ULPGC

Toolkit for seaweed Hatchery operations

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ULPGC
Universidad de Las Palmas de Gran Canaria

I3-4 SEAWEED

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Toolkits for Seaweed Hatchery Operations

Background, Current Practices, and Innovations

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I3-4 SEAWEED

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LIST OF ABBREVIATIONS

AFLP	Amplified Fragment Length Polymorphism
APT	Adenine Phosphoribosyl Transferase
BSA	Bulk Segregant Analysis
COI	Cytochrome Oxidase I
CRISPR	Clustered Regularly Interspaced Short Palindromic Repeats
DMSO	Dimethyl Sulfoxide
DNA	Deoxyribonucleic Acid
FEMS	Federation of European Microbiological Societies
GBIF	Global Biodiversity Information Facility
GBS	Genotyping By Sequencing
GWAS	Genome-Wide Association Studies
IMTA	Integrated Multi-Trophic Aquaculture
ITS	Internal Transcribed Spacer
LSU	Large Subunit
MAS	Marker-Assisted Selection
NGS	Next-Generation Sequencing
PCR	Polymerase Chain Reaction
PES	Provasoli Enrich Seawater
PGR	Plant Growth Regulator
PTFE	Polytetrafluoroethylene
QTL	Quantitative Trait Loci
RAD	Restriction Enzyme-Associated DNA Sequencing
RAPD	Random Amplified Polymorphic DNA
RFLP	Restriction Fragment Length Polymorphism
RNA	Ribonucleic Acid
SBMs	Seaweed Beneficial Microorganisms
SLAF	Specific Locus Amplified Fragment
SNP	Single Nucleotide Polymorphism

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SRAP	Sequence Related Amplified Polymorphism
SSCP	Single Strand Conformational Polymorphism
SSR	Simple Sequence Repeat

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1. SUMMARY

This toolkit provides a comprehensive introduction of the initial phase of seaweed cultivation, during which juvenile algae are obtained and propagated for subsequent production, the hatchery/nursery/seeding/planting or simply **hatchery phase**. It provides a comprehensive overview of the seaweed life cycle, detailing the process of algae propagation in controlled environments prior to their deployment in the production system.

To make this knowledge practical and ready for application, the toolkits will include a set of illustrations for selected seaweed species of economic importance in Europe. The illustrations will present the life cycles of each species and approaches to innovations. In addition, the publication contains fact sheets on hatchery techniques, along with distribution maps. This species-based approach is designed to guide farmers, researchers and entrepreneurs by offering concrete, visual examples they can replicate or adapt.

The document also highlights current tools and methods, as well as promising innovations to make seaweed farming more efficient and sustainable. While the industry is expanding in Europe, many hatchery practices are still underdeveloped. This toolkit supports improvement through six proposed innovations, including lab-based cultivation, the use of natural plant growth regulators, genetic identification, cryopreservation, microbiome enhancement, and biodegradable seeding materials.

A comprehensive European algae company database is available to assist users in exploring potential partnerships, market opportunities and research prospects across the seaweed sector. The establishment of a business in a particular sector is facilitated by the access to a database containing company contact information and activity details.

While the original text was intended for individuals unfamiliar with seaweeds, it also incorporates over 400 references and science mapping for those with more in-depth knowledge, including technicians and scientists.

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2. INTRODUCTION AND BACKGROUND

Concept of the hatchery. The life cycle.

Plants and algae have the capacity for sexual reproduction and vegetative multiplication. The former consists in the mixing of the genetic endowment of a male and a female organism, which requires the production by both sexes of gametes, whose genetic endowment is quantitatively half and qualitatively modified by mixing processes during the formation of the gamete itself.

This process ensures the presence of the necessary subtle variations in the offspring from their parents. The process of gametogenesis involves the reduction and modification of the parental genetic material, which is achieved after a two-stage process of cell reproduction called meiosis (R!). Otherwise, organisms and their cells multiply by a non-reductive process of gene endowment called mitosis (R). Vegetative multiplication is based on this cellular capacity.

In land plants, meiosis for gamete production occurs in one type of individual if it is capable of producing both male and female flowers on the same plant stem (monoecious), or in two types of individuals if each individual produces only one type of gamete (dioecious). Gametogenesis is reduced to one reproductive structure, the flower, which is supported and nourished by the individual.

In the context of multicellular marine algae, the absence of flowers associated with individual organisms is notable. Instead, there are separate, often clearly visible stages (at least one of them) that alternate to complete the life cycle of the organism, producing spores. Overall, the differences between algae and plants can be outlined as shown in Figure 1 (Heesch et al., 2021).

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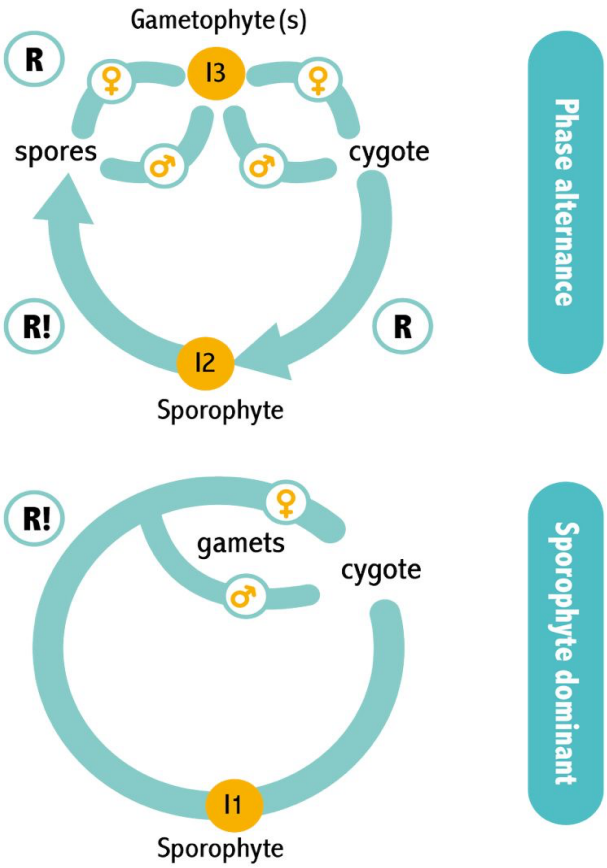

***Figure 1**. Phase alternation and dominance of the sporophyte. In terrestrial plants (below) an individual **I1** sporophyte (with one or both sexes) supports the reproductive organs (flowers) whose gametes fuse to give rise to new individuals. In algae (above) there is no flower-bearing individual, in fact there are no flowers at all, but structures in the **I2**-type individual whose spores form **I3** individuals, which in turn generate the gametes. The different stages are usually free-living and are known as sporophytes (I2) and gametophytes (I3). R! = meiosis; R = mitosis (Heesch et al., 2021).*

The term *"Hatchery"* is very much a word associated with animal production and has been somewhat adopted by the seaweed/plant-based community. In the context of seaweed aquaculture, the early stages of production are critical for ensuring the efficiency and scalability of cultivation systems. These initial phases are often grouped under the general term *"hatchery"* (Table 1), although more precise terminology can help clarify the specific operations involved. Perhaps this community does not always make the association of a hatchery with the cultivation tasks they perform.

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Table 1 *Alternative terms exist for defining the first stages involved in seaweed cultivation that are usually summarised under the term 'hatchery'.*

	Description	Examples
Hatchery (Nursery)	Controlled phase where stages (gametophytes or sporophytes) are obtained and cultured under optimized conditions until they reach a suitable stage for transplantation.	Cultivation of kelp (*Laminaria* spp.) gametophytes in tanks, producing sporophytes for seeding.
Seeding (Planting)	Process of transferring young algae (gametophytes or sporophytes, depending on the species) to the final cultivation environment (e.g., sea farms).	Inoculation of kelp (*Laminaria* spp.) juvenile sporophytes onto ropes for offshore cultivation.

Cultivation of algae consists of the mass production of one of the stages, the sporophyte or gametophyte, which can be obtained by vegetative multiplication or after total or partial completion of the life cycle. Hatchery operations therefore consist of obtaining, maintaining and propagating to juvenile stages the propagules that will then be cultivated, in-shore or off-shore, until algal biomass is obtained. Seeding operations consist of the implantation of these propagules in a substrate for transfer to the culture area.

Science Mapping seaweed aquaculture/ cultivation/ hatchery/ seeding.

Scientific mapping applied to the field of macroalgae cultivation (“macroalga AND cultivation”) makes it possible to visualise the evolution of knowledge around key concepts such as "hatchery" and "seeding". A timely bibliometric analysis (years 1980 to 2025), based on 360 scientific publications indexed in Scopus and conducted following the methodology described in Chapter 8, identified 10 major thematic clusters. Among them, Seeding and Propagation emerge as sub-themes directly related to macroalgal production and establishment, while Algal-Growth acts as the central node articulating the knowledge map.

