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ORIGINAL PAPER

The right tool and the right place for the job: the importance of the field in experimental neurophysiology, 1880–1945

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Abstract This paper seeks to contribute to understandings of practice and place in the history of early American neurophysiology by exploring research with jellyfish at marine stations. Jellyfish became a particularly important research tool to experimental physiologists studying neurological subjects at the turn of the twentieth century. But their enthusiasm for the potential of this organism was constrained by its delicacy in captivity. The discovery of hardier species made experimentation at the shore possible and resulted in two epicenters of neurophysiological research on the American East Coast: the Marine Biological Laboratory and the Carnegie Institution's Dry Tortugas Laboratory. Work done in these locations had impacts on a wide range of physiological questions. These centers were short lived—researchers at the MBL eventually focused on the squid giant axon and the Tortugas lab closed after the death of Mayer—but the development of basic requirements and best practices to sustain these organisms paints an important picture of early experimental neurophysiology. Marine organisms and locations have played an integral role in the development of experimental life sciences in America. By understanding the earliest experimental research done at these locations, and the organisms that lured researchers from the campus to the coastline, we can begin to integrate marine stations into the larger historical narrative of American physiology.

Keywords Experimental physiology · Marine station · Neurophysiology · Jellyfish

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1 Introduction

At the turn of the twentieth century, scientific researchers seeking to investigate marine subjects started traveling as soon as the spring semester ended. For many, the choice of marine stations at which to work was easily made: the closest, the station run by their academic institution, the station frequented by colleagues and friends, or the location that facilitated family visitations (Maienschein 1985; Benson 1988a; Benson 2001; Pauly 2000). Each laboratory within the network of American marine stations promised the same amenities: tables stocked with basic chemicals, glass containers (aquaria or basic bowls and beakers), running water, and access to a wide variety of fresh organisms. Choices were often predicated, not on professional requirements, but personal preferences (Muka 2014). But if all locations offered basic organisms and spaces, why would anyone spend the time and money to go elsewhere? And why would stations exist in less than convenient locations?

Over the past 35 years, historians and sociologists of science have explored the history of marine field stations primarily through the structure and work of the Marine Biological Laboratory (MBL) in Woods Hole, MA. The MBL 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 physiology (specifically experimental embryology). This reputation was largely due to many of the prominent figures that worked at the MBL, including Jacques Loeb, Thomas Hunt Morgan, 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 of local invertebrates and was taught by a rotating cast of researchers. The MBL is often used as an example of the point of infusion for German experimental biology into the American education system (along with Johns Hopkins University) via the mirroring of techniques and laboratory structure developed by Anton Dohrn at the Stazion Zoologica in Naples (Benson 1988b; Groeben 1984; Maienschein 1988).

Robert Kohler's work on the lab-field boundary states that early twentieth century biologists sought to break down the binary of laboratory and field by infusing laboratories with field methods and vice versa. 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 collected materials for courses at these stations, it was a low status job in which upper level researchers did not partake (Kohler does point out that William Morton Wheeler and Thomas Harrison Montgomery collected but are exceptions to the rule). Without the need or desire to collect at the shore, 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 (Kohler 2002, p. 44).

However, more recent work by Raf de Bont has challenged Kohler's assertions. De Bont compares two European stations, Naples (in Italy) and Wimereaux (in France), and finds that the 'ecologies', the natural as well as the social and cultural environment of each location, impacted the work done at these stations. In particular, he argues that Naples' ecology urged researchers to stay indoors and work in a lab that might have belonged in any location; work at Naples resembles that described by Kohler above. However, Wimereaux's ecology provided a more permeable boundary between the lab and field; the station's ecology facilitated the field as laboratory. De Bont's work suggests that historians more closely examine the ecology and research programs of individual stations in order to more fully understand the way that these spaces shaped marine research (and vice versa) (de Bont 2009, see also 2015).

This paper contributes to the discussion regarding the role of laboratory and field culture at marine stations by examining the link between organism choice and field work in these locations. In particular, I trace the rise of two epicenters of neurophysiology research, one at the Marine Biological Laboratory in Woods Hole, Massachusetts and the other at the Carnegie Research Laboratory in the Dry Tortugas off the coast of the Florida Keys. Both of these field stations offered space to a variety of researchers and have become well known for their programs in embryology at Woods Hole and coral research at Tortugas. However, for a short period at the turn of the twentieth century, these spaces, and the jellyfish found nearby, became important spaces for neurophysiology research. Experimentalists traveled to these spaces to work with jellyfish to answer questions regarding the evolution of the structure and function of nervous systems in the animal kingdom. In the process of working on wider research goals, they were required to inhabit a specific environment and understand a highly localized species.

The almost exclusive focus on experimental embryologists and model organisms has skewed understandings of the importance of field work at marine stations during this period. Rachel A. Ankeny and Sabina Leonelli's work on the distinction between experimental and model organisms defines the characteristics of the model organism as "small physical and genomic sizes, short generation times, short life cycles, high fertility rates, and often high mutation rates or high susceptibility to simple techniques for genetic modification." The authors go on to state that the ability to standardize organisms through breeding or genetic manipulation is a "specialized feature" of the model organism (2011, p. 316). In contrast, experimental organisms allow "controlled exploration of a particular biological phenomenon or research question" without the more specific requirements of the model organisms. While all model organisms are experimental organisms, not all experimental organisms attain model status (2011, p. 315). Most of the historical analysis of research at marine stations has focused on experimental embryologists

and their earliest model organisms. In particular, experimentalists at the MBL worked with many available organisms including *Arbacia* (sea urchin) and *Fundulus* (mummichog) embryos, both of which meet many of the characteristics of Ankeny and Leonelli's model organism.[1] These materials offered specific advantages: they were plentiful, small in size, had short generation times and short life cycles, could be manually fertilized, and provided visible growth stages (Oppenheimer 1979).

