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Marine Biological Stations: 150 years seeking knowledge by the sea

Ibon CANCIO
CBET Research Group, Dept. Zoology & Animal Cell Biology; Faculty of Science & Technology and Research Centre for Experimental Marine Biology and Biotechnology (PiE–UPV/EHU), University of the Basque Country, EMBRC-Spain. Areatza 47, 48620 Plentzia, Basque Country
Corresponding author: ibon.cancio@ehu.eus

Abstract: The "Station Biologique de Roscoff" has reached the age of 150 years in 2022, and a life of science, education, outreach, technology transfer and research service provision across three different centuries does not pass in vain. Many lessons on the necessity of marine biological stations in the periphery of the powerful academic, industrial and political hubs can be extracted from looking back into a history of endurance surfing the waves of technological advances and scientific/political priorities. In the case of Roscoff this occurs in the place where the land ends, in "Finistère". The study of biodiversity for a better understanding of its functioning and for a sustainable utilization of its resources requires addressing the enormous diversity in the coastal areas. For this we have been in the necessity to develop specific skills and dedicated infrastructures permanently placed near the seashores. The study of this biodiversity is in fact the mission of marine biological stations since their conception in the 19th century, as early as 1843, with the "*Laboratoire des dunes*" opened in Ostend, Belgium. By 1910 more than 40 such institutions were working across the European coastal geography and most of them are still active today. Presently, 758 marine biological stations in 98 countries have been catalogued by UNESCO in its 2017 "Global Ocean Science Report". These are institutions that were created to shelter travelling scientists; "rest stop sites" offering visitors access to research equipment, ecosystems, bioresources, trained advice and background knowledge. In this 150-year long journey, marine biological stations have provided avenues for basic science at the forefront of research through the utilization of marine model organisms. In the same way, marine life has provided opportunities to exploit resources useful for the humankind (fisheries, marine aquaculture…), while the development of "Blue Biotechnology" holds the promise to contribute to the socioeconomic development of maritime regions. The analysis of the history of these institutions, their missions and visions, their funding streams and their resilience throughout time provides important learning lessons towards the long-term sustainability of marine biological stations as special Research Infrastructures in the 21st century.

Résumé : *Stations de biologie marine : 150 ans de quête de connaissances au bord de la mer*. La Station Biologique de Roscoff a atteint l'âge de 150 ans en 2022 et une vie de science, d'enseignement, de sensibilisation, de transferts de technologie et de fourniture de services de recherche sur trois siècles ne s'est pas écoulée en vain. De nombreuses leçons sur la nécessité de stations marines en périphérie des pôles académiques, industriels et politiques peuvent être tirées en regardant en arrière une histoire d'endurance à surfer les vagues des avancées technologiques et des priorités scientifiques/politiques. Dans le cas de Roscoff, cela s'est déroulé là où "finit la terre". L'étude de la biodiversité pour une meilleure compréhension de son fonctionnement et pour un usage durable de ses ressources nécessite la prise en compte de l'énorme diversité des milieux côtiers. Pour cela, il a fallu développer des compétences spécifiques et dédier des infrastructures permanentes installées près des côtes. L'étude de cette biodiversité est en fait la mission des stations de biologie marine depuis leur conception au 19ème siècle, dès 1843 avec le “Laboratoire des dunes” ouvert à Ostende, Belgique. A partir de 1910, plus de 40 institutions de ce type travaillaient en Europe et la plupart d’entre elles sont toujours actives aujourd’hui. Actuellement, 758 stations de biologie marine dans 98 pays ont été recensées par l’UNESCO dans son “Global Ocean Science report” de 2017. Ce sont des institutions créées pour accueillir des scientifiques en mission, ces “sites de repos” offrant aux visiteurs un accès aux équipements de recherche, aux écosystèmes, aux ressources biologiques, à des conseils avisés et aux connaissances de base associées. Au cours de ce voyage de 150 ans, les stations de biologie marine ont ouvert des voies pour la science fondamentale à l’avant-garde de la recherche grâce à certains modèles marins. De même, la vie marine a fourni l’opportunité d’exploiter des ressources utiles pour l’humanité (pêcheries, aquaculture…), alors que le développement des “technologies bleues” apporte sa promesse de contribution au développement socioéconomique des régions maritimes. L’analyse de l’histoire de ces institutions, de leurs missions et de leur vision, de leur financement et de leur résilience dans le temps fournit des leçons importantes sur la pérennité des stations de biologie marine en tant qu’infrastructures de recherche au 21ème siècle.

Keywords: Marine biological stations ● Marine bioresources ● Coastal research ● Research infrastructures ● History of science

And in the beginning a laboratory was created where the land ends

Félix Joseph Henri de Lacaze-Duthiers (15 May 1821-21 July 1901) was an influential French professor, a prototypical character in Academia. His research interests were centred on the anatomical investigation of different groups of marine animals, primarily corals, mussels and snails, but also tunicates, brachiopods and other invertebrates (Pruvot, 1902; Dayrat, 2016). In any case, his major contribution to science and his legacy for future generations of scientists and biology students was the founding of two of the oldest and most prominent marine biological stations. One is in the Atlantic Ocean where the tidal range is at its highest and it has celebrated its 150th anniversary in 2022, *Station Biologique de Roscoff* (SBR). It was officially founded in 1872 although Lacaze-Duthiers arrived in the coastline of Normandy and Brittany as early as 1854 and in Roscoff (in Finistère, where the land ends) in 1868 (Dayrat, 2016). He was sampling in Roscoff with a reduced number of students, among them Alfred Giard, before and during the Franco-Prussian war (1870-1871). The other institution he created resembling the first one was instead placed in the Mediterranean, where there is nearly no difference between tides and where the climatic circumstances are different, the Aragó Laboratory, now named *Observatoire Océanologique de Banyuls-sur-Mer* (OOB), founded in 1882 (Pruvot, 1902). 2021 marked the bicentenary of the birth of this character of immense personality and 2022 the 150th anniversary of SBR and the 140th of OOB (Fig. 1).

The first name of the station at Roscoff was “Laboratory of Experimental Zoology” (Pruvot, 1902). Lacaze-Duthiers defended a certain vision of zoology against the physiologists (Paul, 1985), championed by Claude Bernard (1813-1878). Experimental physiology was at the forefront of research and the fashionable discipline of those times, as it occurs with genomics nowadays. In 1872, Lacaze-Duthiers also founded the journal “Archives of Experimental and General Zoology” whose main scientific purpose was to help develop research in experimental zoology (Pruvot, 1902; Dayrat, 2016). The experimental method was central and physiology was not the only discipline in biological research using experimentation and not only observation to explain the wonders of life. Funds were not available for all universities and they were fighting for the financial support allowing the incorporation of qualified academic staff for the new biological disciplines being created (Paul, 1985; Van Bennekom, 2013; Hubbard, 2014). Bernard wanted to understand the unity of life while Lacaze-Duthiers wanted to understand its diversity, a goal that became the mission of most of the marine stations in the last quarter of the 19th century (Paul, 1985; Van Bennekom, 2013). Finally, they both had different views on the role of science in society. While Bernard stood for applied sciences, Lacaze-Duthiers defended the value of basic and theoretical sciences, independent of immediate applications (Paul, 1985).

