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The seaweed revolution during 150 years at Station Biologique de Roscoff

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Abstract: During 150 years, research at Station Biologique de Roscoff (SBR) has led to breakthroughs in the understanding of seaweed biology, ecology, systematics, biochemistry, genetics, and biotechnology. The possibility in staying in Roscoff to identify seaweed and their biology contributed at the turn of the XIXth century, to the first local flora encompassing more than 500 species. Renowned SBR's visitors pioneered the use of culture techniques to unravel life histories of not only brown algae but red and green seaweed. Others contributed to establish strong knowledge about kelp physiology or calcareous red algae. Since the turn of the XXth century, the increasing number of SBR permanent researchers contributed largely to a transformative period in studies of the evolution and functioning of seaweed groups, associated microbiota and their potential for novel applications, brought by high-throughput 'omic', genetic methods and system biology. The research at SBR has provided major contributions covering the ecosystemic importance of seaweed communities, the origin of algal groups, the holobiont concept and the link between phenotype and genotype, deciphered algal sex determination and explored the roots of algal multicellularity. The use of seaweed for food, feed, nutraceuticals, agro-solutions, green chemicals, or therapeutics was also promoted thanks to the development of glycobiology, 'omics' and microbial tools.

Résumé : *La révolution des macroalgues pendant 150 ans à la Station Biologique de Roscoff.* Pendant 150 ans, la recherche sur les macro-algues marines à la Station Biologique de Roscoff (SBR) a conduit à des percées dans la compréhension de leur biologie, écologie, systématique, biochimie, génétique et biotechnologies. La possibilité de séjourner à Roscoff pour identifier les algues et étudier leur biologie a contribué, au tournant du XIX^{ème} siècle, à la première flore locale regroupant plus de 500 espèces. Les visiteurs renommés de la SBR ont été les premiers à utiliser des techniques de culture pour démêler les histoires de vie non seulement des algues brunes, mais aussi des algues rouges et vertes. D'autres ont contribué à établir de solides connaissances sur la physiologie des laminaires ou des algues rouges calcaires. Depuis le début du XX^{ème} siècle, le nombre croissant de personnel permanents à la SBR a largement contribué à une période de transformation dans les études sur l'évolution et le métabolisme des groupes d'algues, de leur microbiote associé et de leur potentiel d'applications nouvelles, apportées par les "omiques" à haut débit, les méthodes génétiques et la biologie des systèmes. La recherche à la SBR a fourni des contributions majeures couvrant l'importance écosystémique des communautés de macroalgues, l'évolution des lignées d'algues, le concept d'holobionte et le lien entre phénotype et génotype, la détermination du sexe chez les algues brunes et les racines de la multicellularité complexe. L'utilisation des algues pour l'alimentation humaine et animale, les nutraceutiques, les agro-solutions, la chimie verte ou la thérapeutique a également été favorisée grâce au développement d'outils de glycobiologie, « omiques » et microbiens.

Keywords: Seaweed • Genomics • Population Ecology • Genetics • Glycobiology

Introduction

After all, it's an unusual feeling to walk in immense meadows of *Zostera marina* with abundant fruiting bodies; of *Laminaria bulbosa*⁽¹⁾ of which a single spreading frond covers ten square meters and weighs more than fifty kilograms; of *Laminaria saccharina*⁽²⁾ six and eight meters long; *Himanthalia lorea*⁽³⁾ in endless sticky straps, golden yellow... to speak only of the giantess. And harvest superb samples of all the states of fructification of *Porphyra*, *Ceramium*, *Rhodymenia*⁽⁴⁾, *Plocamium*, *Calliblepharis*, *Polysiphonia*, *Delesseria*, *Hydrolapathum*⁽⁵⁾... to name only the most apparent and the most decorative (Chalon, 1898).

The luxuriance of its seaweed fields (Fig. 1) and seagrass beds made Roscoff as an exceptional place for marine plant biodiversity 150 years ago in spite it was not the major object of interest for the laboratory's founder, the Professor Henri de Lacaze-Duthiers, an eminent zoologist of his time (Debaz, 2004). Jean Chalon was not exaggerating as a Belgian botanist who assiduously frequented the Station Biologique between the end of the 19th century and the first decade of the 20th century (Chalon, 1898). These seaweed beds and forests were hosting an exceptional sessile fauna of hydrarians, bryozoans, sponges, annelids and tunicates, as well as hundreds of motile animal species. They were of course contributing to enrich the hard bottoms and adjacent sandy areas with all the material released during their life and decomposition in the wrack line. Scientists like Lacaze-Duthiers, were therefore attracted to Roscoff by this abundant and highly diverse animal life and were just kind to offer some hosting possibilities for botanists (Debaz, 2004).