The historical analysis of work at marine stations during this period focuses on experimental work with these model organisms; unsurprisingly, Kohler and others see little mixture of lab and field based on these examples. Little was known, or needed to be known, about the native environment or behavior of these species to work with them in the laboratory; Loeb had his materials delivered to his lab table by collectors. Using these model organisms in experiments was divorced from understandings of the natural history and behavior of the organism in its natural environment. In fact, A.C. Redfield highlighted the inadequate understanding of the lifecycle of these popular species in 1958. According to Redfield, when sea urchin eggs became rarer in Woods Hole due to overharvesting, it became apparent that little was known about their life cycle and environment (Redfield 1958).

Widening the focus to another research community and their experimental subject offers a richer view of the work done at marine stations. Neurophysiologists worked with a variety of experimental organisms, including crabs, loggerhead turtles, and various echinoderms before developing programs using jellyfish. At the turn of the century, evolutionists and experimental biologists considered medusae (the scientific term for free swimming jellyfish) an interesting evolutionary case. They were thought to represent one of the earliest examples of nerve tissue, and this made them particularly useful to those investigating the developmental structure of the nervous system. Researchers argued that the jellyfish could be used as a model for the human nervous system and findings using jellyfish were commonly extrapolated to higher organisms. In addition, several species of jelly, and one species in particular- *Aurelia aurita* (moon jelly)–were available at nearly every marine station in the world. Specific interest in evolutionary questions and the widespread availability of the organisms made them, for many, "the right tools for the job" (Clarke and Fujimura 1992; See also Rader 2004; Clause 1993).

However, while prevalent and experimentally interesting, jellies were environmentally bound to specific locations. All jellyfish species required care in transferring them from field to lab. Once in these spaces, the experimental organisms required close attention to detail in order to maintain specimens for long term study. Medusae reproduce both sexually and asexually, there lifecycle is not easily standardized, and even the easiest species to keep in captivity could not be consistently bred and maintained until the second half of the twentieth century. Over time, experimentalists, collectors, and lab technicians developed technology and found species that worked to make these creatures better experimental organisms (Hirai 1958; Abe and Hisada

[1] Ankeny and Leonelli state that the genetic component is not necessary for the model organism definition but it has become prominent in the conception of the model organism by scientists post 1950. Because I examine work prior to this period I lean more heavily on the other variables in the definition (2011).

1969). But they were never able to transfer jellyfish to inland laboratories and many species remained highly localized to specific marine stations. To work with these experimental organisms, one had to travel to them and immerse oneself in the environment and lifecycle of a specific organism. The "right tools for the job" also required that researchers get to the "right place for the job."

This paper contributes to debates regarding the place of marine labs in the lab-field borderlands by focusing on the pairing of organisms to place in American experimental neurophysiology in the first half of the twentieth century. The first section outlines the debate over jellyfish physiology and explains why researchers were so interested in working with this particular organism. The second section outlines the particular difficulties encountered by researchers during the earliest years of research with these organisms. The most prevalent species could be found throughout the world, at nearly every marine station from Japan to Plymouth, but they proved difficult to keep in captivity. The final sections outline the rise of research programs at two marine stations built around specific species of jellies. By combining conversations about place and space in experimental work with those on the history and sociology of research organisms, we can develop a fuller understanding of the impact of experimental design on the role of the lab and field at marine stations.

2 Debating the existence of jellyfish nervous systems

In the late nineteenth century, a debate raged between prominent naturalists regarding the existence and extent of the nervous system in medusae. In 1850, Louis Agassiz described nervous tissue in several species he found during dredging in Boston Bay, including the abundant *Sarsia tubulosa* (clapper jelly) and *Bougainvillia supercilliaris.* Many prominent naturalists, including George Romanes, questioned his findings; Agassiz himself came to doubt his own conclusions (Agassiz 1850; Mackie 2004). Fifteen years later, Ernst Haeckel again described nerves in a hydromedusa, although he did not link his findings with Agassiz's original description (Haeckel 1865). Many, including Thomas Huxley, continued to deny these findings but 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 began publishing on the existence of a nervous structure in medusa (Romanes 1885, pp. 12–23).

Georges Romanes'1885 book *Jelly-fish, Star-fish, and Sea Urchins* brought the debate over the existence and structure of nervous tissue in medusae to a close (Romanes 1885, pp. 269–313). In the years before the publication of his book, both Romanes and Thomas Eimer published articles detailing experiments on the subject. These works utilized similar mutilation experiments to ascertain the extent of the nervous structure (Eimer 1874).[2] Although these publications were cited by other

[2] 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.

researchers, they did not signal an end to the debate. 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 suggested that if jellyfish had nerve and muscle tissues, they were the lowest level on the "zoological 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." (Romanes 1885, p. 11) 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, including determining directionality and speed (both rate of conduction and rhythm of pulsation), 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.[3] 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 (67)." 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 remaining section was linked to a marginal body. 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 (77)." 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 (79).

Romanes' 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 (French 1970a, b). Post- Darwinian researchers also felt that understandings of the function of this system could be extrapolated to larger and more complex systems, including vertebrates (Logan 2002; Clarke 1987) (Fig. 1).

[3] 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".