This conflict between disciplines occurred publicly but in times of war between Prussia and France (1870-1871). This played a major role in Lacaze-Duthiers’s decision to create a permanent marine laboratory. For Lacaze-Duthiers Roscoff was not the ideal place to stablish a permanent marine station, at least not the imagined one. When the war was declared in July 1870, Lacaze-Duthiers was about to send out the first edition

Figure 1. The *Station Biologique de Roscoff* as illustrated in 1891 in the *Archives de zoologie expérimentale et générale* (Vol. 9) and as photographed at low and hide tide in 2022. This is 19 and 150 years after its opening in 1872. The inset photo above shows the caravel that appears in the logo of the institution and that is carved in stone in a building in front of the church of Roscoff.

of his *Archives* and the publication had to be delayed. Lacaze-Duthiers, together with three students, stayed in Roscoff at the *Hôtel du Pigeon Blanc* for most of 1870. He did not go there during 1871 after the Prussian army conquered the city in January to make sure that the *Archives* would be sent on time to the subscribers. However, Alfred Giard (1846-1908), later founder and director of the marine Station of Wimereux (1874), stayed in Roscoff from July to November studying the development of tunicates. Colleagues informed Lacaze-Duthiers about the imminent creation of a marine laboratory in Naples by Anton Dohrn, a Prussian himself (*Stazione Zoologica* Anton Dohrn in Naples (SZN) also celebrated its 150th anniversary in 2022 although it officially opened for visitors in 1874). In early 1872, Lacaze-Duthiers urged the French administration to create a marine laboratory in France and so the Laboratory of Experimental Zoology ran its first season in the summer of 1872 with Lacaze-Duthiers and his student Edmond Perrier (1844-1921), and first external visitors arrived in 1873. The laboratory was first open only from May to October, to become a permanently open working place in 1876 when a villa across the street from the house rented for the laboratory was purchased with help of the French government. In 1877, a fisherman was hired to guard the laboratory, maintain the equipment, and start an official service of delivery of fresh animals during the winter (Pruvot, 1902; Dayrat, 2016). Between 1872 and 1881, 132 researchers visited the coast where the land ends (Dayrat, 2016).

The beginnings of European Marine Biological stations: why marine?

The study of marine biodiversity is the mission of marine biological stations since they were first conceived. The first, rather private, European maritime station was opened in 1843, in Ostend (Belgium) by Pierre-Josef Van Beneden (1809-1894) whose work would be continued, although in a different building by his son Edouard van Beneden (1846-1910) known for having described for the first time the process of meiosis (Hamoir, 2000; Breyne et al., 2010). That first laboratory was called “Laboratoire des Dunes” and was constructed in an oyster house owned by the in laws of P. J. Van Beneden (Kofoid, 1910; Yonge, 1956; Hamoir, 2000; Breyne et al., 2010). The study of marine biodiversity in Ostend was discontinued after the Van Benedens although VLIZ (Flanders Marine Institute) can claim to carry the torch of this first station. Both researchers, the father Professor in the Catholic University of Leuven and the son Professor in the University of Liege, reflect their time and the inflexion point that came with the birth of Biology as

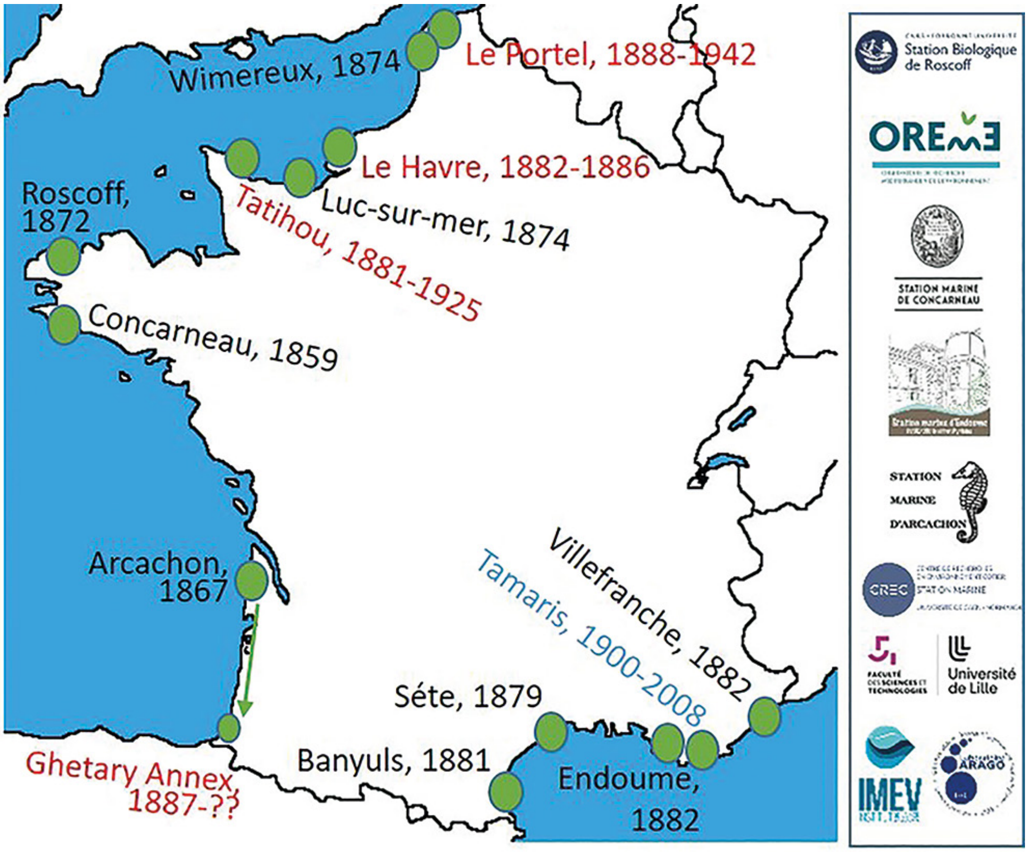

Figure 2. Map of the locations of marine biological stations in France by the year 1910 as published by Kofoid. The ones still open are in black and their logos are depicted. In blue the Michel-Pacha Marine Institute in Tamaris-sur-mer closed due to issues around the ownership of the building is expected to re-open as part of the Universities of Lyon and Toulon. The Arcachon marine station opened an annex in the French-Basque fishing town of Ghetary (Getaria). The ones in red were closed due to bombing during the World War II (Zoological Station of Portel) or dead of the director (Laboratory of Physiology of Le Havre). Part of the functions of the station in the island of Tatihou were retaken by the Dinard Marine Station of the Natural History Museum of Paris in 1935. The present day *Institut de la Mer de Villefranche* (IMEV), is heir of a first French station that was continued by the Russian Zoological Station (University of Kiev) in 1888, to return after being virtually inactive from 1918 to 1931 to be a marine station of the University of Paris in 1932. There was another French station in Algiers opened in 1889. Special mention deserves also the Oceanographic Museum of Monaco opened by Prince Albert I in 1910. Other two stations were mentioned by Kofoid in his book, one in Ambleteuse and the other one in Beaulieu.

a istinct scientific discipline plus the publication of the Evolution Theory in 1859 (Hamoir, 2000; Breyne et al., 2010). Pierre-Joseph was a classical natural historian with a thirst to describe animal forms in coastal habitats (parasites, crustacean and hydroids) and an advocate of fixism while Edouard (although he also systematically described marine fauna in his beginnings) was a convinced evolutionist willing to understand life and its processes (Hamoir, 2000).

The two oldest stations that have remained permanently active are French (Debaz, 2005). The first one was opened in Concarneau, Brittany, in 1859 and the second one in Arcachon, Aquitaine, in 1863 (Kofoid, 1910; Jack, 1945; Yonge et al., 1956; Hiatt, 1963; Egerton, 2014, Tydecks et al., 2016). At the beginning of the 20th century, Charles A. Kofoid (1865-1947), an American zoologist specialist in plankton research, was commissioned by the Bureau of Education of the Department of the Interior of the USA to visit and describe the governance, staff composition, equipment, research focus, ecosystem availability, budget and funding streams of European marine biological stations (Dolan, 2007; Day & Mills, 2012). There were prospects to open and equip similar research stations in USA, specially the Scripps Institution of Oceanography founded in 1903, and they wanted to learn from Europe, the epicentre of marine biological research (Day & Mills, 2012). His report was published in 1910 and he described more than 40 marine stations (he also described stations in continental waters devoted to aquaculture research) spread across the coastal geography of Europe, from Spain to the Russian Arctic and from Greenland to the Adriatic or the Black Seas. Only in the metropolitan France, there were 13 such institutions (Fig. 2), plus another one in Algiers (Kofoid, 1910; Debaz, 2005).

