early focus, and Lillie (1944, chap. 6) provides much more detail up to that point, while annual reports give a good sense of what researchers were asking and what they were doing. Contributions that provided a foundation for courses and for further research included, for example, Whitman's research on cell lineage, along with extensive work on, respectively, Clepsine (leeches, by Whitman), Crepidula (slipper snail) and several ascidians (by Conklin, on whose work see Steinert [2016]), Nereis (by Wilson), and Unio (freshwater clam, by Lillie). Jacques Loeb studied parthenogenesis, regeneration, and fertilization and engaged in lively debates with Lillie and his student Ernest Everett Just about the mechanisms of fertilization that continue to inspire discussion about clashing assumptions informing biology. Morgan's study of regeneration gave way to his focus on heredity and chromosomes. Wilson's study of cells led to his classic The Cell in Development and Inheritance in 1896, with editions in 1900 and 1925, and it inspired the collective study of cells that led to Edmund Cowdry's edited volume General Cytology in 1924. Additional research in physiology, led by Loeb, and protozoology, led by Gary Calkins with a course from 1919 to 1940, added diversity to the research and educational offerings.

Since World War II, the MBL has added important study of ecosys-

tems and the factors that shape a healthy environment. The Ecosystem Center makes up one of three research centers that also include the Eugene Bell Center for Regenerative Biology and Tissue Engineering and the Josephine Bay Paul Center for Comparative Molecular Biology and Evolution. Lively programs in cell biology, imaging, and biodiversity studies through the Marine Resources Department add to the current core areas of MBL research and education.

The MBL in Historical Context: 1888-2018

Director Whitman's initial vision to build a laboratory serving a diversity of researchers and students from different institutions remains intact. His passionate commitment that the MBL remain independent has been replaced by the economic reality that true independence is simply too expensive in the twenty-first century. Nearly every small private independent research lab has affiliated with a university or some other larger institution. The MBL has struggled financially from the beginning but has always managed to find a way to make things work.

Following the Naples model, in its first decades the MBL invited universities to subscribe to tables in exchange for the right to send some students for the summer. Independent investigators rented laboratory space and paid for any equipment or supplies that they needed. Students paid to attend courses. And the relatively modest wooden buildings did not cost much to maintain. Nonetheless, for the first half century, the MBL faced a budget deficit nearly every year because it kept expanding. The archival records make clear that Whitman felt that it was more important to grow than to worry about financial details. Fortunately, philanthropic donations made up the difference, and, in fact, Frank Lillie's brother-in-law Charles Crane made up a very high percentage of the shortfall each year. Crane also funded the first permanent brick building and supported establishment of a permanent library (Maienschein 1985b). Crane died in 1939, and, while Lillie had stepped down as MBL director in 1925, he remained president of the MBL board of directors until he retired in 1942. At that point, the MBL had to develop new funding models (Maienschein 1985b, 1989).

Fortunately for institutions like the MBL, by the 1940s the US federal government had begun to provide funding for scientific research. With external grants, researchers could take their funding with them to independent research stations such as the MBL. A broader range of researchers who had access to these funds could rent laboratory space and housing with grant dollars. Even though these researchers were not actually paying for the full cost of using space, the approach mostly worked because the courses were also bringing in funding and donations added to the mix. By juggling priorities, obtaining special funds to build new space that attracted more people, attracting donors and special earmarked public funding from the state and federal governments, and developing a year-round program, the MBL grew and managed to remain close to solvent but never with a significant financial buffer.

From very early, the MBL has had a national and international impact much larger than its resources would suggest possible. From the 1920s into the 1940s, for example, China sent a number of scientists to the MBL. They studied there and returned to establish marine stations in China (see Luk, in this volume). Lijing Jiang and Kate MacCord have documented this movement in their digital exhibit for the MBL History Project (Jiang and MacCord 2015).

Another connection—this one with Japan—is visible through a document left at the Misaki Marine Biological Station, which had been



FIGURE 1.5. Japan's emperor Hirohito and Sears Crowell at the MBL, 1975. Courtesy of MBL History Archives. https://hpsrepository.asu.edu/handle/10776/12863.

used as a Japanese naval facility during World War II. The document, written by the Japanese researcher Katsuma Dan and found by a US naval officer (see Ericson, in this volume), suggests that dedication to science should outweigh politics and war. Before taking up his position at the University of Tokyo and the Misaki Station, Dan and his American wife, Jean Clark Dan, had spent summers at the MBL studying cell biology and development. Their respect for the MBL inspired Dan's Japanese graduate student Shinya Inoué to pursue what became a distinguished career at the MBL, using exceptional light microscopic techniques to study cellular structure.