The seeding category represents research focused on the seeding or inoculation of macroalgae in cultivation systems. It includes techniques such as spore attachment to ropes, nets or artificial

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substrates, which are essential for the establishment of sustainable crops on a commercial scale. Although this topic has a lower density and centrality in the knowledge network - suggesting that it is still developing or seeking consolidation - its connection to areas such as genetics and physiology indicates its growing importance. References to the topic 'Hatchery' are scarce as specific papers on hatchery are barely found (interesting to note that the term 'seeding' is frequently employed as a keyword).

The mapping shows that themes such as Propagation and Genetics provide specialist knowledge, while Environmental impact and Nutrients provide the ecological context necessary to understand the dynamics of seeding and growth. Algal production is therefore a complex system involving both internal factors (reproductive biology) and external factors (environmental conditions). This analysis highlights the necessity to integrate molecular, physiological and culture techniques in the design of more efficient hatcheries, in line with sustainability and bio-economy objectives (Figure 2).

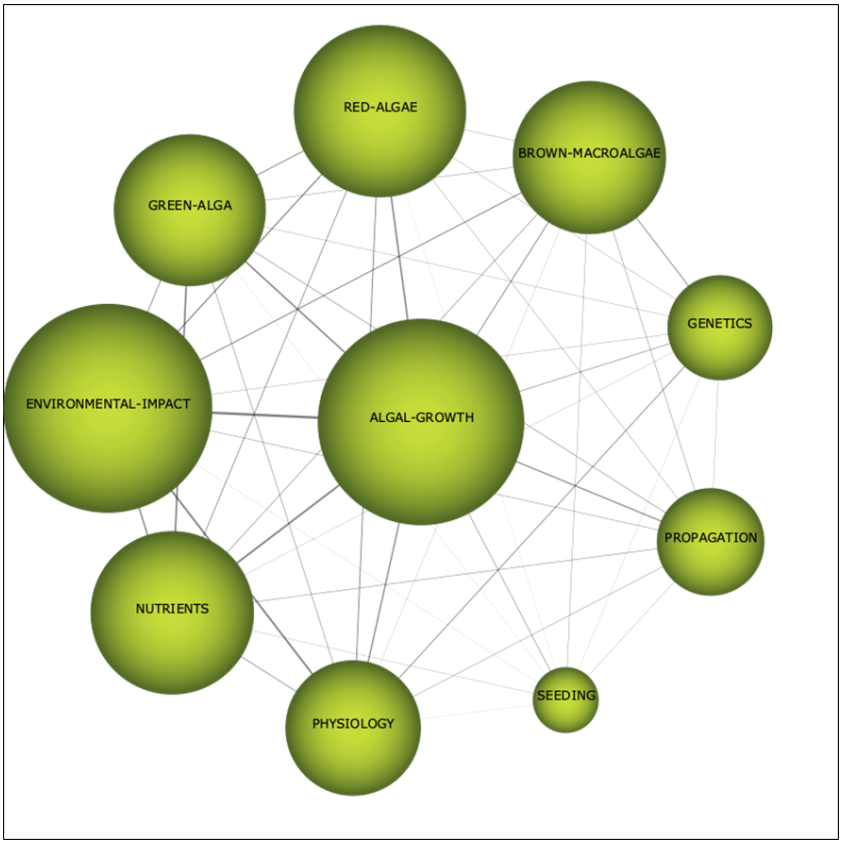

***Figure 2**. Science mapping hatchery/ seeding and conceptual network. Hatchery/seeding has a lower density and centrality in the knowledge network, suggesting that it is still developing or seeking consolidation, its connection to areas such as genetics and physiology indicates its growing importance.*

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3. MAPPING OF EUROPEAN ALGAE COMPANIES: A STRATEGIC RESOURCE FOR SECTORIAL INSIGHT AND COLLABORATION

We have developed a comprehensive and up-to-date mapping of European companies operating within the seaweed sector, covering the entire value chain—from seaweed production to applications in food, cosmetics, and biofertilizers. The dataset has been compiled using a rigorous methodology, combining information from existing databases with targeted manual searches. This approach has enabled both the validation and expansion of the available information.

The databases consulted for the development of this resource include:

- **The European Business Register**: https://e-justice.europa.eu/topics/registers-business-insolvency-land/business-registers- search-company-eu_en
- **The European Commission's "Knowledge for Policy" platform**, specifically the section "Bioeconomy in Different Countries" from which two datasets on the algae industry in Europe were extracted. These datasets cover macroalgae, microalgae, and spirulina; however, a filtering process was applied to retain only data related to the macroalgae industry (Vazquez-Calderon et al., 2022). https://knowledge4policy.ec.europa.eu/visualisation/bioeconomy-different-countries_en
- **Phyconomy Database**: https://phyconomy.net/database/
- A review of companies participating in international conferences such as **Seagriculture**: https://seagriculture.eu/

The primary objective of this initiative is to provide a clear overview of the sector and to facilitate strategic connections between existing stakeholders and new entrants interested in engaging with the algae-based bioeconomy. By identifying active companies and the specific algae species they utilize, this tool aims to enhance visibility, foster connectivity, and strengthen investment opportunities within this rapidly evolving industry.

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The resulting database PhyCo[1]. is publicly accessible at www.phyco.ulpgc.es. It has been designed to be highly user-friendly (Figure 3). Users can retrieve information, either by company name or by algae species through dropdown menus, which helps to avoid typographical errors—a common issue given the complexity of accurately spelling scientific species names. This feature significantly improves accessibility for a broad audience, including investors, industry stakeholders, and users unfamiliar with scientific nomenclature or foreign company names. The database supports a wide range of applications, including market research, partnership development, technological scouting, and policy design.

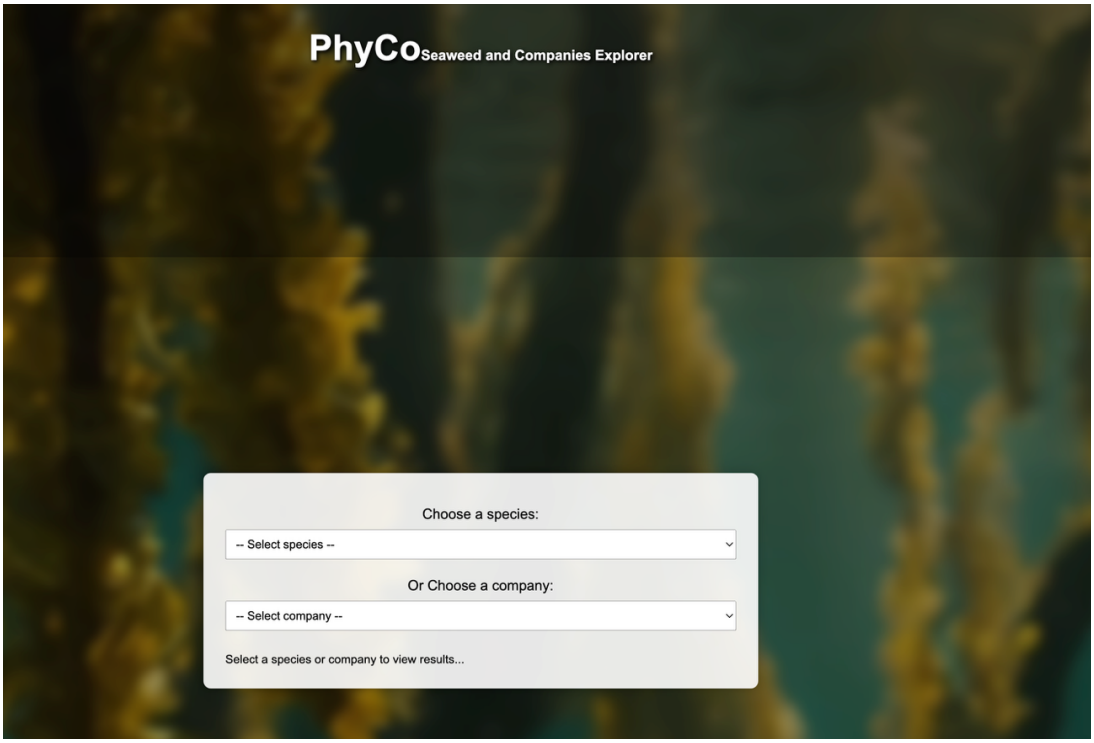

Figure 3. *Frontpage of the European Companies in the Seaweed Sector Database. Publicly accessible at www.phyco.ulpgc.es*

This DATABASE aims to be a valuable tool for stakeholders seeking to understand, invest in, or contribute to the sustainable growth of the European algae sector

[1] **Phyco-"** is a prefix used in scientific terms related to algae (like *phycology*, the study of algae), it comes from **"*Phykos*" (φῦκος)**, the ancient Greek word that means "seaweed" or "alga. The name of the database combines phyco or seaweeds with Co., the abbreviation of company.