Some marine stations were originally created as personal private achievements by convinced researchers needing access to coastal organisms for their research and that of their students and their colleagues. Those were the cases of the stations of Roscoff and Banyuls-sur-mer (Lacaze-Duthiers in 1872 and 1882), SZN (Anton Dohrn, 1872), Wimereux (Alfred Giard in 1873), the first station in Villefrance-sur-mer in France (Hermann Fol and Jules Barrois in 1882) or Tvarminne in Finland (Johan Axel Palmén in 1900) (Kofoid, 1910). Some were created as independent institutions by science-promoting associations such as the *Société Scientifique d'Arcachon* in Arcachon, the Marine Biological Association (MBA) in Plymouth, the Liverpool Marine Biology Committee in Port-Erin, Isle of Man, the Dutch Zoological Association with a wooden hut that moved along the Dutch geography each year (present day Royal Netherlands Institute for Sea Research), or the Saint-Petersburg Naturalists Society in the Solovetsky islands of the White sea (Kofoid, 1910; Jack, 1945; Yonge et al., 1956; Hiatt, 1963; Egerton, 2014). Also, museums opened their marine outposts (see later). Many of such institutions would sooner or later become associated to large Universities, as it was the case of both of the stations opened by Lacaze-Duthiers (University of Paris), Tvarminne (University of Helsinki), Wimereux (first University of Lille, then University of Paris), Arcachon (University of Bordeaux), Port Erin (University of Liverpool). Others were originally born linked to Universities such as Le Portel, Séte, Endoume (France) or Drobak (Norway) to name some (Kofoid, 1910; Jack, 1945; Yonge, 1956; Egerton, 2014), and still now in Europe and worldwide university affiliation is the norm for around 40% of the biological field stations (Tydecks et al.; 2016).

Some of these marine infrastructures were installed in already existing buildings and originally used as schools, hospitals, lazarettos, castles, boat keeping warehouses, oyster houses or monasteries (Kofoid, 1910). Others deserved purpose-built buildings, this being notably the cases of SZN at Naples, Plymouth MBA or the Oceanographic Museum of Monaco (Kofoid, 1910; Egerton, 2014). Some were merely removable wooden huts or took shelter inside moored and floating vessels that allowed mobility and placement by the particular ecosystem across the country that was dimmed interesting for study each season (Adams, 1996; Dral et al., 1998). At the beginning most were operating only seasonally during the periods in which biodiversity flowered and academics and students were on holidays. Others remained open throughout the year, although in most cases with a very limited number of in-house researchers, technicians and administration staff (Kofoid, 1910; Yonge et al., 1956; Egerton, 2014).

UNESCO mapped a total of 758 marine biological stations in 98 countries in the "Global Ocean Science Report" published in 2017 (UNESCO, 2017). Tydecks et al., catalogued in 2016 a total of 1268 biological field stations in 120 countries (https://geo.igb-berlin.de/ maps/169) although the catalogue is much centred in freshwater biological stations, includes many terrestrial stations linked to National Parks and does not detect many marine stations. Biological stations are many times rest stop sites operating to offer shelter to travelling scientists. In doing so they provide research equipment, access to ecosystems and organisms, tanks with seawater to maintain and rear organisms, trained technical assistance, specialised libraries and background knowledge. Which were the reasons to open such research infrastructures by the sea devoted to science, higher education and outreach in Europe? And, how is it possible that these institutions, some of them born in the 19th century, have survived to the 21st century even when their peripheral situation makes them so expensive to maintain?

In this 150-year-long journey, many marine organisms have been the laboratory models explored at the forefront of research (Boutet & Schierwater, 2021) and this has made a difference. Marine biology was developed through access to coastal ecosystems for research and education. Nobel Prizes in Physiology and Medicine and in Chemistry have been awarded to researchers focusing their studies on marine organisms and working in these coastal stations (Groeben & De Sio, 2006). Today, marine biotechnology and aquaculture are two of the five emerging sectors of the Blue-Growth strategy of the European Commission (Piña et al., 2018).

The analysis on the history and durability of marine biological stations in Europe helps to extract lessons on their sustainability into the future. Marine biological stations are peripheral by definition (geographically, economically, politically, scientifically), many of them dependant of bigger and more central institutions such as Universities, this increasing their unit costs. In spite of that, these marine research infrastructures have shown high resilience and capacity to reinvent themselves.

The main reasons for the implementation of marine stations have been:

1.- *In situ* description and analysis of coastal biodiversity
2.- Diversity of marine organisms in defense of evolution theory
3.- Supply of marine organisms and specimens for museums and for research
4.- Training of professionals for the study of Natural History and Biodiversity
5 - Showing the beauty and importance of nature to the public
6.- Fisheries and aquaculture research
7.- Utilisation of marine organisms as laboratory models in biomedical and biotechnological research

Natural History: biodiversity observation and organism classification in the field

The 18th century brought a new component into exploration in the name of the large Empires (Paul, 1985; Van Bennekom, 2013; Reidy & Rozwadowski, 2014). Exploratory voyages had one main mission, the establishment of new transport routes to access natural resources such as spices in territories across the oceans (Egerton, 2014; Reidy & Rozwadowski, 2014). The surgeons on board were tasked with exploration roles into the natural treasures of the wild world. "Natural History" was part of medical academic studies at a period when science was yet not divided in Biology, Geology, Chemistry, Physics. Examples of such early surgeon explorers with naturalistic passion were those of Philibert Commerson (1727-1773), accompanied by first female circumnavigator and botanist Jeanne Baret (1740-1807), in Louis Antoine de Bougalnville's circumnavigation voyage (1766-1769) or William Anderson (1750-1778) on board of the HMS-Resolution expedition (1772-1775) commanded by James Cook (Bowen, 2015). Later in the 19th century we remember surgeon Robert McCormick, tasked also with the samplings of zoological specimens with help for plants by young botanist Joseph Dalton Hooker (1817-1911), on board of the first "HMS-Erebus" expedition to Antarctica (1839-1843). Thomas Henry Huxley (1825-1895) was the surgeon naturalist on the "HMS-Rattlesnake" (1846-1850) voyage to Northern Australia and New Guinea. Needless is to remember here Charles Darwin (1809-1882) on board of the "HMS-Beagle" (1831-1836) (Reidy & Rozwadowski, 2014; Bowen, 2015)

But one voyage was central in initiating oceanographic research and wide marine biodiversity observation and that was the 1873-1876 Challenger expedition. The mission of the "HMS-Challenger" was the physicochemical and biological exploration of the oceans, with the intention of obtaining information to lay the cables connecting Europe and America through telegraphy (Thompson, 1878; Adams, 1996). This vessel let behind the cannons that her predecessors carried and transported only research equipment and a team of researchers. In their trip they gathered 4717 plant and animal species from different seas of the world (Adams, 1996; Egerton, 2014) that were later analysed in the Challenger Society in Edinburgh by a team of invited international (UK, USA, Germany, Norway, Sweden…) taxon authorities (Adams, 1996). This was the first truly transnational research collaboration effort ever, something that is currently implanted in the foundations of scientific activities. The Challenger expedition had other scientific consequences and through the Challenger Society different collections on the expedition and the specific taxa collected were published along the years (Adams, 1996). It suddenly became evident for the Scottish scientists that worldwide biodiversity analysis meant little without understanding the local one, and the first marine laboratory was established in the UK. This first coastal marine laboratory was paid by Sir John Murray (1841-1914) and placed near Edinburgh inside a moored vessel called "The Ark" in 1883 (Hoyle, 1888; Adams, 1996). This was soon moved to the west coast to the isle of Cumbrae and it was a precursor to the SAMS Institution (Scottish Association for Marine Science) in Millport, currently rooted in Oban in the West coast of Scotland (Adams, 1996).