An historical perspective to understand the current trends in the revolution of seaweed research

When the famous French botanists of this time, Thuret and Bornet were also interested by seaweed biology, they were not sharing the zoologist interest for field marine laboratories and were working independently in Paris or in coastal cities such as Cherbourg where they completed the initial investigation of *Fucus* reproduction demonstrating for the first time the role of the spermatozoids in fertilization (Thuret, 1855). It was therefore women who first showed interest in staying in Roscoff for the long term to identify algae and their biology. Nathalie Karsakoff, a young Russian lady, with her friend Anna Vickers, whose family was familiar with early days of the Station Biologique,



Figure 1. The luxuriance of the kelp associated biodiversity at Perharidy Point in August 2022 showing at the surface of *Sacchoriza polyschides* the colonies of botrylloid ascidians as beautiful as a painting from Mathurin Meheut one century before (credit Hagen Buck-Wiese MPI Bremen).

explored the shores every summer for more than ten years and collected precious samples and microscopic observations at the SBR (Feldmann, 1972). They prepared the first seaweed flora of Roscoff, 70 years before the inventory compiled by Professor Jean Feldmann in 1954.

It was another woman, the so-called Madame Paul Lemoine, who was the first phycologist resident from 1912 to 1913 for research on the anatomy of the red calcareous algae of the *Melobesia* and on the growth rate of these algae and many others (Lemoine, 1913). A theme that was pursued by Jacqueline Cabioch from the 1960s, particularly on the ecology and reproduction of the species constituting the maerl beds. Established permanently in Roscoff with a teaching position, she has trained several generations of young phycologists in the identification and ecology of macroalgae during the traditional Easter courses, then summer schools (<https://www.sb-roscoff.fr/en/marine-flora>).

Another famous phycologist Camille Sauvageau provided essential work on the *Laminaria* J.V. Lamouroux genus from 1916 to 1920. He established novel knowledge on their ecology, and their life cycle alternating the giant thalli with the microscopic generation which ensures the sexual reproduction of the species (Sauvageau, 1916). Work whose reminiscence is still important in the research of Susana Coelho and Mark Cock, on the genetics of sex determination and the life cycles of brown algae (Coelho & Cock, 2020), as well as for Bénédicte Charrier on algal morphogenesis (Charrier et al., 2017). These discoveries were also essential for the

⁽¹⁾ Current accepted name : *Sacchoriza polyschides*, (Lightf.) Batters

⁽²⁾ Current accepted name : *Saccharina latissima*, (L.) C.E. Lane, C. Mayes, Druehl & G.W. Saunders

⁽³⁾ Current accepted name : *Himanthalia elongata*, (L.) S.F. Gray

⁽⁴⁾ Very likely *Palmaria palmata*, (L.) Weber & Mohr

⁽⁵⁾ This name is currently regarded as a synonym of *Delesseria*, possibly another member of the Delesseriaceae



Figure 2. A field campaign of measurements of the emissions of volatile molecular iodine (I_2) during the low tide over a kelp bed dominated by *Laminaria digitata*. The Aurelia research vessel is equipped with a spectrometer that use broadband cavity enhanced absorption spectroscopy to quantify iodine in the gas phase. This site for kelp studies is located at Pointe Sainte Barbe at Roscoff (credit Wilfried Thomas).

possibility of cultivating these algae massively after the second world war in the world's leading production of marine plants in China. Today, the Center for Marine Biological Resources ensures with research teams, the conservation of strains and support for genetic work on European species of kelps (<https://www.embrc-france.fr/en/recherche-et-developpement/marine-biological-resources>).

Following in the footsteps of pioneering workers in coastal ecology, Paul Marais de Beauchamp described the associations of living organisms in the intertidal zone and, in 1914, he published "*Les Grèves de Roscoff*" illustrated by the famous painter Mathurin Méheut, while Louis Joubin mapped in 1909 "The oceanographic distribution of marine plants in the Roscoff area". Research in coastal ecology continued through the work of Marcel Prenant and Pierre Drach who developed the scientific diving after the second world war.

Related to seaweed chemistry and physiology, Paul Freundler initiated work on the accumulation of iodine in *Laminaria* undoubtedly linked to the still flourishing industry of iodine extraction from kelps (Freundler & Menager, 1920). Pierre Dangeard published his work on the emission of free iodine by these brown algae which he named iodovolatilization in the 1930s (Dangeard, 1957). Emitting the hypothesis with the

Swedish botanist Kylin that this phenomenon could be modulated by specific oxidases, this will be confirmed in the early 2000s by Catherine Leblanc's team who have identified the family of genes and specific enzymes in *Laminaria digitata* [(Hudson) J.V.Lamouroux 1813] in a pioneering work on structural biochemistry in brown algae, making it possible to revisit the emission of volatile iodine by brown algae (Fig. 2), its accumulation mechanisms and its importance for the coastal climate (Labarre et al., 2010).