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Functionality and Search Options

The type of output depends on the search criteria. When searching by species (Figure 4), the results include:

A brief general description containing: **Genus**; **Colour** (following the traditional classification of macroalgae, even if not taxonomically precise); **Common name**; **Number of Companies** operating with that species in Europe.

Following this summary, a detailed list of companies is displayed including **Company name**; **Country**; **Website; Value Chain; Production Process; Industry** (**Applications**); **Subsector**.

Resultados para la especie: Alaria esculenta

Genus: Alaria
Color: Brown
Common name: Winged kelp
Number: 25

Empresas asociadas:

Company	Headquarters	Continent	Website	Value Chain	Production Process	Industry (Applications)
Alaria AS / Seaweed AS	Norway	Europe	https://www.seaweedfromnorway.no/	Farming & harvesting	Wild harvesting	Food
AlgAran	Ireland	Europe	https://www.seaweedproducts.ie/	Farming & harvesting,Applications	Wild harvesting	Food,Personal care
Algenladen GmbH	Germany	Europe	www.algenladen.de	Distribution		
Arctic Seaweed	Norway	Europe	https://aseaweed.com/	Farming & harvesting	Aquaculture	
Atlantic Mariculture Scotland (Tangled Greens)	UK	Europe	https://tangledgreens.co.uk/	Farming & harvesting,Applications	Aquaculture	Food,Plant & soil nutritio
C-weed Aquaculture	France	Europe	https://www.c-weed-aquaculture.com/	Farming & harvesting,Applications	Aquaculture,Offshore	Personal care,Food
Donegal Bay Seaveg	Ireland	Europe	https://organicseaweedireland.com/	Farming & harvesting	Wild harvesting	
Eat Seaweed	UK	Europe	https://www.eatseaweed.co.uk/	Farming & harvesting,Applications	Wild harvesting,Aquaculture	Food
Hortimare	Netherlands	Europe	https://www.hortimare.com/	Breeding & propagation,Consulting	Aquaculture	
Kelpinor	Norway	Europe	https://www.kelpinor.no/	Farming & harvesting	Aquaculture	
Little Samphire Island	Ireland	Europe	https://www.littlesamphireisland.com/	Farming & harvesting	Wild harvesting,Aquaculture	
Lofoten Seaweed	Norway	Europe	https://lofotenseaweed.no/	Farming & harvesting	Wild harvesting	Food
Ocean Forest (Lerøy Ocean Harvest / Maer)	Norway	Europe	https://www.leroyseafood.com/en/sustainability/ocean-harvest/	Farming & harvesting,Applications	Aquaculture,IMTA	Food
Ocean Rainforest	Faroe Islands	Europe	http://www.oceanrainforest.com/	Farming & harvesting	Aquaculture,Offshore	
Plant Ecology Beyond Land (Pebl)	UK	Europe	https://www.plantsbeyondland.com/	Breeding & propagation,Infrastructure & equipment	Aquaculture	
Quality Sea Veg	Ireland	Europe	https://qualityseaveg.ie/	Farming & harvesting	Wild harvesting	Food
Seaweed Farming Scotland	UK	Europe	https://www.seaweedfarmingscotland.com/	Farming & harvesting	Aquaculture	
Seaweed Solutions	Norway	Europe	http://www.seaweedsolutions.com/	Farming & harvesting,Applications,Infrastructure & equipment,Breeding & propagation	Aquaculture,Offshore	
Tango Seaweed AS	Norway	Europe	https://www.tangoseaweed.no/	Farming & harvesting	Aquaculture	Food
TARI	Faroe Islands	Europe	https://tari.fo/	Farming & harvesting	Aquaculture	Food
Tekslo Seafood (Sjosaker)	Norway	Europe	https://teksloseaweed.no/en/	Applications,Farming & harvesting	Wild harvesting	Food,Personal care
The Irish Seaweed Company	Ireland	Europe	https://irishseaweed.co.uk/	Farming & harvesting	Wild harvesting, Aquaculture	Food
Ting med Tang	Norway	Europe	https://tingmedtang.no/	Farming & harvesting	Wild harvesting	
West Algues	France	Europe	http://www.westalgues.fr/	Farming & harvesting	Wild harvesting,Aquaculture	
Zeewaar	Netherlands	Europe	https://www.zeewaar.nl/nl/	Farming & harvesting	Aquaculture	

Figure 4. *Example of a species-based search result for Alaria esculenta.*

The database also features an interactive map (Figure 5), which displays the geographical distribution of companies by country. By clicking on each country, users can view the list of companies working with the selected species.

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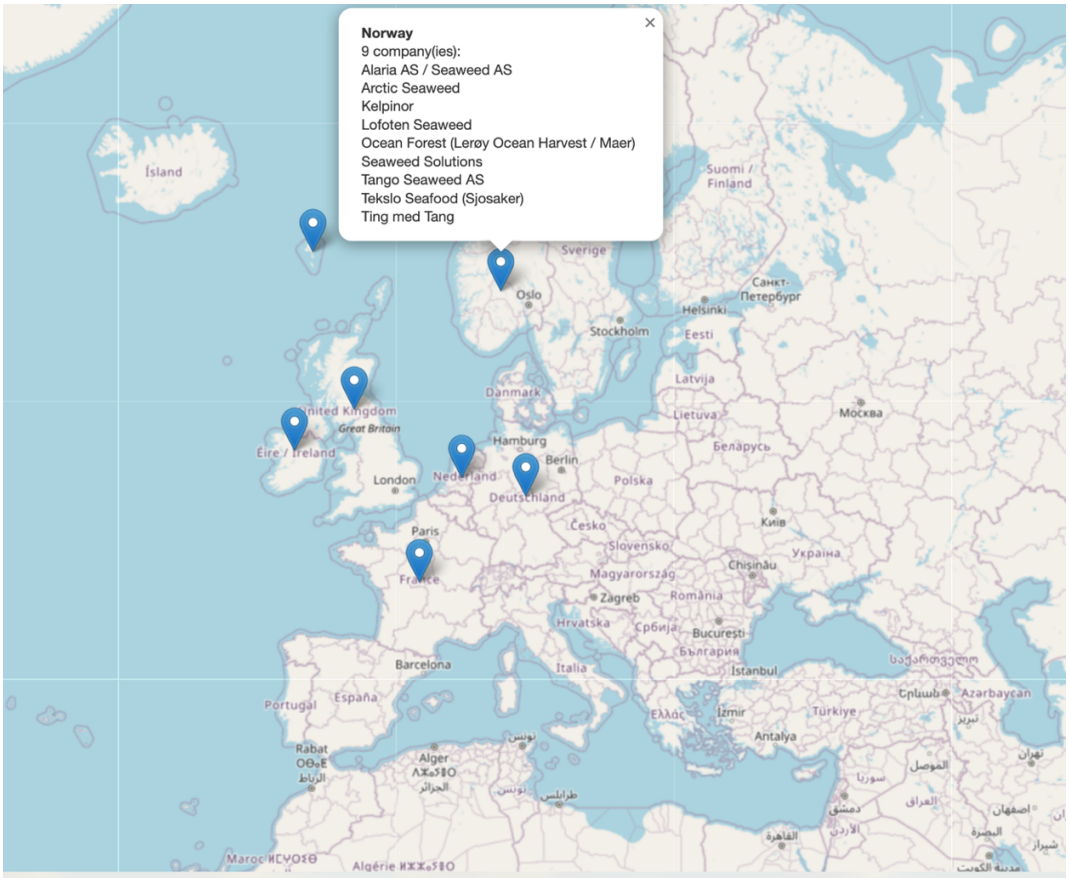

Figure 5. *Interactive map showing the distribution of companies operating with Alaria esculenta across Europe. The figure highlights all countries with relevant companies and displays the list of nine companies based in Norway.*

When performing a company-based search (Figure 6), the output is a table that includes: Company Name; Country (Headquarters); Value Chain; Website; Production Process; Industry Applications; Algae Species utilized by the company.