Collections are an invitation to compare species and a passion to establish relationships was born that would allow ordering nature depending on the similarities and differences among creatures. The Professor of the University of Berlin, Johannes Müller (1801-1858), mentor of some of the most important scientist in Prussian and world history, is considered the father of comparative microscopy and physiological research (Otis, 2007). His research always included the analysis of marine animals and this relied in summer excursions to the island of Helgoland, or to the French and Italian coast, to collect samples (Otis, 2007). The necessary methodological approach he defended was the microscopic analysis of organisms and biological tissues from a comparative perspective. Subsequently, his students would do the same incorporating chemical and biochemical approaches, at the beginning of such disciplines, extending the field of research to comparative embryology and cytology.

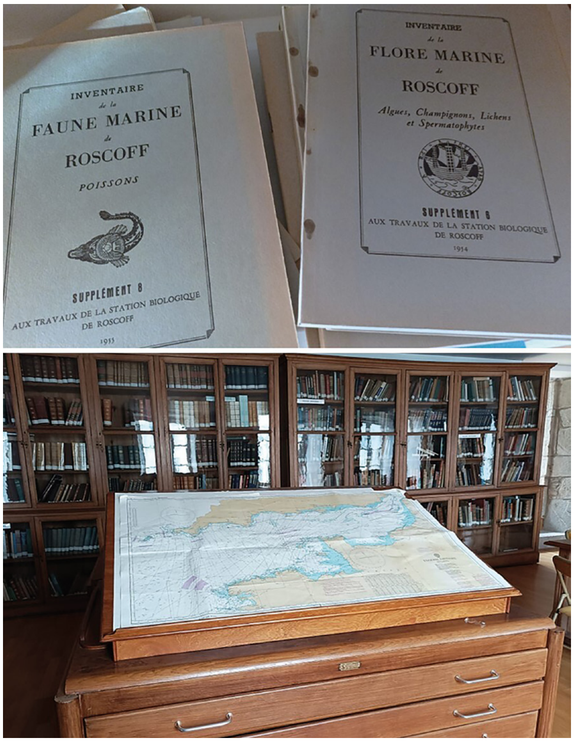

Figure 3. Old library of the Station Biologique de Roscoff as in 2022, with two copies of the years 1954 and 1955 of the Inventory of Marine Fauna and Flora of Roscoff. In the library a map of the English Channel and the coast of Brittany with its large tidal range can be examined.

Indeed, comparative embryology would provide new resources and tools to classify some unclassifiable invertebrates (Fantini, 2000a & b).

These summer excursions to the coast can be considered as scientific tourism. This is the case for example, of the expedition of Ernst Haeckel and Nikolai Miklouho-Maclay to Lanzarote and Morocco, or those of Anton Dohrn, N. Miklouho-Maclay and Élie Metchnikoff to Italy (Webster, 1984; Egerton, 2014). Before stablishing SBR Lacaze-Duthiers constantly visited in summers coastal sampling sites in France and abroad installing a provisional laboratory that he carried on his trips (Dayrat, 2016). Lacaze-Duthiers first visited the Balearic Islands to study molluscs in 1853. In 1854, he travelled from Caen to Saint-Jacut-de-la-Mer on the coasts of Normandy and Brittany for two months. In 1855, he returned to Saint-Jacut, and in 1858, he stayed in Corsica from April to June and in the Balearic Islands from June to August. His trip to Corsica allowed his first dredging studies using the coral dredge to sample corals and other benthic animals. Then a series of expeditions for coral fishing in Algeria followed from 1860 to 1863. The samples collected in Algeria provided the material for his 1864 book on corals, "*Histoire naturelle du corail*", in which he described for the first time the development of hexacorallians and octocorallians. He then visited different sites on both coasts of metropolitan France, Port-en-Bessin and Saint-Quay-Portrieux in 1864, Arcachon and Cette in 1865, and Roscoff in 1868, 1869 and 1870 (Dayrat, 2016). In all cases the same problems emerged; the lack of sampling gear and material, the lack of tools and resources to analyse collected samples, the lack of knowledge about the life cycles of studied organisms and about the ecosystems that were sampled. In summary, a lack of working conditions for biological research.

The first approach to coastal biodiversity was descriptive and it was important to study marine organism close to the place where they live. Marine stations would allow this *in situ* investigation of the life cycles throughout the whole year (Dohrn, 1872; Maienschein, 1988). On the other hand, they guaranteed the possibility to describe coastal ecosystems and to study local biodiversity and the relationships between the different organisms. Thus, scientific journals were created in marine biological stations to describe this biodiversity: "*Fauna und Flora des Golfes von Neapel und der angrenzenden Meeresabschnitte*" in Naples, "*Inventaire de la Flore et de la Faune Marines de Roscoff*" (Fig. 3), "*Journal of the Marine Biological Association of the United Kingdom*" in Plymtouth or "*Bulletin of the Station Biologique d 'Arcachon*" in Arcachon to put some examples. This emphasized the need to open marine stations for the study of unique coastal ecosystems. In this context, examples such as the mega-tidal areas of Brittany (Figs 1 & 3) studied in SBR at Roscoff (1872) can be mentioned, or also the Baltic Sea that is studied in the Tvärminne Zoological Station (1904) and the gateway to the study of the White Sea and Arctic allowed by the station of the Saint-Petersburg Naturalists Society in the Solovetsky islands (1881) and the Murman Marine Station at Alexandrovsk (1899) (Kofoid, 1910; Lajus, 2013).

The Evolution Theory, a revolution for the understanding of life from marine stations

In 1859, the Evolution Theory of Darwin changed not only Biology, but also our way of understanding living organisms and life in general. Darwin was also a marine biologist and dedicated the years after his voyage on board of the Beagle to a monograph on cirripeds, exclusively marine crustaceans (Buchanan, 2017). He published his findings in four books between 1846 and 1854. He used his microscope to analyse specimens that he received at Down house from museums, collections, naturalists, researchers and scholars from around the world.

Researchers studying the diversity of marine invertebrates strongly aligned with the theory. Anton Dohrn (1840-1909), who had been Haeckel's student, was convinced that scientists needed research stations located on the coast to allow such investigations and that would be the mission of SZN in Naples that he constructed with his own money and with help from the Prussian government and friends in 1872 (Groeben, 1985). Darwin congratulated Dohrn on his achievement creating his marine station and contributed with money and with books for its outstanding library. In Dohrn´s vision of marine stations had to form a network of marine observatories as a kind of hostels or train-stations for scientists around the world to visit.He reported so in a meeting of the Association for the Advancement of Science of Great Britain in 1871 (Dohrn, 1872).

SZN would become a hub for scientists all around the occidental world. Anton Dohrn has been called the "Statesman of Darwin" (Groeben, 1985), but he really was a catalyser of scientific progress (Sloan, 1978; Fantini, 2000a; Groeben & De Sio, 2006; Groeben, 2013; Groeben & Forkin, 2013). In a totally privately managed institution he established a table access system. A research table in Naples offered a workplace, equipment, experimental specimens from the Bay of Naples and local knowledge on the nature of the Neapolitan flora and fauna. Each table was rented for the whole year or 6 months by institutions. In 1910, a fee of 500$ was paid for an annual table and 50 tables were rented (Kofoid, 1910). One such table was the "Naples Table Association for Promoting Research by Women" that from 1897 to 1933 allowed research in Naples to 40 American women (Sloan, 1978). The renters of these tables were different European and American Universities, scientific associations and institutions and governments. The annual rent entitled the right to send scientists to Naples to conduct marine research. Dohrn did not supervise the research to be done, and the system resulted in an international climate similar to that of a never-ending congress (Groeben, 1985 & 2013). Visiting researchers were invited to write monographies on different phyla, and their research was published in scientific journals specially created in house. These scientists upon return to their institutions would sent publications available to them in their Universities, helping in the continuous growth of the contents of the library in the station (Groeben, 1985 & 2013). On the other hand, Dohrn was a close friend with Ernst Abbe (1840-1905) and Carl Zeiss (1816-1888) and this made Naples a hub where the microscopy and histological processing techniques that we know today were developed and tested (Zeiss, 2005). This happened at a time when microscopy, physiology and comparative embryology, before molecular biology or genomics, became the fore-front branches of biological research. In SZN 19 Nobel Prize winners in Medicine and Physiology or in Chemistry (1 in Peace, Fridthof Nansen) have been hosted (Groeben & De Sio, 2006).