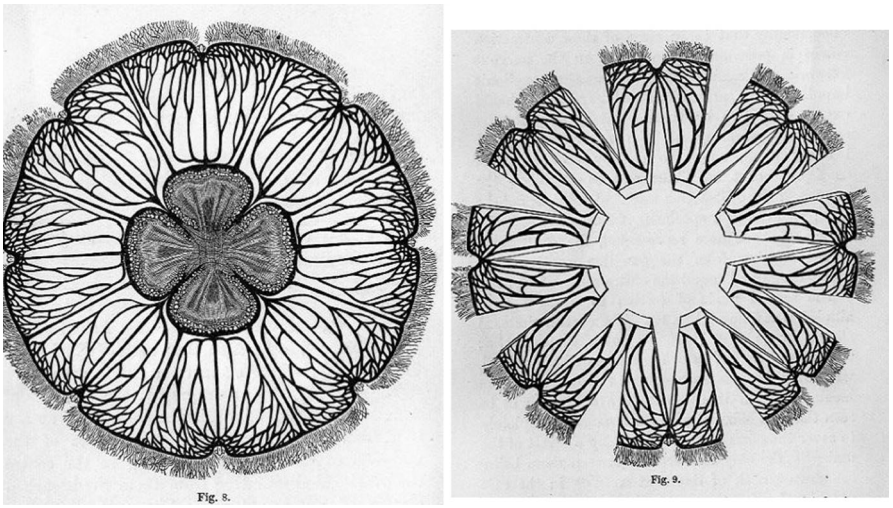

Fig. 1 A side-by-side comparison of a jellyfish before and after mutilation experiments. George Romanes (1885) *Jelly-fish, Star-fish, and Sea Urchins: Being a Research on Primitive Nervous Systems.* New York: D. Appleton and Company, pp. 66–67

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 (Brooks 1883a; Hargitt 1902; Mayer 1910, 1923). Jellyfish have a distinctive 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 (Hargitt 1910). At Woods Hole, Charles and George Hargitt found that all forms of reproductive materials were consistently available throughout the summer. They collected throughout the day in various locations and found, for any given species, "embryos in all stages of growth (222)." 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, Morgan specified in his work on regeneration that he used jellies between 10 and 20 mm diameter with somewhere between 40

and 60 tentacles (Morgan 1899, p. 941). The high volume and continuous lifecycle of the specimens made this specificity possible and marked the jellyfish as a valuable experimental tool.

At many marine stations 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 neurophysiological investigations. However, an abundance of material did not ensure that it could be converted into usable material for controlled experimentation. While the physiological structure of medusae could help researchers explore the basic biological phenomenon of nerve conduction, each species required a varied set of interventions to facilitate experimentation and the transfer of these physiological reactions into publishable data. Researchers had to find a variety of methods for converting these delicate creatures into durable experimental organisms.

3 Making jellyfish useful

Jellyfish were difficult to work with as either freshly killed or living specimens. This section will highlight the various practices, including technology and feeding regimens, developed by researchers to convert them into experimental organisms. Developing these technologies and regimens required careful observation and analysis of jellyfish in their native environment. Even when researchers succeeded in maintaining jellies in the laboratory for extended periods, this did not disconnect them from the field. The inability to keep captured specimens alive 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* (1899) to the attention required to preserve medusa (Fantini 2000, p. 526).

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 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 jellyfish (a rare occurrence after deep sea dredging) should begin immediately onboard ship (Lo Bianco 1899, pp. 20–21).

Closely following these methods still did not ensure preservation of important characteristics; no technique succeeded in the retention of 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 (Agassiz 1850, p. 222).

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 drawback being that otoliths are frequently dissolved" (Bigelow 1909, pp. 10). By 1887, physiologists had 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 neurophysiologists (Murbach 1903). 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.

One option for extending the experimental lifespan of jellies was to build a viable aquarium environment around their 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 jellies 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. 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 explore his methods in his publications (Brooks 1883a, b). 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 medusae was a key problem for experimentalists (Reiß et al. 2015; Brunner 2012).

3.1 Browne's plunger jar

One major problem with maintaining jellyfish in captivity revolved around the inability to keep them healthy for extended periods. Researchers with captive specimens reported similar physiological ailments in their specimens. Adult forms collected and placed in laboratory aquaria regained vigorous pulsations within a few minutes, but over the course of hours, days, or even weeks the specimens slowly lost vitality, growing visibly malformed, pulsating erratically, and eventually settling 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" (1904, p. 75). Hargitt initially believed that these specimens had been weakened by the 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. (1904, p. 75).

Hargitt was not the only investigator to report this problem. Jakob von Uexküll, the German biologist who theorized the *Umwelt*, or the theory of perception of the world as it appears to a particular organism, encountered these "whitish blotches" while working with jellyfish at Naples in 1900 (Uexküll 1934). Uexküll believed that the blotches produced a type of nervous stimulation but Hargitt doubted this, suggesting that they were merely a symptom of pathology (1901).

In addition to Uexküll and Hargitt, Edward T. Browne, a researcher at the Marine Biological Association laboratory in Plymouth, England stated that he had only 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 reported 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. (Browne 1898, p. 176).

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 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 pulley system to create a constant wave movement within the jar. Filling and emptying the bucket raised and lowered a wooden beam creating a constant motion within the jar. Allen said in response to the successful creation that he "was not a little pleased to have produced an efficient piece of apparatus from just 'a treacle tin and a stick." (Kemp and Hill 1943, p. 361) (Fig. 2).

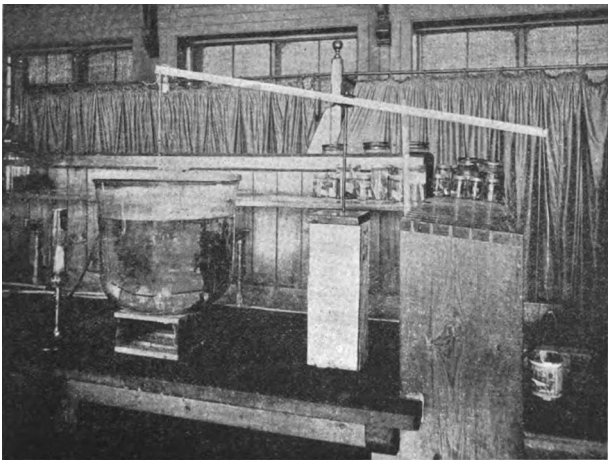

Fig. 2 E.T. Browne's original plunger jar. You can see the repurposed treacle tin (*far right*) in this picture. Edward T. Browne (1898) "On Keeping Medusae Alive in an Aquarium," *Journal of the Marine Biological Association of the United Kingdom* 5, pp. 176–180

Browne's system proved extremely effective. He started the first plunger jar in the Plymouth laboratory on Sept. 4th, 1899 and 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 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 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." (Browne 1898, p. 179).