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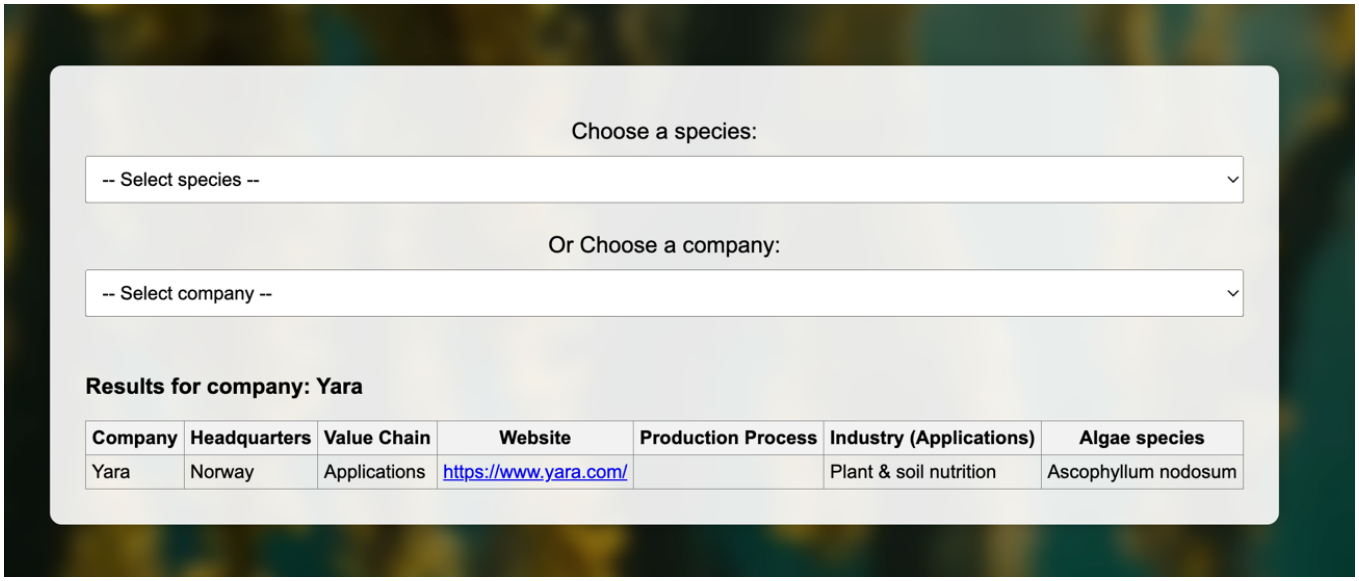

Figure 6. *Example of a company-based search result for* ***Yara****.*

Maintenance and Updates

If blank fields appear in the search results, it indicates that the information is currently unavailable at the time of publication. This database is conceived as a **living resource**, subject to continuous updates and improvements based on contributions from companies and institutions willing to share new or updated information.

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4. ALGAE HATCHERY OPERATIONS. CASE STUDIES

Given the diversity of groups, morphologies and biological cycles that feed the culture, there is no single procedure, so we will cover this section by describing the existing procedures for each type of algae, expecting that the information provided may guide the use of other species in the future. The cases have been selected according to the relevance of the species in the European context (Araujo et al. 2021).

Pyropia/Porphyra spp.

Pyropia J.Agardh, 1899 and *Porphyra* C.Agardh, 1824 are closely related genera of red algae (Phylum Rhodophyta, class Bangiophyceae, order Bangiales) extensively cultivated for their nutritional value and bioactive compounds with antioxidant and anti-inflammatory properties. Additionally, they are rich in carotenoids –notably xanthophylls like lutein and zeaxanthin–, amino acids, and other nutrients, making them important for human consumption (Diehl et al., 2017; Xu et al., 2024). These genera are among the most commercially important macroalgae globally, used extensively in food products such as nori. Their cultivation is increasing due to demand and the need for sustainable marine resources (Piña et al., 2023; Knoop et al., 2019; Marin et al., 2023; Piña & Contreras-Porcia, 2021).

Both genera typically inhabit upper intertidal zones, with distribution influenced by temperature, humidity, light, and desiccation stress. Different morphotypes and species show preferences for specific microhabitats (e.g., rocky walls vs. flat platforms) (Meynard et al., 2019; Zapata et al., 2019; Contreras-Porcia et al., 2022).

These macroalgae have a broad cosmopolitan distribution, with high species diversity and complex evolutionary relationships revealed by molecular studies. Their presence spans multiple continents and diverse coastal environments, shaped by both natural and anthropogenic factors (Figure 7). *Porphyra* and *Pyropia* are found in both hemispheres, with confirmed presence in Asia (notably Korea, Japan, and China), Oceania (New Zealand), the Americas (North America, South America — including Brazil and Chile), and Europe (Diehl et al., 2017; Zapata et al., 2019; Contreras-Porcia et al., 2022; Guillemin et al., 2016; Yang et al., 2020; Meynard et al., 2019; Milstein et al., 2015; Sánchez et al., 2014; Piña & Contreras-Porcia, 2021; Lindstrom et al., 2015).

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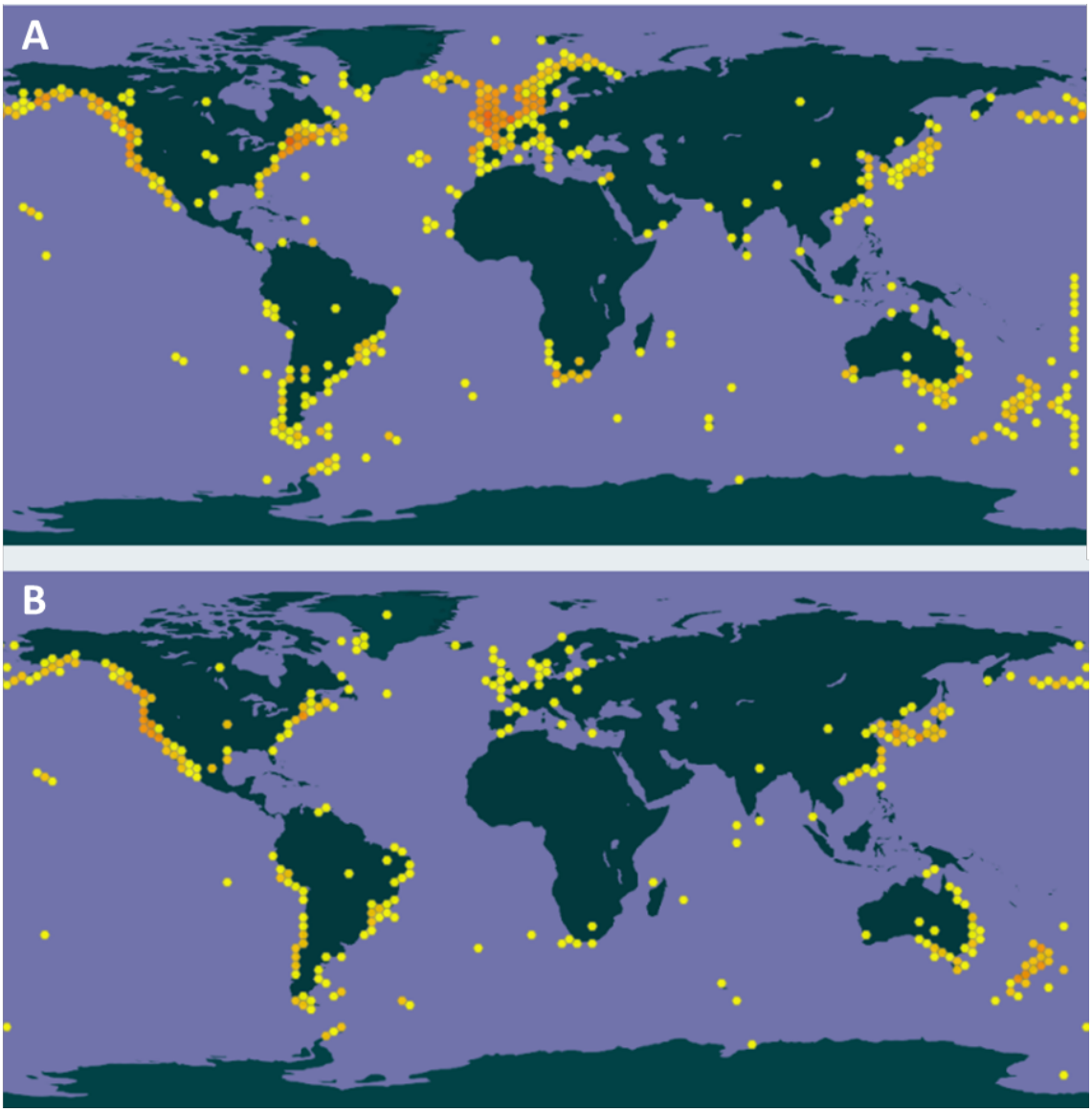

***Figure 7**. Worldwide distribution of **A.** Porphyra spp.; **B.** Pyropia spp. The points represent georeferenced occurrences of species: orange / reddish-orange: Data published as observations or specimen records (e.g., field observations, museum specimens); and, yellow: Literature-based records or other secondary sources; Light Green: Sensor-based data or camera trap records (GBIF Secretariat, 2023).*

Life cycle

These red algae exhibit a heteromorphic haploid–diploid sexual life cycle in which the macroscopic leafy gametophyte (thallus) alternates with the microscopic filamentous sporophyte (conchocelis), with conchospores bridging the two. Understanding these stages is crucial for increasing the production in mariculture farming of this economically significant

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marine resource (Knoop et al., 2019; Wang et al., 2019; Wang et al., 2020; Piña et al., 2023; Niu et al., 2024).