The antithesis of Anton Dohrn can be observed in Henri Lacaze-Duthiers. In his view marine stations should be open free to all scientists (Dayrat, 2016). In fact, most of the marine stations required no payment for the use of their services. Prussia won the Franco Prussian war and Lacaze-Duthiers would never forgive Prussians such as Dohrn. Therefore, no table would ever be rented by French researchers or institutions (Kofoid, 1910; Paul, 1985). This could partly explain the proliferation of the marine stations in France before 1910 (Fig. 2).

A lot has been written on the correspondence of Darwin with Dohrn (Groeben, 1985), also in relation to the creation of SZN, but those were not the only letters of Darwin in relation to marine stations and organisms. Various letters were also exchanged with Lacaze-Duthiers and Barrois for instance.

In a letter sent to Lacaze-Duthiers in Sept 1872 Darwin wrote:

"I must trouble you with a few lines to thank you for sending me the two papers on the Embryology and Relationship of the Ascidians. I read them with the greatest interest in the Archives to which I am a Subscriber. Some of the expressions in your paper made me believe that you accepted the principles of evolution, and I rejoiced at this."

In a letter sent to Jules Barrois in 1882 Darwin wrote:

"I am very glad to hear of the proposed establishment of a Biological Laboratory at Villefranche. The great scientific results already obtained & the number of Naturalists who have gained experience, in Dohrn's Institute at Naples & in the Laboratories founded by your Lacaze-Duthiers on the shores of France, shows beyond a shadow of doubt how important an aid to Natural Science are these establishments.

Foreigners of every country ought to be grateful for the liberality of the French Government, which is willing that all should profit by their new foundation.

Nor is there any danger of too many Laboratories being founded; for the amount of Scientific Work which has to be done in the several great Invertebrate classes is almost infinite."

The Darwin Correspondence Project:
https://www.darwinproject.ac.uk/

Marine stations to supply marine organisms for museums, universities and researchers

Some marine stations were created as outposts of natural history museums, mainly for the provision of marine specimens. The fever to classify organisms after Carl Linnaeus (1707-1778) grew around museums and there was a shortage of marine biological species among the more than 4000 animals and about 7000 plant species that this first taxonomist classified. The Natural History Museum in Paris and its "*Jardins des plantes*" were founded in 1793. Many scientists in the museum in Paris were keen on the investigation of marine animals, and the Laboratory of Zoology and Maritime Physiology of Concarneau opened its doors in 1859 with a connection to the Museum, and is today one of its official sites open to the public. The same occurred with the Maritime Laboratory of Tatihou in Normandy that closed in 1925. In 2008 the museum got associated to yet another station near Tatihou, the *Station de biologie marine de* Dinard (CRESCO) as a site exclusively for research (https://www.mnhn.fr/en/the-museum-s-sites). Outside France the Marine Laboratory of Trieste (Austro-Hungarian empire at the time), where a young medical student Sigmund Freud (1856-1939) conducted his first investigations on the gonads of the European eel during a stay of several months in 1877, was opened in 1875 to supply marine organisms to the Museum of Vienna (Kofoid, 1910). The present day "Center for Marine Research of the Ruder Boskovic Institute" at Rovinj was established in 1891 as a zoological station of the Berlin Aquarium (Zadovnik et al., 2001). The Bergen Marine Station (1891) was opened in connection to the Bergen Museum (Bock & Helle, 2016), or the Marine Station of Santander (1886) was linked to the Natural history museum of Madrid (Kofoid, 1910). Few know that the Oceanographic Museum in Monaco was created (1910) as a research centre by the Prince Albert I, a marine naturalist himself (Kofoid, 1910).

Marine stations have also collected organisms for shipment to researchers and universities in Europe. When in 1877 a fisherman was hired in SBR to guard the laboratory permanently a service of free delivery of fresh animals started that until 1891 shipped 1,099 boxes in France and abroad with an average of two or three jars per box (Pruvot, 1902; Dayrat, 2016). Recipients only had to pay for the shipping and send back jars and boxes. In Naples, at the Zoological Station methodologies were developed for the preparation of organisms and tissues (for example microscopic slides), with a public catalogue for the supply of samples already available in the 19th century. A similar catalogue of samples was available at the Marine Biological Laboratory (MBL) in Woods Hole, Massachusetts.

Examples of researchers receiving samples for investigations in their own institutions from marine stations are the Nobel Prize winners Fridthof Nansen (1861-1930) and Santiago Ramón y Cajal (1852-1934). Both defended the neuron theory extending the cell theory to the nervous tissue that was considered a reticular system not formed by cells. Nansen´s PhD thesis, presented in Bergen in 1887, was devoted to the central nervous system of various invertebrate and vertebrate marine species, many of them analysed at SZN through a visit in 1886, some of them analysed on samples shipped from Naples for him (Bock & Helle, 2016). Cajal had visited the marine stations of Porto Pi and Santander (Spain) and Banyuls-sur-Mer, later publishing a monograph on the retina and optical nerve centres of cephalopods (Cajal, 1917). His microscopic investigations were carried out utilising cephalopod samples supplied from Santander and Porto Pi (Cajal, 1917), currently part of the Spanish Oceanographic Institute, IEO.

An important part of the beginnings of Cell Biology as the characterization of the secretory function of the Golgi complex and the axonemal structure in flagella and cilia, were based on the analyses by electron microscopy of different species of microalgae by Irene Mantorn (1904-1988). She often analysed microalgae strains isolated and deposited by Mary Park (1908-1989) in the Plymouth MBA Microalgae Culture Collection (Leadbeater, 2004). Marine biological stations hold today some of the most important culture collections of microorganisms (The Roscoff Culture Collection, The Basque Microalgae Culture Collection, the SAMS Culture Collection of Algae and Protozoa, CIIMAR Blue Biotechnology and Ecotoxicology Culture Collection…) and provide specimens for research as one of their main services (https://trace-embrc.eu/).

Marine stations to train and educate professionals: Natural History and biodiversity

Teaching and outreach was the main reason for the creation of the first maritime stations in the United States; training teachers for schools (Benson, 1988 & 1995). Louis Agassiz (1807-1873), considered the father of American zoology opened the first marine summer station on the East Coast of the United States, the Anderson School of Natural History in the island of Penikese in 1873, seed of what later would become the Woods Hole MBL (Dexter, 1980; Zinn, 1980; Maienschein, 1988 & 1989). Summer courses were taught to train Natural History teachers, in order to promote an understanding of nature in schools (Dexter,