By combining observation and tinkering, Browne successfully simulated tidal movement in 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 the tank and other organisms. 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.

3.2 Feeding schedules and requirements

Some 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. Browne fed his jellies copepods (small crustaceans) but suggested that a specialized diet might be required for long term care. Two years after the publication of Browne's paper, Maude Delap, a naturalist and associate of Browne's living on Valencia Island in County Kerry, Ireland, published "Notes on the Rearing of 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 and focused on the diet and feeding schedule of the specimen throughout its lifecycle.

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 because she had been unable to collect food due to foul weather (Delap 1901; McMillan and Rees 1958).

Delap reported her experimentation with feeding regimens for each form. Her article assiduously recorded the food sources, including those 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* (25)." 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." (27) During the mature medusa stage, 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. 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 succeeding six years she published accounts of rearing *Aurelia*, *Pelagia perla* (mauve stinger jelly) and *Cyanea lamarcki* (bluefire jelly), providing detailed descriptions of diet, life cycles, and water temperatures in each subsequent publication (1905, pp. 20–22, 1907).

Delap influenced other investigators interested in extending the life of captive jellyfish. Mary Lebour, a researcher and colleague of Browne's at Plymouth, combined Delap's findings on food sources with Browne's plunger jar to ascertain if certain species actually did consume fishes. Lebour maintained several jelly species in plunger jars (one specimen per jar) and experimented with the diet of each species. Lebour found that many jellyfish do eat fish, especially *Aurelia, Phialidium,* and *Obelia*. She reported that jellies were "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 (Lebour 1923, p. 75, 1922). Lebour noted 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 (Russell 1972).

Although investigators worked out the process of rearing and maintaining certain medusae in the laboratory, the advances in husbandry did not severe the connection of the organism from their environment. The advancements made by Browne, Delap, and Lebour allowed researchers to tinker sometimes successfully with local species with general understandings of the lifecycle and technological and dietary requirements of jellies but it did not provide concrete steps to blackbox the process. Researchers were still required to observe the specimen in its native environment to ascertain normal pulsation rates and to identify the wide array of food sources available; an understanding of local water chemistry and temperature were also important to the long term survival of jellies. Only through these localized observations could experimentalists create systems that worked for species at each separate marine station. While successful experimentalists found it easier to maintain specimens with these technological and dietary guidelines, the experimental jellyfish and the experimentalists themselves were still bound to the marine location around each individual marine station.

4 Pairing location and species: neurophysiology at marine stations

An alternative to developing new technologies or following a rigorous feeding schedule was to find species more amenable to captivity. This section will highlight the two most commonly utilized medusae in neurophysiological investigations between 1895 and 1930: *Gonionemus vertens* (clinger jelly) and *Cassiopea xamachana* (upside down jelly). Found in abundance in Woods Hole, MA and the Dry Tortugas (respectively), these species' physiological requirements (or lack thereof) allowed them to survive in captivity without specialized technology or feeding schedules. However, they were not widely available, and demonstrate the link between place and space in experimental studies at marine stations. Even working with a species with fewer requirements required researchers to travel to

specific locations and become familiar with those environments in order to gather their experimental organisms and work with them effectively.

4.1 Gonionemus murbachii

Gonionemus murbachii was first seen by Louis Murbach at Woods Hole, Massachusetts during the summer of 1894. During that year, a number of small jellies were noticed in the Eel Pond, a shallow tidal salt pond with little water movement on the MBL campus. 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." (1895, p. 494) Murbach initially identified the jelly as *Gonionemus vertens*, a species described by Alexander Agassiz in 1862 in the Gulf of Georgia in Washington State. However, 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."(494) The popularity of this medusa as an experimental organism was enhanced by several variables: availability, limited dietary requirements, and plasticity of captive habitat (Fig. 3).

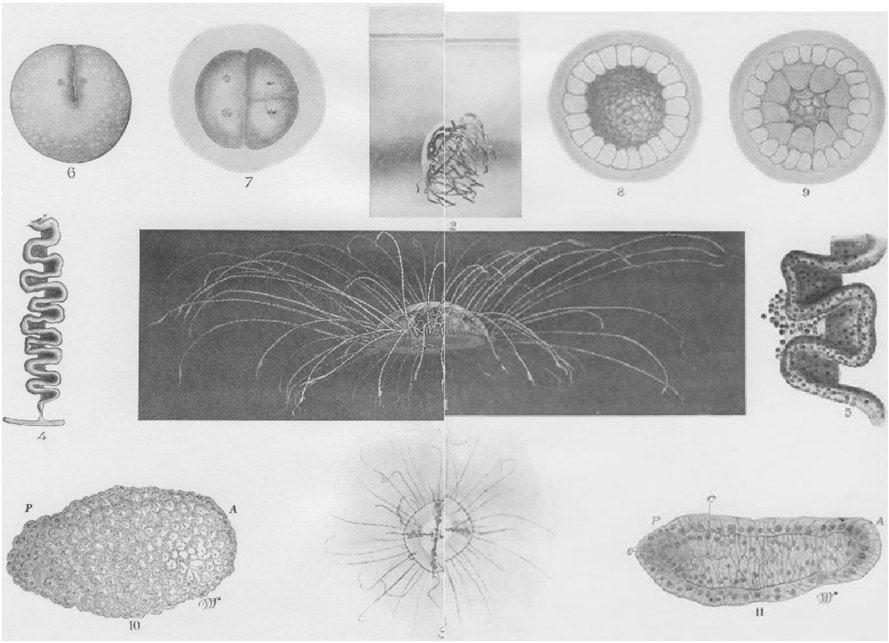

Fig. 3 An image of *Gonionemus murbachii* reviewing development from fertilization to maturity. Henry Farnham Perkins. "The Development of *Gonionema murbachii*" Proceedings of the Academy of Natural Sciences of Philadelphia 54:3 (Sept–Dec. 1902) pp. 750–590