The simplified life history of *Pyropia* and *Porphyra* starts with male (spermatium) and female (carpogonium) gametes on the thalli fertilize to form diploid carpospores contained carposporangium (spore-producing structure) (Figure 8). The released carpospores penetrate a shell, where they undergo development into filamentous conchocelis (tetrasporophyte), residing within the shell. The conchocelis further matures into conchosporangia, eventually releasing conchospores. These spores undergo meiosis, ultimately leading to the development of gametophytic thalli. (Piña et al., 2023; Niu et al., 2024).

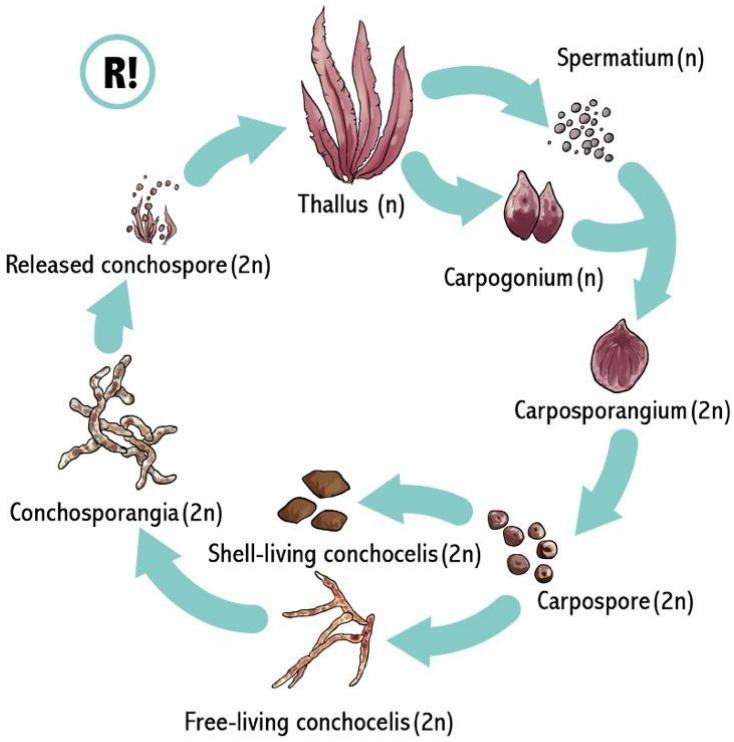

***Figure 8**. The simplified life cycle of Pyropia and Porphyra (Niu et al., 2024).*

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Hatchery techniques

Modern *Pyropia/Porphyra*, and all species, hatchery techniques depend on precise control of life cycle stages —particularly the conchocelis phase— optimization of abiotic factors like temperature, photoperiod and salinity. Environmental factors, particularly temperature and photoperiod, play a crucial role in regulating transitions between reproductive stages, including conchospore release and blade development (Knoop et al., 2019; Wang et al., 2019; Wang et al., 2020; Piña et al., 2023).

Overall, the conchocelis phase grows on shells under controlled conditions and, in autumn, releases conchospores that adhere to nets for cultivation in the sea. These conchospores subsequently grow into thalli, which are later harvested (Polne-Fuller et al., 1984; Pattiasina et al., 2023; Piña et al., 2023).

The following fact sheets present hatchery techniques for *Pyropia/Porphyra*, with further details available in the cited bibliography.

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Pyropia / *Porphyra* hatchery

	Start material	Spore released and seeding	Sporeling growth and yield	Out-growth
Propagules	**Conchospores** Produced by mature **Conchocelis** (filamentous sporophyte). Cultured on substrates (e.g., oyster shells Hannach & Waaland, 1989) or in suspension. (Stekoll & Lin, 1999; Piña *et al.*, 2023).	**Conchospore release:** 9–15°C (Piña *et al.*, 2023). **Conchospore germination:** 9°C (Knoop *et al.*, 2019). **Light intensity:** low light intensity increases conchospore germination. **Conchocelis culture conditions** **Light intensity**: 40–80 µmol photons m^{-2} s^{-1} (Hannach & Waaland, 1989). **Photoperiod:** 8:16 h (light:dark) (Piña *et al.*, 2023). **Temperature:** 11–20°C, varies by species (Nam Gil, 1999; Stekoll & Lin, 1999; Knoop *et al.*, 2019; Piña *et al.*, 2023).	Optimal spore stocking densities for cultivation are generally between 5,000-10,000 spores mL^{-1} (Flavin *et al.*, 2013).	
Sporeling production	**Gametophyte**		**Blade growth:** 5–20°C, young blades (gametophytes) prefer lower temperatures; consistent blade development at higher temperatures (20 °C) (Nam Gil, 1999; Knoop et al., 2019; Piña *et al.*, 2023). **Light intensity:** lower light intensity increases conchospore germination.	Gametophyte fronds can be cultivated in land-based tanks (inshore) or natural upper intertidal zones, where they naturally grow. Substrate for blades: Nylon or cotton traditional ropes; synthetic seedstrings such as Gore C type which improve efficiency (Xing *et al.*, 2025).

Conchospores: the germination of conchospores into young blades is a major bottleneck. Even with optimized conditions, germination rates remain very low, indicating this is the stage where propagation is least successful (Knoop *et al.*, 2019).

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Alaria esculenta

Alaria esculenta (Linnaeus.) Greville, 1830 (Phylum Ochrophyta, class Phaeophyceae, order Laminariales), also known as dabber locks or winged kelp, is a brown seaweed valued for its high productivity and rich content of carbohydrates, proteins, vitamins, minerals, and bioactive compounds. It is cultivated for food and biomass, especially in Europe, and is recognized for its rapid growth and potential as a source of phlorotannins and other beneficial compounds (Duarte, 2017; Kerrison et al., 2020).

This macroalga primarily colonizes wave-exposed, subtidal rocky shores in cold, clear waters, where light is abundant and sedimentation is low (Kraan & Guiry, 2000; Kraan, 2020). Its distribution is limited in sheltered, turbid, or sediment-rich environments, and it is sensitive to changes in temperature and salinity, especially during early development.

Alaria esculenta is predominantly found in temperate to cold waters of the Northern Hemisphere, inhabiting the Atlantic and Pacific coasts of Canada and the USA, as well as northern Europe — specifically the United Kingdom, Greenland, the Faroe Islands, and the Nordic countries— (Figure 9). Its distribution is largely restricted to areas where the water temperature does not exceed 16°C, explaining its absence from warmer southern regions such as the southern North Sea and beyond the English Channel (Murúa et al., 2018; Inaba et al., 2022; Kraan & Guiry, 2000; Kraan, 2020; Kraan et al., 2001).

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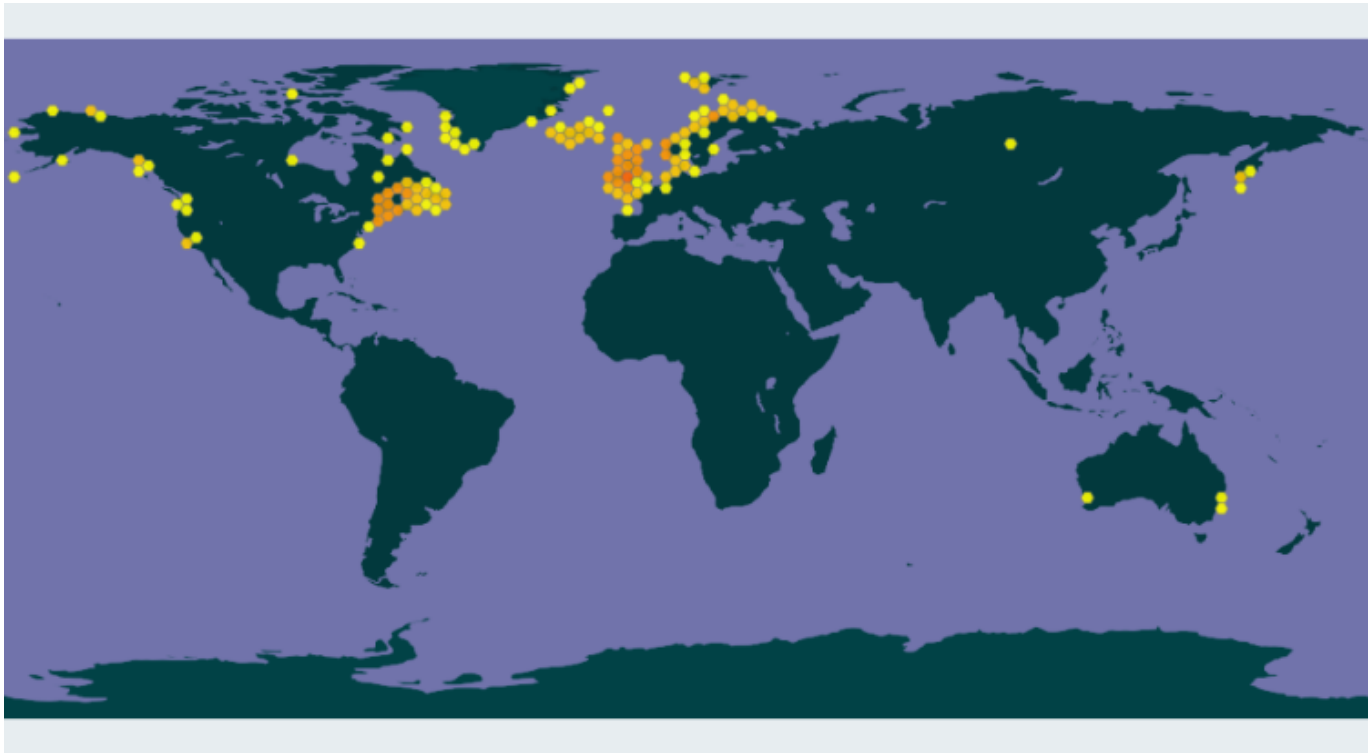