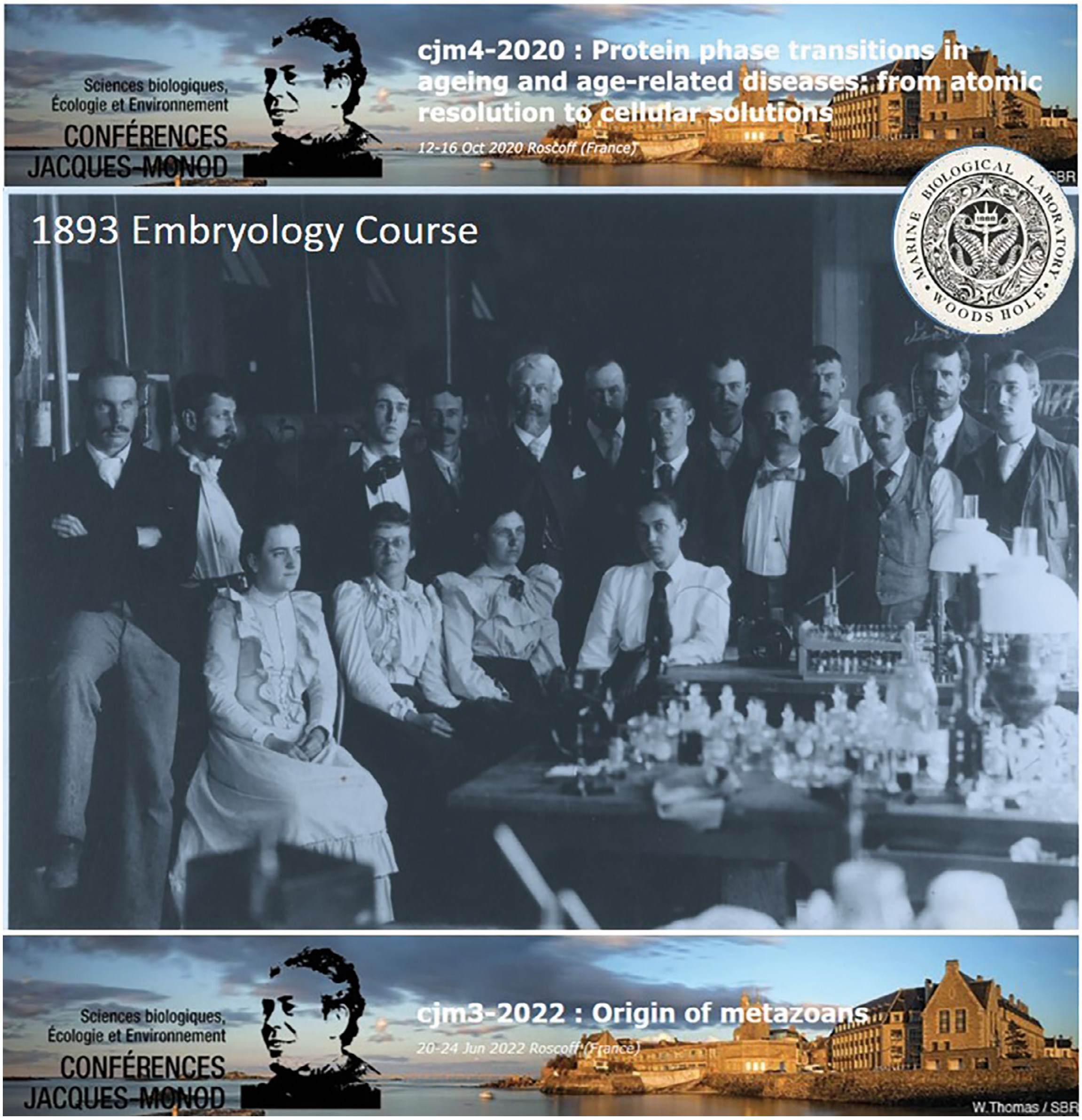

Figure 4. Two examples of the 2020 and 2022 editions of the Jacques Monod Conferences that were initiated in 1988 with a mythic conference and experts gathering on the cell cycle. The central photograph shows the faculty and students of another mythic course, that on Embryology at Woods Hole MBL in its first edition of 1893 (MBL archives, Attribution 4.0 International).

1980; Benson, 1988 & 1995). Some of the greatest figures of the Marine Biology in America took these summer courses in the coast. Among the first students we can even find a future Nobel Prize winner, Thomas Hunt Morgan (Kenney & Borisy, 2009). Afterwards more than 50 Nobel Prize winners have been working in the MBL, stably or as visitors, in research and/or teaching (Maienschein, 1988 & 1989). There was also important participation of women in these first courses at MBL (Benson, 1988 & 1995) (Fig. 4).

In Europe, the primary role of marine stations was research, and the advancement of science. In most cases, and especially in France, the marine stations were institutionally linked with universities combining education with research (Paul, 1985) and contributing not only to undergraduate training but also to laboratory based doctoral studies conducted between the field and the laboratory (Paul, 1985). T.A. Huxley laid the foundations of science education in universities as we know it nowadays, centred on experimental work in the laboratory (Paul, 1985). Basically, sciences transitioned from mere theoretical and descriptive disciplines to become experimental marking the birth of modern Biology. Following such changes Biology became specialised and different disciplines were born: Zoology, Botany, Physiology, Embryology, Cytology, Biochemistry. In this scenario and being the coastal areas, a biodiversity hotspot, laboratories needed to be brought to the coast (Paul, 1985). Huxley became for instance the first president (from 1884 to 1890) of MBA (born 1884) and of its laboratory when it was opened in Plymouth in 1888.

Marine stations have also been deeply involved in lifelong education and training, offering specialized courses (in taxonomy, sampling and other laboratory techniques...), or training workshops for professionals from different fields apart from teachers: fishermen, aquaculture professionals, environmentalists, public servants... (Benson, 1988; Egerton, 2014). Education and training have always been activities that have contributed to the sustainability of marine stations and, additionally, to the socialization of science. More specialised, are the famous summer courses and conferences of institutions such as SBR at Roscoff (Jacques Monod Conferences), SZN at Naples (Advanced phytoplankton and zooplankton courses) or MBL at Woods Hole (Embryology course or Analytical and Quantitative Microscopy Course) to name some (Fig. 4).

Marine stations to share the beauty and importance of nature with the citizenship

The initiation of tourism and the start of weekend trips to the coast can also be traced to the first days of marine biological stations. The rapid expansion of the railway network in Great Britain made the coast accessible to the common public and in a short time it became common in the Victorian society to collect shells and coastal organisms. Then, the first public aquaria were stablished; in London (1853), Paris, Vienna, Berlin or Washington (Rehbock, 1980).

For outreach, it is significant and it deserves highlighting the commitment of many marine stations in Europe to run public aquaria. This is the case of the SZN at Naples, one of the oldest (1872) and most prominent. One of the reasons for the location of the station in Naples was the size of the city and its vitality attracting many visitors to the city throughout the year. For all these people the Aquarium would become another attractive entertainment. Monaco on the other hand, is known for its aquarium. Marine Stations such as those of Arcachon, Plymouth, Port Erin, Helgoland (1892), Varna in Bulgaria (1932) to mention some also opened public aquariums. These aquaria were in many cases the first approach to Marine Biology for the public, and contributed funds for the maintenance of the stations. To visit the “The Ark”, that was the first laboratory of the Scottish Marine Association, one penny was charged per visitor while it was anchored in Port Loy Millport. This helped in the maintenance of the facility, until in 1900 it was swept away by a storm.

The last 20 years, and especially with the inrush of citizen science and public awareness on environmental issues and the oceans, outreach has become one of the major functions of marine stations.

From fish shortage to fisheries research: from plankton to ecology and to biodiversity observatories

In the 19th century there was a vivid debate about the situation of fish and shellfish stocks (Royce, 1988; Lee, 1996; Hubbard, 2014). In Great Britain Edwin Lankester (1847-1929) defended the need to concentrate research efforts to study the life cycles and habitats of fish. He advocated for the creation of a scientific association to supervise such research aided by a coastal laboratory. The MBA was born in 1884 at a meeting of the Royal Society with the aim of promoting scientific research in Marine Zoology and Fisheries (Lee, 1996; Southward, 1996). Plymouth was chosen, due to its coastal biodiversity, for the building of the laboratory on Citadel Hill, opening its doors in 1888 (Lee, 1996; Southward, 1996) 12 Nobel laureates have worked inside its walls.

Fisheries research at its origin, focused on very basic biological aspects such as the study of the life cycles of fish and their reproduction, trophic chains, ecology, and oceanographic conditions that impact stocks (Royce, 1988; Adams, 1996; Lee, 1996, Lajus & Pantiulin, 2012; Lajus, 2013; Egerton 2014; Hubbard, 2014;). First quantitative studies of ichthyofauna were carried out by C.G. Johannes Petersen (1860-1929), first director of the Danish Marine Station (Egerton, 2014). In the investigation of the trophic chains relevant to fish stocks scientists realised about the importance of plankton, especially in the “*Laboratorium für die Intenationale Meeresforschung*” at Kiel, Germany, and such studies contributed to the birth of Ecology as a scientific discipline (Egerton, 2014). The investigation of the dynamics of plankton acquired prominence and annual plankton samplings were widely implemented. Today some of the most extensive historical series of biological data were born with plankton research, and best example is the continuous plankton recorder initiated in 1931 and that now is housed in Plymouth MBA (Vezzulli et al., 2022). The study of the life cycle, reproduction, taxonomy and distribution of copepods, as main component of zooplankton, became central and marine biological stations grew in connection to this mission.