In addition to being abundant, the jellies proved easy to collect. Robert Yerkes, a graduate student interested in behavior and nervous reactions in lower organism and later known for his pioneering work on primate intelligence, 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 (1902, p. 436).

Yerkes also noted that the jelly did not only migrate to the water's surface nocturnally; while many species required collecting at night, *murbachii* was equally available during the daylight hours. Though the adult specimen was abundantly available, planulae 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 sea. Others believed that these stages were either too quickly cycled through or the intermediate forms too minute to be collected by dip netting (Hargitt 1902, p. 28).

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." (1902, p. 436) 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 these jellies to adapt to its captive environment easily and made the species useful for neurophysiological experimentation.

Researchers published brief sketches of their experimental techniques for maintaining these jellies. 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. Yerkes stated that he kept his experimental organisms in "shallow dishes" and "jars" (1903, 1904, 1906). 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) (1909). Morgan, who was interested in testing Hargitt's original assertions about the hardiness 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 2 weeks in "excellent condition." (1899, p. 943).

This species prompted researchers who had previously rejected jellyfish as ill-suited for experimental work to bring them into the laboratory. 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 (1902, p. 28)." 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 (pp. 32–33).

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." (354) Physiologists working at Woods Hole utilized *Gonionemus* for physiological experiments, even though there were at least 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.[4] Because it required little upkeep in the laboratory and was easy to collect, *Gonionemus* became the organism of choice for neurophysiologists at Woods Hole and many researchers worked with the species for multiple seasons.

4.2 Cassiopea xamachana

In 1892, Brooks reported the summer work of the Marine Zoological Laboratory of Johns Hopkins at Port Henderson, Jamaica to the president of the university. Brooks, a morphologists and physiologists at JHU, identified a new jelly 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 collected from 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 stalled after Johns Hopkins relocated their laboratory to another portion of the island due to a yellow fever epidemic (Brooks 1892). 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 species for experimentation. Similar to *Gonionemus*, *Cassiopea xamachana* was easy to collect, had a simple diet, and could survive in a wide range of laboratory environments (Fig. 4).

Collecting *Cassiopea* was an easy process. The species thrived in the shallow waters surrounding the main island of the Dry Tortugas. The moat was shallow enough for wading and unlike *Gonionemus*, individual upside down jellies were

[4] 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.

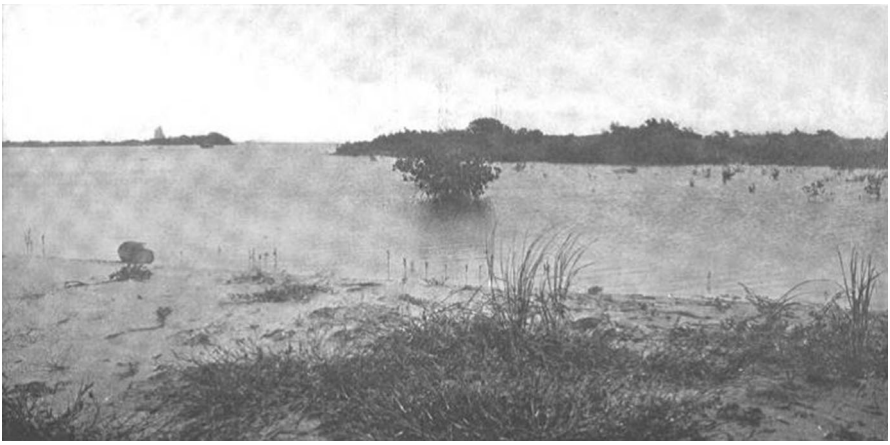

Fig. 4 The "moat" from shore. The photograph is captioned by Mayer as "Where *Cassiopea* Lives". Alfred Goldsborough Mayer (1908) "The Cause of Pulsation" *Popular Science Monthly*, p. 486

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." (1916, p. 3) Collectors chose their desired specimens and then utilized a dip net to gently pick them out of the water for transport to the laboratory. *Cassiopea* were reliably available in all sizes in the moat, meaning that investigators had direct access to the organism and could collect with specificity (Fig. 5).

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 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!" (Series 4 Box 9, Alfred Goldsborough Mayer Papers, Syracuse University: Syracuse, NY) It appears that most researchers took for granted that *Cassiopea* thrived without an apparent food source; it was not until much later it was found that the species hosts zooxanthelle, a symbiotic dinoflagellate, 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 have to deal with a loss of vitality or the byproducts of feeding such as excess of mucous or detritus in the laboratory aquarium (Verde and McCloskey 1998).