***Figure 9**. Worldwide distribution of Alaria esculenta. The points represent georeferenced occurrences of species: orange / reddish-orange: Data published as observations or specimen records (e.g., field observations, museum specimens); and, yellow: Literature-based records or other secondary sources; Light Green: Sensor-based data or camera trap records (GBIF Secretariat, 2023).*

Life cycle

Alaria esculenta has a heteromorphic life cycle, alternating between a microscopic gametophyte stage and a macroscopic sporophyte stage (Fredersdorf et al., 2009; Silva et al., 2022; Zacher et al., 2019; Ebbing et al., 2021) (Figure 10).

The large visible kelp (sporophyte) produces zoospores through meiosis (meiospores). These zoospores settle and develop into microscopic male and female gametophytes (Fredersdorf et al., 2009; Zacher et al., 2019; Silva et al., 2022). Gametophytes produce gametes (eggs and sperm). The fertilization of the gametes results in a zygote, which develops into a sporophyte, completing the cycle (Zacher et al., 2019; Ebbing et al., 2021; Silva et al., 2022).

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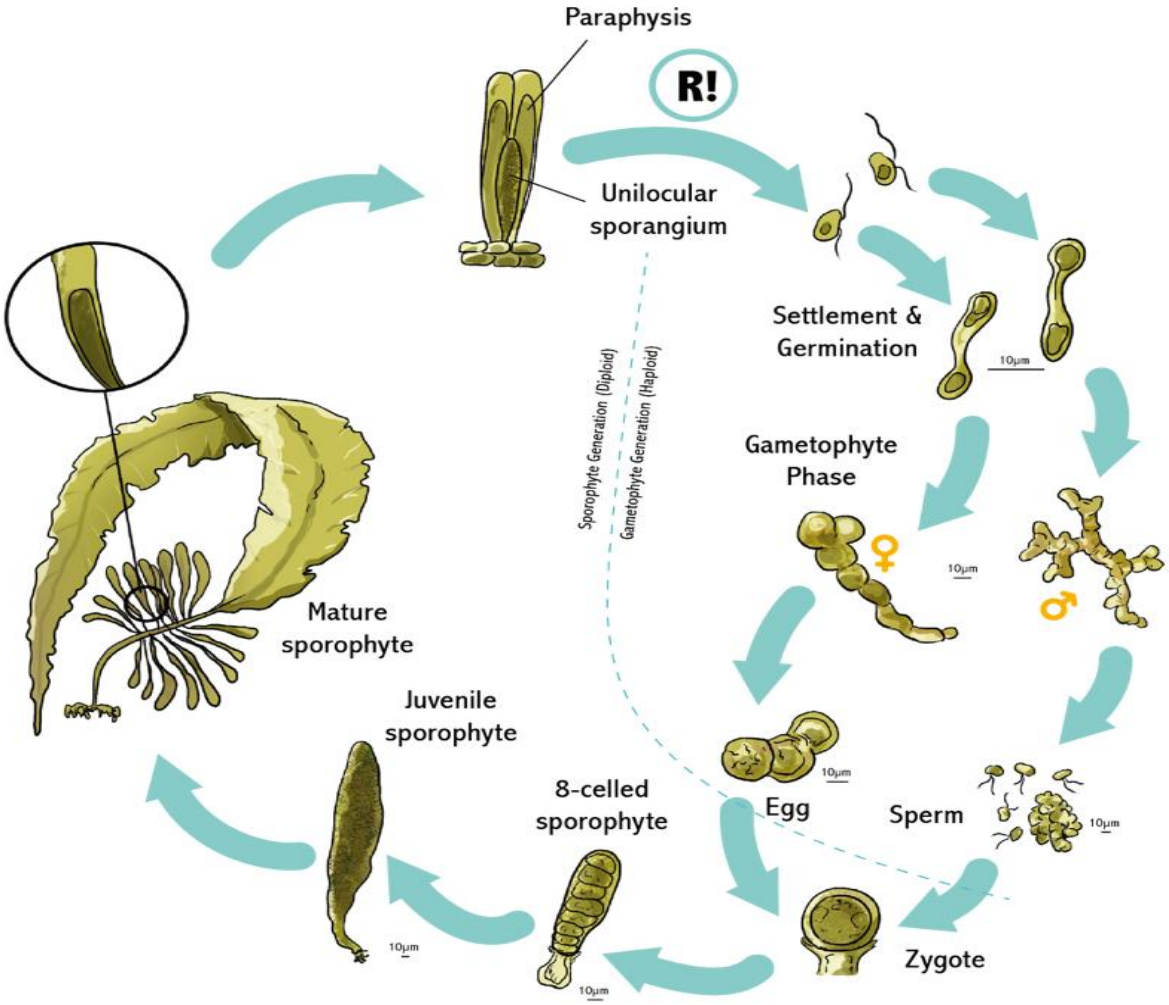

***Figure 10**. The life cycle of Alaria esculenta (adapted from Redmond et al., 2014).*

Related to seasonal timing, in Arctic conditions, gametophyte growth and reproduction are halted during winter darkness and resume in spring and summer. In *A. esculenta*, sexual reproduction and sporophyte recruitment mainly occur in summer and autumn (Silva et al., 2022).

Hatchery techniques

Hatchery and seeding techniques for *Alaria esculenta* are central to its cultivation for food and biomass. Research has focused on optimizing seedling production, comparing traditional and innovative seeding methods, and understanding how these affect yield and morphology.

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Alaria esculenta hatchery

	Start material	Spore released and seeding	Sporeling growth and yield	Out-growth
Propagules	**Zoospores** main dispersal and reproductive propagules. They are produced in the sporangia of the adult sporophyte through meiosis, making them haploid cells. These zoospores or meiospores are motile and can germinate to form gametophytes (Duarte, 2017).	**Photoperiod:** A 16:8 h light:dark **Temperature:** 7–13 °C are optimal for zoospore photosynthesis, germination, and early development (Roleda, 2009).	Optimal spore stocking densities for cultivation are generally between 5,000-10,000 spores mL^{-1} (Flavin *et al.*, 2013).	
Sporeling production		**Gametophytes** This method allows for a constant, year-round supply of propagules, unlike the seasonal limitation of zoospore release (Duarte, 2017).	**Photoperiod:** 16:8 h (light:dark) photoperiods yield higher sporophyte production and growth (Martins et al., 2021). **Binder-Seeding:** Binder-seeding onto specialized textiles (AlgaeRope, AlgaeRibbon) can reduce costs. Biomass yield is similar across natural and artificial materials, but higher sporophyte density on AlgaeRibbon lead to shorter, thinner fronds. (Kerrison *et al.*, 2020).	Juveniles are grown on twine in hatcheries and then deployed at sea. *Alaria esculenta* can grow and be cultivated in both inshore and natural environments (Kerrison *et al.*, 2020).

Vegetative gametophyte stage: Gametophytes can remain in a vegetative (non-reproductive) state and cannot be used for reproduction in hatcheries until fertility is induced by specific conditions, such as changes in light or temperature (Duarte, 2017; Martins *et al.*, 2021).

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Ulva spp.

Ulva spp., commonly known as sea lettuce, are green seaweeds (Phylum Chlorophyta, class Ulvophyceae, order Ulvales) valued for their high productivity, environmental tolerance, and nutritional properties. They are increasingly cultivated for food, feed, and biofuel applications, with commercial interest growing globally due to their versatile uses and ease of cultivation in various systems, including photobioreactors and open sea farms (Steinhagen et al., 2022; Balar & Mantri, 2019).

These green macroalgae have a broad global distribution inhabiting a wide range of marine habitats from intertidal to subtidal zones, and even some freshwater environments, due to their tolerance to light, temperature, and salinity variations (Kirkendale et al., 2013; Mantri et al., 2020; Yohannan et al., 2024) (Figure 11). Studies report high species diversity in specific regions:

Jeju Island, Korea: Nine *Ulva* species identified, with *U. australis, U. ohnoi,* and *U. procera* being predominant (Kang et al., 2019).

Australia: Overwhelmingly cosmopolitan flora with both native and nonindigenous species, and several new records and range extensions (Kirkendale et al., 2013).