When shortage of fish stocks revealed as an evidence in the end of the 19th century, marine aquaculture was explored as a possible solution in the recovery of marine stocks. Flat fish farming techniques, such as those used today in turbot farming, were developed at the Port Erin Marine Station on the island of Mann, UK (1892-2005) and Tatihou Marine laboratory of the Natural History Museum in Normandy (1889-1925) where flatfish metamorphosis was described.

Through a convention, some European nations decided to implement the International Council for the Exploration of the Seas, ICES, in 1902 (Royce, 1988; Adams, 1996; Lee, 1996; Lajus & Pantiulin, 2012; Lajus, 2013; Egerton 2014; Hubbard, 2014) as an intergovernmental research association to study marine fisheries. Fish stocks are distributed along the territorial waters of different states so their monitoring needs to be approached transnationally. The associated nations needed to contribute with fisheries, biological and oceanographic data so this required the opening of coastal research infrastructures that could guarantee these studies (Royce, 1988; Adams, 1996; Lee, 1996, Lajus & Pantiulin, 2012; Lajus, 2013; Egerton 2014; Hubbard, 2014). For the first time public funds arrived into the already existing marine stations. Consequently, marine stations experienced a growth, both in resources and in the possibilities of hiring new and stable personnel (Paul, 1985; Hubbard, 2014).

At this historical moment, governments realized the importance of scientific research, because "*Scientia potentia est*" (Knowledge is power), largely catalysing the establishment of the national funding mechanisms we know nowadays to finance scientific activities (Paul, 1985; Hubbard, 2014). Most of the research carried out in universities and research centres around the world is based on the use of public funding schemes, for which countries set their research priorities and programs. Marine biological research can be placed playing an important role in the naissance of public scientific funding.

Today plankton research in the era of genomics, coupled to marine microbiome research and environmental DNA analysis, are the fields more tightly linked to technological advances in biology and are central research focus in marine stations in connection to the biomonitoring of environmental health within a context of global climate crisis (Obst et al., 2020; Abreu et al., 2022; Rogers et al., 2022). In general, marine biological stations setting permanent biodiversity observatories are custodians of historical place-based datasets that now need to be made available under the FAIR principles (Findable, Accessible, Interoperable and Reusable).

Marine model organisms for transformative biological science and blue biotechnology

Biomedical research needs to concentrate efforts studies on model organisms. These are bacterial, plant or animal species that are easy to handle, offering possibilities to analyse diverse molecular, cellular, physiological and developmental processes within simplified anatomical structures (National Research Council, 1999; Boutet & Schierwater, 2021). This conceptual revolution emerged during the 19th century and the marine biological stations were at its origin. Recall the importance of comparative physiology or embryology in the shaping of present day biomedical research (Otis, 2007; Fantini, 2000a & b). No embryological explanation can be given without presenting the studies carried out on marine cnidarians, molluscs or echinoderms by Thomas Huxley, Hans Driesch, Hans Spemann, Alexander Kowalevsky, Theodor Boveri; Thomas Hunt Morgan, Ernst Everett Just, Jacques Loeb, …, and in marine stations (Boveri, 1912; Manning, 1983; National Research Council, 1999; Fantini, 2000a & b; Groeben & Sio, 2006; Kenney & Borisy, 2009; Byrnes & Newman, 2014).

Take the fruit fly *Drosophila melanogaster* Meigen 1903, a favourite species in Genetics. It was brought to the spotlight by the Nobel Prize winner (1933) Thomas Hunt Morgan (1866-1945). He was a marine biologist, affiliated from 1890 to 1945 to the Woods Hole MBL (also trustee of the institution), where he carried out his work nearly every summer. He also visited SZN in Naples four times (from 1894 to 1902) and stablished the Kerckhoff Marine Laboratory of the Caltech at Corona del Mar, California, in 1928 (Kenney & Borisy, 2009). He worked with many different species, most of them marine invertebrates from molluscs, to crustaceans or ctenophores and notably echinoderms. He proposed the "Chromosome Theory", as did also Theodor Boveri who used sea-urchins as model species in his eight visits to Naples (Boveri, 1912; Laubichler & Davidson, 2008).

Sea urchins are wonderful model organisms because they produce oocytes easy to obtain and manipulate that are fertilized externally. For example, Otto Warburg (1883-1970) visited Naples five times between 1908 and 1914, and working with sea urchin embryos he would discover a tremendous increase in oxygen consumption upon fertilization (Groeben & Sio, 2006). This oxidative burst is responsible for the formation of the fertilisation envelope. As a result of these studies, his posterior work on cellular respiration was awarded the Nobel Prize in 1931. Warburg´s friend Otto F. Meyerhoff (1884-1951) described the oxidation of glucose and the production of lactic acid in the muscle, obtaining the Nobel Prize in 1922 together with colleague and friend in the distance Archibald Vivian Hill (1886-1977). Meyerhoff contrasted his metabolic studies carried out previously in frogs in the sea urchin in two visits to Naples in 1910 and 1913 (Groeben & Sio, 2006). Hill, who had received training in Plymouth as a fresh graduate would be president of the MBA from 1955 to 1960.

Sea urchins and echinoderms in general have been mainly a fundamental model in the investigation of fertilization. Herman Fol (1845-1892), the first director of the marine station in Villefranche sur Mer with Julian Barrois, observed in a sea star the entrance of a single sperm into an oocyte and one of Ernest Haeckle´s advanced students, Oscar Hertwig (1849-1922), witnessed the same process in sea urchins during a research stay in the Mediterranean coast in 1975. Hertwig described the fusion of male and female pronuclei at the beginning of embryo development underlining the contribution of the nucleus, and the importance of the material it provides, in the development of the embryo. Ernest Everett Just (1883-1941) who developed his entire research career as summer visitor of the marine stations of Woods Hole first, Naples next and Roscoff last described the slow and fast block of polyspermy mainly in echinoderms (Manning, 1983; Byrnes & Newman, 2014) At the beginning of research in Development Biology, August Weismann (1834-1914) discovered in Naples in 1881-1882 that the tissues that produce gametes (germ plasma) develop separately from other pioneer tissues that will produce body tissues.

Another example is the discovery of the proteins that universally command cell cycle progression in eukaryotes in the first years of Molecular Biology. During his first visit to Woods Hole MBL in 1982 Tim Hunt studied the early cell division steps during embryo development in the urchin *Arbacia punctulata* (Lamarck, 1816) and the Atlantic surf clam, *Spisula solidisima* (Dillwyn, 1817). He found cyclins, proteins whose concentrations go through production and destruction cycles prior to mitosis (Hunt, 2004). In his 1991 visit to Woods Hole from Israel, Avram Hershko analysed the dividing embryo cells of the Atlantic surf clam and observed the proteolytic cleavage of cyclins during the cell cycle leading to the discovery of ubiquitins. Hershko obtained the Nobel Prize in Chemistry of 2004 while Hunt obtained the one in Medicine in 2001. Both discoveries can be presented as pioneering and at the origin of the molecular study of cancer.