The Misaki Marine Biological Station was founded in 1896. The Japanese admiration for marine studies played out at the highest political levels with the emperor Hirohito's work. In 1975, when Hirohito was planning the agenda for a trip to the United States, he asked to visit the MBL. There, he declined afternoon tea and the proposed socializing because he preferred to spend his time looking through the microscope at the hydroids and related organisms that he had studied and summarized in *The Hydroids of Sagami Bay* (Hirohito 1988, 1995).

The MBL Today

In 2013, the MBL institutional situation changed. From its founding, the MBL Corporation had owned and technically managed the MBL. Corporation members were scientists who had spent time at the lab and paid annual dues to belong. Yet, by 2013, financial strains had become untenable. At a special meeting, the corporation overwhelmingly voted to make the University of Chicago the sole member and hence owner. With the long and rich connections between the university and the MBL, as documented in all of the histories of the MBL, the alliance appears to make sense (Maienschein 2014). Such a change, after more than 125 years, has also brought challenges. The initial mission to provide opportunities for instruction and investigation remains the guiding vision. But the institution has returned to a core focus on marine science, a commitment that had been lost at times when summer visitors brought diverse research projects to the lab.

Discussing the Chicago-MBL affiliation, the university president, Robert Zimmer, pointed to the lab's long success as a "convening power." The MBL draws people—because of the location, the rich history of discovery and education, and the opportunities it provides for networking and working with other scientific leaders. As MBL scientist Ron Vale put it, "how lucky can one get" to have the opportunity to spend time in this place with these people (Vale 2012).

In addition, the new mission emphasizes streams of strategic focus on new discoveries emerging from the study of novel marine organisms, encompassing research in regenerative biology, neuroscience, sensory physiology, and comparative evolution and genomics; the study of microbiomes and microbial diversity and ecology in a variety of ocean and terrestrial habitats; cutting-edge imaging and computation, illuminating cellular function and previously unknown biology; and organismal adaptation and resilience in the face of global change and rapidly changing ecosystems.⁵

The MBL's three centers and focus on marine organisms and related scientific programs, along with expansion of the year-round program, are attracting a dynamic group of scientists at all levels from distinguished researchers to energetic postdoctoral fellows to undergraduate assistants. These are all changes from the situation that prevailed before the 1970s. Then, only very few researchers stayed longer than the summer, individuals colonized small projects rather than far-reaching centers, and courses still included some undergraduates becoming familiar with biology (e.g., through the invertebrate biology course). Today, the year-round faculty is in the dozens, the centers provide new ways for individuals to connect ideas and explore cross-cutting projects, and the courses attract diverse international groups of enthusiastic and hardworking students.

The MBL has adapted. The future remains to be written, of course, and the affiliation with the University of Chicago has occurred so recently that its success remains to be seen. Yet the optimism for and energy devoted to innovation is palpable. Accepting the fact that the old models needed changing has brought new vitality and creativity to the MBL. New imperatives to study ecosystems or organisms perceived as being under siege by climate change, such as corals or saltwater marshes, suggest the need for changing priorities. An initiative is looking at ideas of regeneration across the scales of organisms, ecosystems, and microbial communities. The MBL hosts the National Xenopus Resource. And a new director has brought his own initiatives and research directions to inspire additional research and education. It will be fascinating to watch as the MBL and other marine stations continue to evolve and marine studies take new directions at the beachside and at the benchside. As the New York University physician, writer, and longtime MBL resident Gerald Weissmann puts it.

the MBL is "the place where a lot of people fall in love with science" (Goldberg 1997).

Notes

- 1. See, e.g., https://marinebio.org/creatures/marine-biology/history-of -marine-biology.
- 2. See http://www.szn.it/SZNWeb/showpage/107?_languageId.
- For Whitman's letters, see http://www.mblwhoilibrary.org/sites/default/ files/Whitman.pdf (finding aid) and https://hpsrepository.asu.edu/handle/ 10776/11546 (the documents themselves).
- 4. See http://peabody.yale.edu/collections/invertebrate-zoology/george-m -gray-museum-collection.
- 5. See https://www.mbl.edu/strategic-themes.

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