New Caledonia: Fifteen species found, including ten newly described species, highlighting significant undiscovered diversity in tropical regions (Lagourgue et al., 2022).

India: 28 taxa recorded, with seven endemic taxa and highest diversity in Gujarat (Yohannan et al., 2024).

China: Six new records, with both temperate and subtropical species expanding their ranges, especially *U. meridionalis* (Xie et al., 2020).

Brazil: Ten taxa identified, including new occurrences and cryptogenic species, with evidence of misapplied traditional names (Carneiro et al., 2023).

Northeast Atlantic and North America: Multiple species present, but with significant misidentification issues in public databases (Fort et al., 2021; Lamb et al., 2019).

In Europe, *Ulva* spp. are broadly distributed across marine, brackish, and freshwater environments, with species composition and distribution patterns shaped by local ecological conditions. Among these, *Ulva flexuosa* is the predominant freshwater species, exhibiting distinct

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ecological preferences across its subspecies: *U. flexuosa subsp. pilifera* is commonly found in inland freshwater systems, while subsp. *flexuosa* and subsp. paradoxa are more frequently associated with marine and coastal habitats. *U. flexuosa* is considered indigenous and can form blooms under certain conditions (Mareš et al., 2011; Czerwik-Marcinkowska et al., 2020). Another prominent species, *Ulva rigida*, is among the most frequently encountered *Ulva* taxa in European coastal seawaters. Due to its abundance and resilience, *U. rigida* is often included in studies focused on macroalgae applications in food production, aquaculture, and environmental management, underscoring its ecological prevalence and growing commercial relevance across the continent (Neto et al., 2018; Research et al., 2020; Da Costa et al., 2020; Califano et al., 2020; Moreira et al., 2021; Gao et al., 2018; Karray et al., 2017; Naldi & Viaroli, 2002).

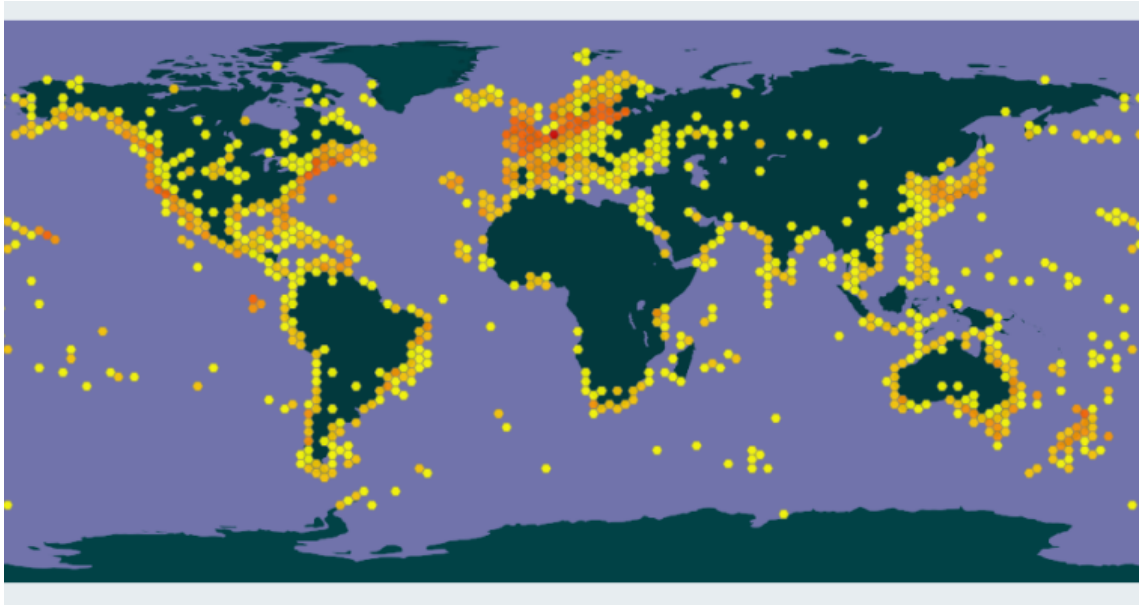

***Figure 11**. Worldwide distribution of Ulva spp. The points represent georeferenced occurrences of species: orange / reddish-orange: Data published as observations or specimen records (e.g., field observations, museum specimens); and, yellow: Literature-based records or other secondary sources; Light Green: Sensor-based data or camera trap records (GBIF Secretariat, 2023).*

Life cycle

Reproduction in these macroalgae occurs both sexually and asexually (Figure 12). The life cycle is biphasic, consisting of two distinct phases: the gametophyte and the sporophyte. It is also isomorphic, meaning that the gametophyte and sporophyte generations are morphologically similar yet genetically distinct. (Graham & Wilcox, 2000; Mantri et al., 2020).

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Sexual reproduction involves the production of haploid biflagellate gametes that fuse during fertilization, resulting in the formation of a diploid zygote. This zygote then develops into a diploid multicellular adult sporophyte thallus. As these typical vegetative cells mature, they transition into spore or zoospore mother cells, which undergo meiosis to produce haploid quadriflagellate zoospores (Figure 12). These zoospores germinate and give rise to haploid male and female isomorphic adult gametophytic thalli (Costa, Cotas & Pereira, 2024). At maturity, these thalli once again produce their respective gametes through mitosis. This reproductive process is termed a "haplodiplontic" life cycle (Figure 12). Both zoospores and gametes have no cell walls and are described as naked and are produced mainly in cells at the end of the thallus (Graham et al., 2000; Mantri, et al., 2020).

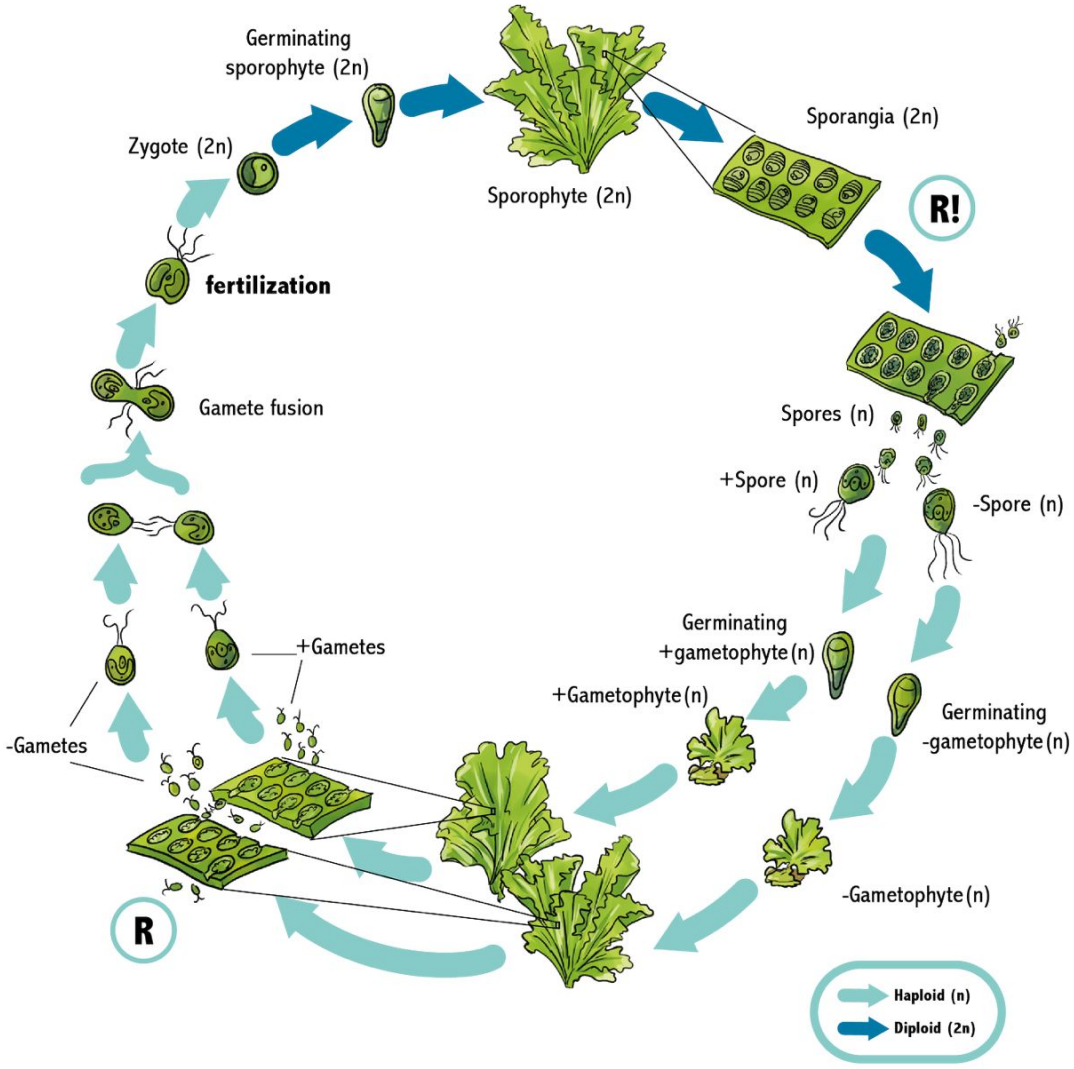

***Figure 12**. Typical life cycle of Ulva spp. (Fusco & Minelli, 2019).*

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Some *Ulva* species, such as *Ulva rigida*, are capable of parthenogenetic reproduction, whereby their gametophytes can produce clonal gametes even in the absence of a mating partner (Steinhagen et al., 2022; Balar & Mantri, 2019). Notably, parthenogenesis—where offspring develop from unfertilized gametes—is a widespread and ecologically significant reproductive strategy among several *Ulva* species. This mode of reproduction contributes substantially to their life cycle flexibility, population resilience, and ecological success. It is particularly relevant in the context of species that drive large-scale green tide events and those utilized in aquaculture, as it enables rapid population expansion and persistence under varying environmental conditions.