Similar to *Gonionemus*, *Cassiopea* thrived in simple 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

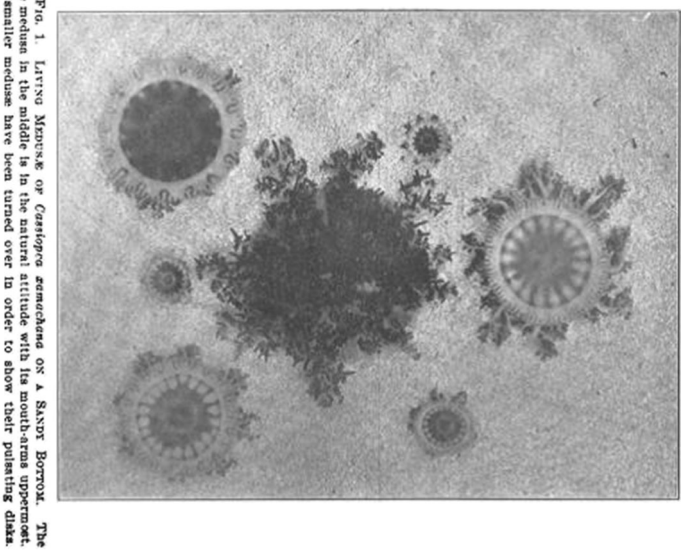

FIG. 1. LIVING MEDUSAE OF *Cassiopea xamachana* ON A SANDY BOTTOM. The large medusa in the middle is in the natural attitude with its mouth-arms uppermost. The smaller medusae have been turned over in order to show their pulsating disks.

Fig. 5 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. Mayer "The Cause of Pulsation" *The Popular Science Monthly* (Dec. 1908), p. 482

> 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. (1916, p. 4).

In addition to not needing water changes, Mayer felt that *Cassiopea* was the best organism on which to study the impact of water temperature and chemistry on nerve conduction rates. 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 suggested it was 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 (Mayer 1914a, b). With no need to feed them, no reason to change the water consistently, and the ability to narrow variables about temperature requirements, *Cassiopea* became a useful species for physiologists.

Finally, *Gonionemus* and *Cassiopea* shared another important trait: they recovered and regenerated throughout multiple mutilation experiments. Loeb and Morgan both performed experiments on *Gonionemus* cut into four parts, Morgan

keeping those mutilated sections for up to 3 weeks in captivity (1899, p. 943). Hargitt states that he knew 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 4 to 6 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. (1904, p. 74).

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 (Mayer 1906, p. 25). 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 (Fig. 6 and 7).

While these species survived and thrived in captivity, they did not disconnect experimentalists from the environments around marine laboratories. Neither species traveled well, tethering experimentation to the coastline. In addition, most experimentalists did their own collecting both because of the ability to choose specific organisms in the field and also the ease of doing so without specialized equipment (especially because of the access without a boat). Finally, these two species were only found close to these two laboratories. This distinction meant that

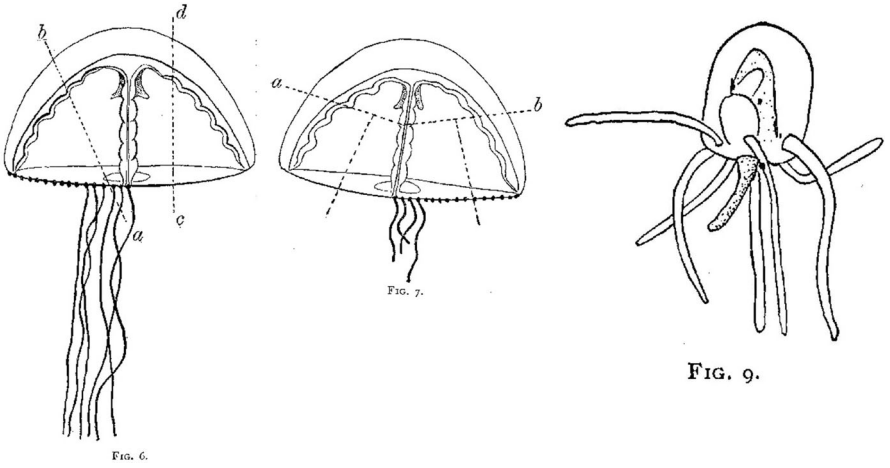

Fig. 6 These three figures appear in Morgan's paper on regeneration in *Gonionemus.* The first two images show the cuts made by Morgan and the third is a drawing of the "regenerated" organism from 1/4 of the original specimen. Its tentacles were malformed but the organism continued to pulsate normally for almost 1 month. T. H. Morgan "Regeneration" *The American Naturalist* (Dec. 1899) pp. 939–951

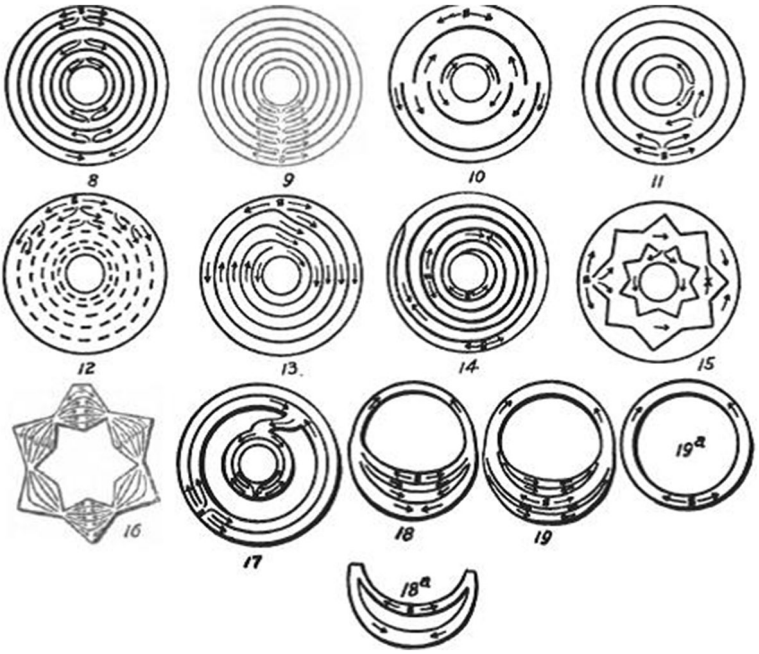

Fig. 7 These are only some of the disks Mayer excised from the umbrellas of the *Cassiopea.* The arrows indicate the direction of nerve conduction through the tissue. Alfred Goldsborough Mayer (1906) *Rhythmical Pulsation of the Scyphomedusae Washington, D.C.: Carnegie Institution of Washington.* p. 25

researchers interested in working with them had to travel to these marine stations to do so. The tethering of research agendas to specific organisms in specific locations resulted in the growth of neurophysiology at these stations in the early twentieth century.