The most shinning contribution of molluscs to biosciences has been made in the field of neurophysiological research. The giant axon of the squid in the genus *Loligo* was discovered by neurophysiologist John Z. Young (1907-1997) in his work across Woods Hole, Plymouth and Naples. Its large diameter, up to 1.5 mm, allows easy manipulation and experimentation. Nobel Prize, winners (1963 & 1970) Alan Lloyd Hodgkin (1914-1998) and Andrew Huxley (1914-1998) on one side, Bernard Katz (1911-2013) on the other, utilised this structure in their studies on action potentials and neuronal signalling in Plymouth MBA and SZN (Groeben & Sio, 2006; Schwiening, 2012). Sea hares of the family Aplysidae have also provided cutting-edge biological models. Its simple nervous system allows the investigation of sinaptogenesis, synaptic transduction and memory. Eric R. Kandel was introduced to the model in an early career visit to France when he was taken to Arcachon marine station to sample *Aplysia depilans* Gmelin, 1791 (Allport, 2016). Later he concentrated most of his studies *Aplysia californica* J. G. Cooper, 1863 in California, obtaining the Nobel Prize in Medicine in 2000 (Allport, 2016). Other marine model organisms have contributed to important achievements in biomedicine but to summarise we can recall the work done on vision and photoreceptors on fish, molluscs such as *Mya arenaria* Linnaeus, 1758 or the horse shoe crab, Nobel Prize in Medicine 1967.

There are numerous examples of marine organisms that can be used in the molecular and cellular research to understand processes such as aging, stem cell biology and regeneration to just call a couple of examples (Plickert et al., 2012; Boutet & Schierwater, 2021). There is a jellyfish colonial species in the Mediterranean Sea that can be considered biologically immortal, *Turritopsis dohrnii* (Weismann, 1883) (Pascual-Torner et al., 2022). which curiously is named after Dohrn. Under stress their adult phase displays the capacity to return to the immature polyp stage through cell transdifferentiation. There are marine vertebrates such as the whale *Balaena mysticetus* Linnaeus, 1758 that can live for hundreds of years. The genome of this cetacean has been sequenced and this information begins to provide clues of its longevity. For example, an important gene in DNA repair, PCNA, is duplicated in its genome (Keane et al., 2015). Acoela are a small group of worms in the phylum Xenacoelomorpha that live in the sand. *Symsagittifera roscoffensis* (Graff, 1891) performs photosynthesis through strict symbiosis with a unicellular algae, *Tetraselmis convolutae* (Parke & Manton) R.E.Norris, Hori & Chihara, 1980 (Bailly et al., 2014). These worms possess a frontal accumulation of serotonergic and photo- and mechano-receptor neurons that form a primitive brain. Cutting these brains means that the worms lose their borrowing capacity, but their neuroregenerative capacity allows them growing their brain back in 20 days. This may be a wonderful biological model to study neural regeneration in the future (Bailly et al., 2014).

Let us consider more directly applied science, biotechnology. The General Directorate for Maritime Affairs and Fisheries of the European Union (DG-MARE) has identified 5 emerging activities in its Blue Growth strategy. Two rely on biological resources: Marine Aquaculture and Marine Biotechnology (Hurst et al., 2016; Piña, et al., 2018). The OECD also refers to these two activities in their report "Oceans Economy in 2030" (OECD 2016). Marine biotechnology has very diffuse boundaries, but it should engulf any activity using marine biological resources to obtain products or services beneficial to humans. Marine organisms have always provided value-added products. The purple colour, a classical symbol of power associated to kings and cardinals, was obtained from marine gastropods of the Muricidae family extracting the bromoindigo dye that the snails use in their immune protection. In the 19th century a revolution for microbiology was the discovery of agar from red algae for microbe culture in Robert Koch´s laboratory. More recently, we only need to recall the examples linked to light and vision again. Since the enzymatic reactions lead by luciferase-luciferin system responsible for bioluminescence were described in 1877 by Raphaël Dubois (1849-1929), director of the Michel Pacha Institute for Marine Biology in Tamaris-sur-mer, luciferase reporter assays have been developed and extensively used to investigate whether a protein can activate or repress the expression of a target gene (Greer & Szalay, 2002). Among the most used assays we find those based on the use of the luciferases of the sea pansy *Renilla reniformis* Pallas, 1766 or the marine bacteria *Vibrio harveyi* Johnson & Shun, 1936 (Greer & Szalay, 2002). Osamu Shimomura isolated a bioluminescent protein aequorin from the marine hydrozoan *Aequorea victoria* Murbach & Shearer, 1902 that turned out to be the first photoprotein (luciferase) to be isolated. It emits blue light in the presence of calcium (Zimmer, 2009). Another protein co-eluted with aequorin. Instead, this protein fluoresces in green, and it was called the green fluorescent protein (GFP). Osamu Shimomura managed to isolate this fluorescent protein at the University of Washington Friday Harbor Laboratory, during the 1960s and 70s (Zimmer, 2009). Aequorin was used in between the 60s and the 90s as one of the best calcium probes in research. GFP is used in most transgenic analyses, allowing to observe gene expression processes life. This brought a terrible revolution to the investigation of germline cells, to cloning processes, to organ transplants, to neurosciences...and it gave Shimomura its Nobel Prize in chemistry in 2008 (Zimmer, 2009).

Today, and above all, with the possibilities that parallel mass sequencing techniques allow, and the ability to perform multiple screening of biological functions, marine bioprospection has become the last frontier (Newman & Cragg, 2012 & 2014). We look for food, nutraceutical or probiotic products. Think for instance on the benefits of omega-3 fatty acids. We have begun to look at algae as part of our diet. But screening projects look for different specificities in all kinds of molecules and metabolites that can only be found in marine creatures. Some act as immunosuppressants, immunostimulants, growth suppressants, anti-cancer drugs antibiotics or fungicides (Newman & Cragg, 2012 & 2014). We also look for moisturizing compounds, antioxidants or photo-protectors for the cosmetic industry and others (Guillerme et al., 2017). We also look for specially performing enzymes, oligosaccharides, lipids. The options are enormous, because as life initiated in the sea 4 billion years ago Evolution has been playing for a long time there.

There is a huge potential, but the biotechnology industry does not pay too much attention to the sea, in part because marine bioresources are not that easy to access and manipulate. This will be, to a large extent, the new framework to be developed by marine biological stations, and this has been the goal of the European ESFRI roadmap of research infrastructures launching the pan-European research infrastructure "European Marine Biological Resource Centre" (EMBRC, www.embrc.eu). This is an infrastructure disseminated in nine countries, consisting of more than 40 sites, most of them marine stations. The goal is to make marine bioresources and marine biological research accessible to all researchers and industry, offering services for their molecular, cellular and biotechnological utilization, catalysing the Blue biotechnology to be developed in Europe (Piña et al., 2018; Gras et al., 2019).

Conclusions

Learning from the past of marine biological stations, many clues to understand their resilience over the years and learning lessons to underpin their future long-term sustainability can be gained. Oldest marine biological stations were born mainly as a consequence of the personal drive of individual academics/ researchers, sometimes initiating activities as private institutions or most times linked to universities or to naturalist, scientific or fisheries associations.

Marine biological stations, have shown capacity to reinvent themselves along the years and to survive in times of crisis. They have served as places to conduct experimental biological research, to train the trainers, to educate undergraduate and postgraduate students or for outreach and science popularisation. Most marine stations have worked pursuing different aspects of such missions often exploiting the triple helix research/education/outreach as a basic approach to their sustainability. With fisheries ecological research (and historical datasets) was initiated and it brought a first approximation to applied research that included also aquaculture. Marine biological stations have lived in many circumstances linked to small maritime communities where they were stablished, contributing to the socioeconomic development of peripheral maritime areas (Piña et al., 2018; Gras et al., 2019). The promise of the development of the emerging field of "marine biotechnology" it is an opportunity not only for the sustainability but also for the growth and socioeconomic impact potential of these research infrastructures.

Still the United Nations felt the need to call in 2020 for a "Decade of Ocean Science for Sustainable Development (2021-2030)" since marine biodiversity is largely unknown (Rogers et al., 2022). In the last 20 years the marine biological stations have initiated a networking process through associations such as MARS and WAMS to work towards common objectives in marine observation, that finally, and for a subset of European Marine Biological Stations, has resulted in the creation of an ESFRI-roadmap pan-European research infrastructure, EMBRC-ERIC (www. embrc. eu), to offer access to marine ecosystems and advanced biological research platforms and services for marine biologists, administrations and industry (Piña, et al., 2018). The future looks blue ahead of us standing on the shoulders of giants that were before ourselves during the last 150 years.

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