Jean Feldmann not only left an inventory of the flora of Roscoff, but for more than 50 years of research and algological teaching in Roscoff and in France, he contributed to founding a school which has trained a whole new generation of researchers, some of whom, like Yvette Berger-Perrot, settled permanently in Roscoff to study green seaweed taxonomy and life cycles and others were hired in other universities and returned regularly to Roscoff, like Marie-Thérèse l'Hardy-Halos for early work in scuba diving. Susan Loiseaux de Goër, for her part, made a contribution during her doctoral thesis to the study of the Myrionemataceae, tiny crusts of brown algae living on the surface of other algae and *Zostera* leaves. Then she became a pioneer in establishing a first brown algal model for the molecular biology of chloroplasts and mitochondria, the brown alga *Pylaiella littoralis*

[(Linnaeus) Kjellman, nom. cons. 1872: 99 (as 'Pilayella')] during the 1980s, far from Roscoff at Grenoble University (Oudot et al., 2001).

A revolution could be defined as a movement in a closed curve around an axis or a point, real or fictitious, whose return point coincides with the starting point. From the few examples that were described above, the seaweed research history at Station Biologique exemplified how the modern researches have revisited ancient concepts, experiments and theories that were in the roots of the Laboratory.

1980-2000 The Kloareg's school : from the ecosystem to the molecule

Rooted in life history traits and taxonomy, seaweed research has developed markedly at Roscoff during the last 50 years, focusing on brown and red algae and integrating a variety of approaches such as physico-chemistry, biochemistry, molecular and cell biology, as well as genetics and genomics. Since the early 1980's, Bernard Kloareg had already founded a new school of research on the biochemistry and functions of seaweed polysaccharides that is continued today by Cécile Hervé, Elisabeth Ficko-Blean, Gurvan Michel and others that the arrival of Mirjam Czjzek from Marseille

allowed to crystallize in the marine glycobiology team twenty years ago.

Combining biochemical techniques and physico-chemistry, Bernard Kloareg and colleagues established that polyanionic wall components in brown algae are major players in ionic and hydric regulation. One of the characteristics of brown multicellular algae is the abundance (50% or more in dry weight) and variety of extracellular-matrix (ECM) polysaccharides, such as fucans and alginate (Mazeas et al., 2023). Differences in the cation selectivity of alginate and sulfated fucans, combined with their distinct *in situ* localization, are likely to result in gradients of cation distribution throughout the wall (Kloareg et al., 1986). Although the molecular mechanisms involved are unknown, such gradients might confer an adaptive advantage to resist desiccation or osmotic shocks at low tides. The sulfate content of the cell wall polysaccharides in brown algae was also seen as a driving force for species zonation (Mabeau & Kloareg, 1987). Based on their functional properties and biological activities, these poly-anionic macromolecules are instrumental in regulating hydric potential (Kloareg, 1981), in shaping tissue texture and organ morphology as well as in the regulation of development and in innate immunity (Mazeas et al., 2023). This research culminated by the publication of a seminal review entitled: "Structure of the cell walls