5 Neurophysiology programs built around *Gonionemus* and *Cassiopea*

The MBL and the Carnegie Institution Tortugas Laboratory became centers of neurophysiological research centered on the jellyfish species available in those locations. Neurophysiological experimentation at Woods Hole revolved around *Gonionemus* and its regenerative abilities. Morgan, Loeb, and Hargitt did extensive experimentation in Woods Hole and their work was cited in major studies on neurophysiology; Morgan's work with *Gonionemus* figured heavily in his 1901 book *Regeneration* and neurophysiologists cited this work over the next 20 years (Morgan 1901). At the Carnegie laboratory, Mayer courted young physiologists interested in nerve research. He made a yearly list of researchers to invite to the laboratory, actively recruiting 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* ("Notebooks" undated; unpaginated. Series 4 Box 9, Alfred Goldsborough Mayer Papers, Syracuse University: Syracuse, NY). Mayer, Cary, E. Newton Harvey, and Stockard's work on nerve conduction rates was also widely cited.

Researchers considered jellyfish good experimental organisms for a wide variety of physiological questions. The growth of exercise physiology and the acceptance of the metaphor of the body as a machine resulted in experimentation that sought to optimize that machine. Neurophysiological researchers during this period worked on exercise physiology problems through investigations on the causes of fatigue. In particular, questions about whether fatigue was a mental or physical process, and if physical, by what process did it physically manifest, were questions that those working with jellyfish sought to answer. (Johnson 2009, pp. 127–184) E. Newton Harvey used *Cassiopea* to do fatigue experiments. The ability to cut *Cassiopea* into strips of muscle that could live without requiring food allowed Harvey to test nerve conduction and fatigue over a long period. He placed a ring of jellyfish subumbrella tissue in water and induced pulsation via an electrical current. He found that the muscle contracted, uninterrupted, for 11 days and traveled an estimated 457 miles. Harvey altered water chemistry and found little difference in conduction rates, but did find that the velocity of conduction was greater at night- something he attributed to higher concentrations of oxygen during that period (Harvey 1912). While Harvey did not offer a theory of fatigue based on these findings, his work intersected with the larger conversation surrounding exercise physiology during this period.

Work at these locations advanced understandings of human physiology and directly impacted medical research of the period. At Tortugas, much of Mayer's work sought to produce abnormal pulsations in the jellyfish to ascertain the exact point when mineral imbalance caused musculature failure. Between 1906 and 1922, he performed a series of experiments on nerve conduction in *Cassiopea* by altering the ionization of the water in which they lived using a kymograph[5] to record contractions that would indicate the "weak, exhausted, or pathological character of conducting tissue." (Mayer 1917a, b, p. 5) He tested nerve conduction in untreated cistern and distilled water and found that pulsation declined as conductivity declined, suggesting that nerve function depended on the electrical conductivity of the surrounding medium. Mayer also wanted to find out if different ionization impacted multiple aspects of jellyfish physiology simultaneously (Mayer 1906). In his 1915 notebook, he writes that during the season he will "treat the water with iodine and see if it affects the rate of segmentation with *Cassiopea*. If so, does it also augment the rate of nerve conduction?" ("Notebooks" unpaginated. Series 4 Box 9, Alfred Goldsborough Mayer Papers, Syracuse University: Syracuse, NY) Both Harvey and Mayer's work inspired George Ralph Mines' and W.E. Garrey's work on heart arrhythmias. They repeated their experiments with similar circular sections of heart muscles from a variety of species, including canine hearts and eventually

[5] 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.

used these experiments to develop a successful theory of heart fibrillation (Kass and Clancy 2006, p. 18; Garrey 1914).

Researchers at Woods Hole used *Gonionemus* to test mechanistic theories of muscle contraction and nerve conduction. Jacques Loeb, commonly known for seeking to identify and alter the mechanisms of movement and behavior using lower organisms, experimented with the jelly during summer trips to Cape Cod (Pauly 1987). In 1900, Loeb published two papers on the influence of water ionization on rhythmical pulsations in jellyfish. This work was part of a sequence performed by Loeb to try to determine if it was possible to change the physiological properties of tissue by adjusting the ions in them. Loeb worked primarily with *Gonionemus* and *Fundulus heteroclitus* eggs while graduate students in his laboratory used frog and turtle hearts (Loeb 1902). 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 mineral ions (Na, Ca, K, and Mg) existing in definite proportions in the tissues." (Loeb 1900a, b, p. 383).

Similar to those researchers working at the Carnegie lab, these experimentalists sought to extrapolate jellyfish to higher systems. 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 vinosus, whose ventricle is however free from ganglia but contains scattered ganglion cells. (Loeb 1905, p. 383).

Medical physiologists also took up Loeb's findings. Meltzer and Auer extrapolated jellyfish pulsation to the peristaltic movements of human intestines (Meltzer and Auer 1907; Alvarez 1922).