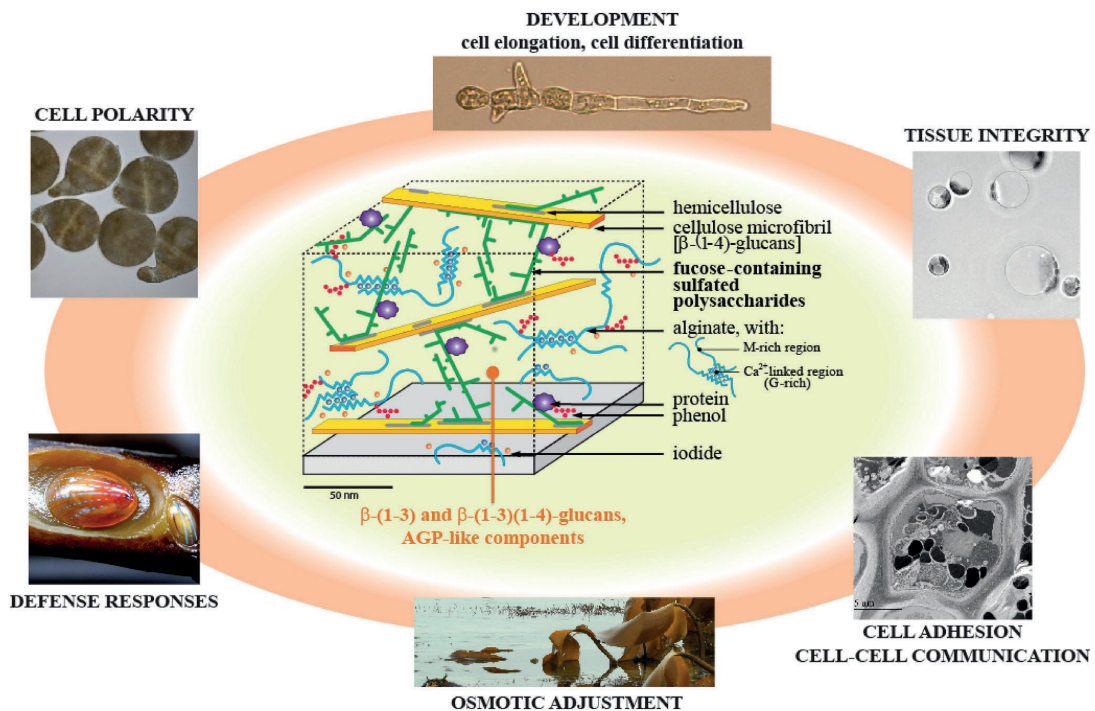


Figure 3. Schematic representation showing the general organisation and key roles played by the cell-wall in brown algae. The cell-wall model for brown algae is shown as the central core of the figure. It is representative of species of Fucales and was initially drawn by Kloareg & Quatrano (1988).

of marine algae and ecophysiological functions of the matrix polysaccharides” (Kloareg & Quatrano, 1988).

In late 1980s, pioneering cell biology approaches to obtain brown algae protoplasts and working on the biochemistry of alginate degradation enzymes from abalone and marine bacteria, Catherine Boyen was preparing the transition from physico-chemistry to cell and molecular biology. Moreover, Erwan Ar Gall published ground-breaking protocols for protoplast isolation in red seaweeds, especially in the red alga *Chondrus crispus* (Stackhouse, 1797) and flow cytometry methods with Dominique Marie to measure seaweed ploidy, DNA content and evaluate genome size (Le Gall et al., 1989 & 1993). A small research group was constituted and with the arrival of Tristan Barbeyron in 1986, trained in microbiology and DNA sequencing at Pasteur Institute and the transfer of Susan Loiseaux de Goër from Grenoble to Roscoff, the team was ready to hire new PhD students and post-docs.

However, when you are a small research group, how can you boost your research potential? Indeed, it should be done through scientific cooperation and fortunately, the support of CNRS to create research networks benefited to the Kloareg’s team including the creation of a network on the genetics and biochemistry of marine macroalgae between 1992 and 2000 involving different biological disciplines from the Universities of Lille and Brest, the Paris Ecole Normale Supérieure, Ifremer Nantes and CERMAV at Grenoble. Other supports were from European Cooperation programs which initiated the first joint project with the Department of Ecology of the Pontificia Universidad Catolica de Chile in 1994 and also, from the translational research of the team which involved applied research on polysaccharides as texturants and oligosaccharides as a booster of the immunity of agronomic plants and seaweed cultivation (see below). Then, the laboratory has grown thanks to new recruits and the attractiveness of Roscoff for established researchers.

Seaweed polysaccharides constitute the major carbon source in coastal ecosystems, recycled by networks of heterotrophic bacteria (Brunet et al., 2022). An ATIPE team was provided to William Helbert in the early 2000s and this research group provided many new structural features for the red algal galactans deploying the expertise of polysaccharide chemistry and structural characterization using Nuclear Magnetic Resonance (Guibet et al., 2007). Research concerning these biomolecules, unique to the marine environment, was based on a dual approach: biodegradation, including the isolation of polysaccharide-degrading bacteria, the purification and cloning of a number of

glycoside hydrolases, the sequencing of the genomes of remarkable polysaccharide-degrading bacteria such as *Zobellia galactanivorans* (corrig. Barbeyron et al., 2001) (Barbeyron et al., 2016) as well as the expression and the biochemical and 3-D structural characterization of polysaccharide-degrading enzymes or operons (Hehemann et al., 2010; Thomas et al., 2017; Ficko-Blean et al., 2017); and biogenesis, mainly the study of the origin and evolution of the ECM constituents (Michel et al., 2010a & 2010b) and their assembly in the cell wall during early development or tip growth (Hervé et al., 2016)

This research axis was parallel of a strong emphasis on the phylogenetic origins of algal lineages and the evolution of organellar genomes (Boyen et al., 2001). The research initiated by Susan Loiseaux de Goër on the model brown alga *Pylaiella littoralis* was continuing by the cloning of chloroplast genes, followed by the sequencing of entire algal mitochondrial and plastidial genomes in red and brown seaweeds (Leblanc et al., 1995; Oudot et al., 2001).

This shift in the molecular biology of brown and red algae catalyzed by Bernard Kloareg was decisive for entering the genomic era in the 2000s.

2000-2010 The movement toward genomics and genetic approaches

Application of genomic approaches to macroalgae can be considered as recent in comparison to other model species. Thanks to a strong integration effort between 2010 and 2020, at the local (3 successive Infrastructure national-regional plans at Roscoff, scientific networks BiogenOUEST and Europole Mer), national (Scientific network Institut de la Génomique Marine) and European level (Network of Excellence Marine Genomics Europe coordinated by C. Boyen), Station Biologique, in collaboration with Genoscope at Evry, has engaged in a number of genome sequencing projects as the leading partner, including the first genome for a multicellular brown alga, *Ectocarpus siliculosus* (Dillwyn) Lyngbye 1819 (Cock et al., 2010), a close relative of large kelp species. Using traditional sequencing techniques, it took 6 more years of an international effort coordinated by M. Cock to assemble and annotate the 200-Mbp genome of *E. siliculosus* (Cock et al., 2010).

Relative to nuclear genome sequences and algal genetics, a strategic move was to propose the filamentous brown alga *Ectocarpus* as a model organism for the brown algal lineage (Peters et al., 2004). The availability of the complete genome sequence of *Ectocarpus* has strongly orientated

the research focus of Station Biologique's teams on brown algae, and has greatly enhanced its visibility and leading position at the international level in the field of the genomics of algae (Brodie et al., 2017). The *Ectocarpus* project has involved the development of molecular, genomic and genetic tools including a large EST collection, whole genome tiling microarrays, EST-based expression microarrays (Dittami et al., 2009), high-throughput small RNA sequencing, mutant screens (Le Bail et al., 2010) and genetic maps (Heesh et al., 2010; Avia et al., 2017). Additional tools being developed at Roscoff include work on genetic transformation and on protocols for proteomic (Ritter et al., 2010) and metabolomic studies (Gravot et al., 2010). These efforts have generated considerable amount of data that provide a comprehensive view of the carbohydrate metabolism of brown algae (Michel et al., 2010a et b), and have shine new light on the secondary metabolism of these organisms (Cock et al., 2010, Meslet-Cladière et al., 2013). It also allowed the development of forward genetics, which allow the identification of structural or regulatory genes based solely on mutant phenotypes (Coelho & Cock, 2020).

Genome sequences also provide large-scale resources allowing the targeting of metabolic pathways or physiological processes amenable for improvement in seaweeds, and this data also represent a rapid and convenient way to identify useful molecular markers, such as microsatellites (Heesch et al., 2010) for the nuclear genome and cytoplasmic markers inferred from mitochondrial or chloroplastic genome sequences (Engel et al., 2004; Voisin et al., 2005., Le Corguillé et al., 2009). Then the Phaeoexplorer project (<https://phaeoexplorer.sb-roscoff.fr/home/>) was initiated in 2016 with the objective of exploring the evolution of biological complexity in brown algae by generating genomic data for a range of more than 40 brown algal species covering all orders of *Phaeophyta* and their closest relatives among *Ochrophyta*.

Another land mark was the completion of the 105-Mbp genome of the red alga *Chondrus crispus*, which features an unusual structure characterized by gene-dense regions surrounded by transposable elements. It displays 9,606 genes and small gene families that contrast with many other lineages which possess more than 20,000 genes. This reference genome sheds light on the biology of red seaweeds, which are key components of coastal ecosystems and are economically important as industrial sources of food and gelling agents (Collén et al, 2013), and now new genomes of Gracilariaceae and Palmariales are released (Lipinska et al., 2023).

This school of molecular biology and genomics was also essential to establish the structural biology

of enzymes active on seaweed carbohydrates with Gurvan Michel and the arrival of Mirjam Czjzek from Marseille to build a whole new research platform in protein crystallography.

From genes to ecosystems

Evolutionary biology and ecology

This need for molecular biology and then genomics for cell biology and structural biochemistry became also essential for work in ecology and evolutionary biology. The skills in population genetics that had made Roscoff famous with the School of Georges Tessier on invertebrates will be rediscovered from the 2000s by the arrival of two women CNRS researchers from the University of Lille, Frédérique Viard and Myriam Valero.