Jellyfish also proved useful for studying regeneration of the nervous system during this period. 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 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 more severe the injury the faster the organism started regenerating. Extensive experiments with jellyfish able to withstand multiple excisions over a long period of time found mixed results on this question (Hargitt 1897; Morgan 1899; Hargitt 1902; Stockard 1909; Goldfarb 1913).

Extrapolating these studies of nerve trauma became incredibly important during WWI. During WWI, marine stations struggled to contribute to the war effort by donating boats, working on food supply issues, and working on marine safety (Muka 2014, pp. 236–238). In addition, Mayer joined human physiologists in trying to further understand the role of the nervous system in injury and regeneration in returning troops (Lanska 2009). Utilizing *Cassiopea* grown and caged in the moat outside the station, he exploded dynamite at varying distances from the cages. After the explosions, he recorded the physical damage to the bell of the jelly and the time it took to resume normal pulsation rate of each specimen. Finding that even jellies with extensive bell damage eventually resumed normal pulsation, Mayer concluded that shell shock was probably not caused by nerve damage, but by mental trauma and could be cured only through Freudian measures (1917a).

In addition to these clear groups of research questions utilizing jellies, physiologists interested in a wide array of theoretical questions involving the nervous system traveled to these stations. For instance, Robert Yerkes used *Gonionemus* in a group of studies that sought to isolate the mechanism by which organisms receive and process stimuli, specifically taste and tactile stimuli. He exposed jellies to a variety of stimuli, including food sources, chemicals, mechanical, and phototactic stimuli. By touching a pipette to different areas of the jelly, he created a hierarchy of areas of "increasing sensitiveness" finding the exumbrella the least sensitive and the tip of the tentacles the most (1902, p. 444). Yerkes also used *Gonionemus* to study theories of phototaxis (1903, 1904, 1906).

In the end, these neurophysiological programs were short lived. The station at the Dry Tortugas faltered following the death of Mayer. The Carnegie laboratory was extremely difficult to reach, located on an isolated area off the coast of Florida, and vulnerable to hurricanes throughout the research season. The time and expense required to visit the laboratory far outweighed the ease of working with *Cassiopea*. Research, including the neurophysiological work with jellies, was largely sustained through Mayer's enthusiasm. His death in 1922 crippled the station; T. Wayland Vaughn's (Mayer's second in command at the station) move to California to head the Scripps Institution of Oceanography was the *coup de grâce* that led to the closure of the station in 1939 (Ebert 1985; Stephens and Calder 2006). While *Cassiopea* continued to be an organism of interest, especially at public aquaria where it proved to be one of the easiest jellies for public display, work in the academic neurophysiology community declined rapidly upon the collapse of the station.

Experimental neurophysiologists continued to work at the MBL, but moved away from the field and further into the laboratory. 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 with the axons at Woods Hole. While the maintenance of squid in the laboratory proved similarly difficult to that of jellyfish, squid were more widely used in the laboratory. Squid eggs were used by experimental embryologists because of their large, visible life cycles. As juveniles and adults, their axons could be excised and utilized for neurophysiological research. Overall, collection could be done from already deployed collecting boats and required less care than jellyfish

after collection. And finally, the excised flesh of the squid makes a fantastic food for other organisms in the laboratory (Arnold et al. 1974). Even with the difficulty of closing the cycle in the laboratory, the squid quickly rose to prominence as a model marine organism, displacing jellies at MBL. 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 in America and in Europe (Rasmussen 1997; Hodgkin 1992).

6 Conclusion

The neurophysiological research with medusae at marine stations highlights the inextricable link between marine organisms and the environment during this period. At most marine stations, medusae served as an available, if finicky, experimental organism that linked both lab and field. Maintaining jellyfish in captivity forced researchers to emulate the natural environment in the laboratory. Browne, Delap, and Lebour spent hours building understandings of the needs and behaviors of jellyfish and constructing model systems to mimic the environments surrounding marine stations. In this sense, a laboratory filled with jellyfish resembled the surrounding environment. While the technologies and techniques for maintaining a wide variety of jellies worked in the short term, few became reliable experimental organisms. In fact, *Aurelia,* one of the most widely distributed species of jelly, was the only medusa mentioned in later laboratory manuals on easily cultured invertebrates (Lutz et al. 1937, p. 143).

However, even the hardier model species linked the environment and lab. According to Ankeny and Leonelli's definition of model organisms, both *Cassiopea* and *Gonionemus* were model organisms. Both could be reliably kept in the laboratory and could be fashioned into a (somewhat) consistent biological structure by excising the subumbrella and tentacles; regardless of the initial specimen, most researchers worked with a disc of the umbrella, effectively standardizing the organism. In addition, findings were extrapolated to higher organisms and systems including the human nervous, cardiovascular, and digestive systems, suggesting that researchers saw their experiments as illuminative of universal phenomena. While neither was bred in the laboratory or genetically standardized, we can still see the shape of model organisms or systems in the use of these species during this period.

These model organisms still contained environmental constraints. Neither species could be successfully moved inland, meaning that researchers were forced to travel to a specific station to work with these jellies. At those locations, collecting these jellies fell to the experimentalist, meaning that they gained intimate knowledge of the native environment, even if that knowledge was not required to maintain it in the laboratory. Finally, at Tortugas the moat surrounding the laboratory eventually became a laboratory itself when Mayer began monitoring and experimenting on *Cassiopea* in situ.

Studying neurophysiological experiments at early marine stations illuminates a nuanced narrative that complicates the assertion that these spaces were basically mobile university laboratories separate from the seashore. When we delve into the

impact that organism choice had on interaction with the environment, we see that working with jellyfish served to both bring the environment into the laboratory and also to shift the laboratory into the surrounding environment. It is only through closer attention to a wider variety of experimental and model organisms and research programs in these locations that we can truly start to build an understanding of how they operated and shaped current experimental programs.

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