The original interests of the group in Lille was the reproduction biology of the red alga *Gracilaria gracilis* [(Stackhouse) Steentoft, L.M.Irvine & Farnham 1995] (Valero et al., 1992). Myriam Valero together with Christophe Destombe has carried out original work on the evolution of sex in red algae, particularly on the species *G. gracilis*, and she has founded a joint international CNRS laboratory with two Chilean universities which for nearly two decades has been providing very original results on the genetics of the populations of large kelps and agar-producing red algae from the European and Chilean coasts and the consequences of global change and human pressures, including the harvesting of these algae.

Since the 1990s, the team investigated the population structures of *G. gracilis* and of the brown algal kelp *Laminaria digitata*, using the development of microsatellites, a pioneering method in seaweeds (Billot et al., 1998; Luo et al., 1999). At the SBR these research interests broadened to wider phylogeographic analyses, in the Fucales and Laminariales (Olsen et al., 2010; Robuchon et al., 2014), thanks to various European or regional research projects.

Finally, within the general topic of conservation biology, they addressed the case of seaweed domestication, focusing on *Gracilaria chilensis* C.J.Bird, McLachlan & E.C.Oliveira, *Macrocystis pyrifera* (Linnaeus) C.Agardh and *Saccharina latissima* (Valero et al., 2017).

Frédérique Viard focused her research on the topic of introduced species and has produced results of international importance on the population genetics of two seaweeds introduced from Asia, *Sargassum muticum* [(Yendo) Fensholt 1955] and *Undaria pinnatifida* [(Harvey) Suringar 1873] (Wakamé), the latest introduced voluntarily by the Ifremer in Ouessant

in 1984 for cultivation trials (Voisin et al., 2005). This species quickly escaped from cultivation to establish spontaneous populations which today ensure the expansion of this species throughout Europe via the relay of marinas (Guzinski et al., 2018).

This research reminds us of another disturbing event that could have permanently damaged the scientific credibility of the Station Biologique. In 1973, a year after its centenary, the SBR hosted a team of phycologists from ISTPM (Institute of Fisheries which merged in 1981 with CNEXO to form Ifremer). In agreement with the seaweed harvesters and alginate manufacturers, an experiment was carried out to monitor the growth of seedlings of the giant kelp *M. pyrifera* originating from Chile in the channel of the island of Batz (Braud et al., 1974). Under international scientific pressure, these experiments were halted before the very rapidly growing algae developed reproductive structures. This voluntary introduction did not have any negative consequences, but with the hindsight of the last 50 years, it is difficult to understand what could have motivated such choices if not the parallel with other transfer practices, very common in terrestrial and even marine systems as shown with the massive importation in 1970s of the Japanese oyster *Crassostrea (Magallena) gigas* (Thunberg, 1793) to save oyster farming in ruins with the massive mortality of the flat oyster native to European waters *Ostrea edulis* (Linnaeus, 1758). This introduction brought with the oysters, its procession of Japanese invertebrates and species of algae including *S. muticum* (Le Cam et al., 2019) and nearly fifty other species of macro-algae.

Beyond the aspects of conservation of biodiversity and habitats, this work on population genetics provides insight and essential tools for the management of marine protected areas, ecological restoration and the development of sustainable seaweed farming and the design of new vectors of biodiversity such as ports.

In addition, more recently, wider remaining evolutionary questions were addressed by the group of Myriam Valero, such as the hypothesis that the transport of red algal gametes by isopods could be an important mechanism for reproduction because the spermatia lack flagella and otherwise rely on water currents to transport them (Lavaut et al., 2022). This discovery suggests that animal-mediated fertilization could have evolved independently in terrestrial and marine environments and raises the possibility of its emergence in the sea before plants moved ashore.

Ecology of rocky coast ecosystems

The benthic oceanography tradition starting in the 1950s at Roscoff mainly focused on the subtidal soft and hard bottoms of the English Channel but hardly investigate the rocky intertidal and subtidal environments. Thanks to the recruitment of Pascal Riera as an Assistant Professor, and the arrival of Dominique Davout and Aline Migné from the Wimereux Marine Laboratory, the research on the functioning of rocky coast ecosystems benefited of a renewal 20-25 years ago. Combining experimental and/or field approaches, their research investigated the functional diversity of benthic communities, the structure and functioning of food webs and production



Figure 4. *In situ* photorespirometry for direct measurement of primary production in a kelp forest in the vicinity of Roscoff operated by Lydia White (credit Wilfried Thomas SBR).

and the impacts of global and local environmental changes on the functional and structural properties of coastal ecosystems such as kelp forests, rocky bottom macroalgal communities and the communities dominated by calcifying organisms, on biogeochemical fluxes, primary production and the fate of organic matter through the trophic networks.

This research implemented a multiplicity of field and laboratory experimental approaches as well as field observations, including the development of *in situ* benthic chambers to measure benthic metabolism (CO₂ and O₂ fluxes, Bordeyne et al., 2017), mesocosms dedicated to lab experiments (Noisette et al., 2013) as well as the use of stable isotopes to describe trophic networks (Leclerc et al., 2015). More recently, *in situ* photorespirometry provided a more direct measurement of primary production (Fig. 4), unaffected by exudation of dissolved carbon or tissue loss, that can account for sub-canopy and stipe components of the kelp forest, commonly excluded from traditional studies (White et al., 2021). They make it possible to address key-issues on the relationships between biodiversity and ecosystem functioning and on the responses of benthic organisms and communities to the increasing anthropisation of coastal areas and climate change, the most important of which are global warming and acidification. The originality of this latter research led by Sophie Martin is to determine the combined influence of direct environmental impacts on individual species and indirect effects mediated by changes in interspecific interactions to discriminate between the community-level effects of climate change and the more local environmental changes (eutrophication, urbanisation, kelp harvesting) on diversity and ecosystem functioning (Legrand et al., 2017).

Translational research on seaweeds

Applied seaweed research for their uses emerged when, at the end of the 80s, a company from St Malo, *Les Laboratoires Goëmar* (now integrated in the Indian multinational group, UPL) approached SBR seeking help in order to understand why, when spraying seaweed extracts on crops, this promoted disease resistance. *Laminaran*, a structural analog of fungal and oomycete ECM glucan polysaccharides, as well as sulfated fucans, which are homologs of microbial exopolysaccharides, were eventually identified as elicitors of the natural defenses of plants (Klarzynski et al., 2000 & 2003). This led to the development of the first natural defense stimulators to be homologated in Europe as pest biocontrols.

These products, referred to as “Vacciplant”, are now used on ca. one million acres in France and Europe. More generally, it is recognized today that seaweed extracts can act either as Pathogen Associated Molecular Patterns (PAMPs) or as Damage Associated Molecular Patterns (DAMPs), which bind to the Pathogen Recognition Receptors (PRRs) of plants and animals, stimulating their innate immunity. Remarkably, the CNRS fully supported the formal association of SBR with the Goëmar Laboratories, offering more opportunities to dig into the innate immunity systems of the brown algae and the red algae themselves (Potin et al., 2002).

This new line of research clearly showed that cell wall mediate innate immunity in brown algae and red algae (Potin et al., 2002). In *Laminaria digitata*, oligoalginates released from the wall elicit an oxidative burst and activation of defense responses (Küpper et al., 2001). This research culminated in the demonstration that kelps are endowed with both systemic signaling and interplant communication mechanisms (Thomas et al., 2011 & 2014). The oxidative stress is often associated with a massive production of volatile halogenated organic compounds. Their release is catalyzed by haloperoxidases, which oxidize the halide compounds present in the wall (i.e. iodide, bromide and chloride), leading to the halogenation of various organic substrates (Labarre et al., 2010).

In the genus *Ectocarpus*, one strain isolated from a genuine freshwater environment was shown to have retained its ability to grow in normal seawater (Dittami et al., 2012). The transition between high and low salinities is reversible, yet it is accompanied by profound morphological, transcriptomic and metabolic changes. Interestingly, drastic changes in gene expression were observed regarding metabolism of cell wall polysaccharides and phlorotannins (Dittami et al., 2012; Meslet-Cladière et al., 2013).

From the genomes to the socio-ecosystems 2011-2022

With the project IDEALG funded by the Investment for the Future national program (2011-2021) and the European project GENIALG (2017-2021) and many other regional and international projects, the Station Biologique has resolutely turned towards the transfer of its seaweed research to society. In particular, for the management of wild seaweed resources in partnership with professionals with Dominique Davoult's team, but also for the development of seaweed farming for which many biological locks must be lifted and genetic knowledge is in its infancy. The European research



Figure 5. Sharing the seaweed knowledge from the Station Biologique de Roscoff. From left to right: *Algues des Mers d'Europe* (Cabioch et al., 1992); *Algues de Roscoff* (De Goer & Noailles, 2008) et *Alice et la forêt d'algues* (Valero et al., 2018). The background picture presents *Kallymenia crouaniorum* in its subtidal environment at Basse Plate Ile de Batz, a novel species of red alga described in 2009 by Line Le Gall and Marine Robuchon (credit Wilfried Thomas SBR).

infrastructure in marine biology and ecology EMBRC, of which Roscoff is an essential place for algae resources, should sustain all the research efforts undertaken since the creation of the SBR for the next 25 years. But these more finalized projects have also constituted formidable opportunities and a financial support for interdisciplinary research. In particular, the field of systems biology has exploded over the last decade thanks to the decisive contribution of Anne Siegel from the Computer Science Institute of Rennes to provide the tools and mathematical concepts ensuring a reconstruction of the metabolic pathways of algae. At the genome-scale the modeling of the metabolic interactions between an alga and its microbiota can reveal the metabolic complementarity or the contribution of an holobiont to acclimatization or adaptation to stress conditions. Completed with multiple approaches in the acquisition of data on genes, their expression, proteins and products of algae metabolism, but also by lifting a lock on the specific extinction of genes in brown algae by genomic editing, new data are acquired. They will concern in particular the interactions of algae with their physical and living environment. New generations of researchers are

opening these new research frontiers in a sustainable way in Roscoff.

Sharing the Seaweed Knowledge

Research on seaweeds in Roscoff has been widely communicated to the general public through numerous conference events or interventions for school children, but also through the leadership of Jacqueline Cabioch in the publication of the Guide to marine macroalgae of the Atlantic coasts and the Mediterranean (Cabioch et al., 1992). A book for the general public “*Algues de Roscoff*” was also published in 2009, initiated by Susan Loiseaux de Goer and magnificently illustrated with her original photos and those of Marie-Claude Noailles who also provided her line drawings of microscopic details of algal cells patiently drawn during her participation in Roscoff phycological courses for several decades. More recently, in 2017, a beautifully illustrated children’s book was written by Myriam Valero and Christophe Destombe to shed light on the importance of kelp forests in Brittany and Chile for a very young audience. Let’s not forget either the fabulous work of photographic and videographic documentation by the divers Wilfried Thomas and

Yann Fontana, who enriched numerous publications and exhibitions for the general public (Fig. 5).

Conclusion

During the last two decades, the study of algae has undergone a revolution (Brodie et al., 2017), largely due to the development of increasingly sophisticated omics technologies (e.g., genomics, proteomics, epigenomics, and metagenomics), bioinformatics, systems biology, and novel reverse genetic approaches, such as the use of CRISPR-Cas9 for editing their genomes (Badis et al., 2021). Here, I have documented the transformative impact of modern 'omics' and genetics for seaweed research at Station Biologique.

Macroalgal research at SBR has become one of the flagships of the marine station. The study of *E. siliculosus* (Cock et al., 2010) and *C. crispus* (Collén et al., 2013) genomes has paved the way for the establishment of modern algal genetics in *Ochrophyta* and *Rhodophyta*. These approaches can now be used to study fundamental aspects of seaweed biology, such as adaptation and evolution, or to pursue more applied goals, such as the stock improvement of cultivated species or the provision of innovative bioproducts and services.

The Station Biologique currently is likely to represent the largest pool of fundamental research on macro-algae in Europe and probably in the world. Three grants from European Research Council (ERC) were attributed to two women scientists at Roscoff since 2015 indicative of their personal recognition in their field at the national and international level, and of their capacities to run innovative, high-risk projects that open up new avenues in their discipline. A new chair for a Junior Professor was also granted in 2022 by the CNRS to develop a new blue sky project on the molecular basis of tidal rhythms in brown algae. This diversity of approaches and the excellence of its research on seaweed have also brought to SBR an international recognition that has gone beyond scientific notoriety to interest companies in developing new processes, improving knowledge of existing products and developing new applications of algal molecules. Seaweed research at SBR holds the potential for completing the current seaweed industry based on commodities such as polysaccharide ingredients by the development of specialties with higher added value, for aquaculture, plant and animal nutrition as well as health and cosmetics. In particular, through the development of enzyme-based processes to refine the algal biomass, which presided to the

creation of the start-up company Aber Actives in late 2021 (<https://www.aberactives.com/>).

In 2020, the Station Biologique was also recognized by the British foundation Lloyd's Register to ensure the setting up and scientific management of an unprecedented international coalition to develop cooperation on the development of seaweed cultures, their safety for consumers, the environment and respect for the health of workers in the sector (www.safeseaweedcoalition.org). Under the aegis of the United Nations Global Compact (UNGC) Ocean platform, the contribution of Station Biologique is essential to ensure that future decisions will be based on very solid scientific bases, particularly when it comes to enlightening citizens' choices on Nature-based solutions to respond to the climate emergency, ensure global food security and promote the seaweed revolution.

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