The seasonal timing of *Ulva* spp. reproduction is influenced by environmental factors such as temperature, light, and photoperiod, as well as endogenous biological rhythms. *Ulva* species display distinct seasonal reproductive patterns, with peaks in reproduction and biomass often linked to specific times of year and environmental cues.

Hatchery techniques

Effective hatchery and seeding practices for *Ulva* spp. rely on high seeding densities, optimal nursery periods, and efficient in vitro seeding methods. Environmental factors like salinity and phosphorus play supporting roles, while life cycle selection can further enhance productivity. These insights support the development of reliable, large-scale *Ulva* aquaculture.

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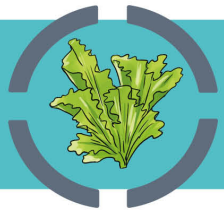

Ulva spp. hatchery

	Start material	Spore released and seeding	Sporeling growth and yield	Out-growth
Propagules	**Germ cells** Thallus is directly used by segmenting or chopping, which can induce the formation of germ cells (zoospores or gametes) or allow for vegetative regrowth (Vesty *et al.*, 2015; Tao *et al.*, 2021).	**Light intensity:** 100–400 µmol m^{-2} s^{-1}. **Photoperiod:** 8:16 h and 12:12 h (light:dark), depending on the species. **Temperature:** 15–22°C.	Stocking thallus fragments at 5–20 g fresh weight L^{-1} results in a doubling of growth each week (Pettett, 2009).	
Sporeling production	**Sporophyte or gametophyte blades** Germ cells can germinate and develop into new thalli, with high germination rates observed under optimal nutrient and salinity conditions. Induction protocols allow reproducible and standardized inoculum production (Vesty *et al.*, 2015; Bastos *et al.*, 2019).		**Nutrients and Water:** Nitrogen (N) and phosphorus (P) are essential; growth increases with higher DIN (Dissolved Inorganic Nitrogen); excess phosphate can be toxic; high nitrate is well tolerated. Continuous water flow enhances seedling coverage and nutrient removal efficiency (Teichberg et al., 2009 Salvi *et al.*, 2021; Nederlof *et al.*, 2022) . **Temperature:** Some species are more cold-tolerant, but warmer conditions generally boost biomass (Yoshida *et al.*, 2015). **Seeding:** 621,000 swarmers/m rope, 5-day nursery (optimal growth) (Castelar *et al.*, 2014).	*Ulva* spp. are highly adaptable and grow well in both natural and land-based (inshore) environments. Controlled seeding of juvenile sporophytes on nylon nets or ropes enhances biomass yield, with nylon outperforming natural fibers such as jute or bamboo in terms of coverage and growth, especially under continuous water flow (Castelar *et al.*, 2014; Li *et al.*, 2014; Geng *et al.*, 2015; Salvi *et al.*, 2021).

Thalli used for cultivation may be either **sporophytes** (2n) or **gametophytes** (n) as they are morphologically identical. Gametophyte-origin fragments generally lead to faster blade development, however **Late-stage or senescent thalli** as well as clonal gametophytes, are generally not used for hatchery starts, as they do not support optimal growth or biochemical quality in *Ulva* crops (Van Der Loos *et al.*, 2024; Steinhagen *et al.*, 2022). Optimizing the choice and management of life-history phases could significantly benefit *Ulva* aquaculture in the future.

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Saccharina latissima

Saccharina latissima (Linnaeus.) C.E. Lane, C. Mayes, Druehl & G.W. Saunders, 2006 commonly referred to as sugar kelp, is a perennial brown macroalga belonging to the phylum Ochrophyta, class Phaeophyceae, and order Laminariales. This species plays a critical ecological and economic role in temperate marine environments. Renowned for its physiological adaptability, high nutritional value, and contributions to coastal ecosystem services, *S. latissima* is increasingly recognized as a keystone species in marine habitats and a promising candidate for sustainable aquaculture and bioproduct development (Diehl et al., 2023; Rey et al., 2019; Burgunter-Delamare et al., 2023). Beyond its resilience, *S. latissima* is highly regarded for its rich nutritional profile, comprising a high amount of carbohydrates, proteins, and health-promoting lipids, particularly polyunsaturated fatty acids known for their beneficial effects on human health (Rey et al., 2019; Vasconcelos et al., 2024).

This kelp dominates many temperate coastal ecosystems as a canopy-forming species — growing tall and extending its fronds outward to form an overhead canopy— thereby playing a pivotal ecological role as an ecosystem engineer. By modifying its environment and creating complex habitats, it supports biodiversity and enhances ecosystem structure and function (Diehl et al., 2023; Tourneroche et al., 2020; Burgunter-Delamare et al., 2023).

Saccharina latissima is widely distributed across the cold and temperate coastal waters of the Northern Hemisphere, from the Pacific to the Atlantic, including Arctic and sub-Arctic regions (Figure 13). The species shows high adaptability to local environmental conditions, supporting its broad distribution.

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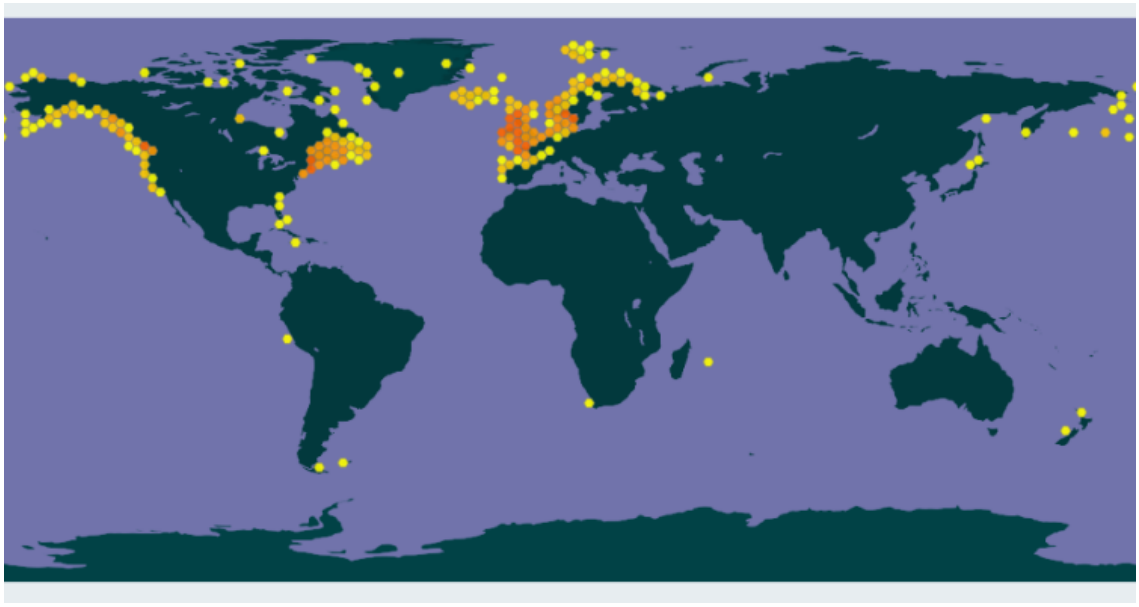

***Figure 13**. Worldwide distribution of Saccharina latissima spp. The points represent georeferenced occurrences of species: orange / reddish-orange: Data published as observations or specimen records (e.g., field observations, museum specimens); and, yellow: Literature-based records or other secondary sources; Light Green: Sensor-based data or camera trap records (GBIF Secretariat, 2023).*

Life cycle

Saccharina latissima has a complex biphasic life cycle that alternates between a large diploid sporophyte and a microscopic haploid gametophyte stage (Figure 14). The sporangia located in sporophytes, during meiosis, form zoospores (n) by a large multicellular sporophyte (2n). The spores settle onto the seafloor and develop into male and female gametophytes (n). Sterile gametophytes can be clonally propagated and used as seed stock for further breeding and cultivation. Male and female gametophyte form antheridia that produce sperm and oogonia that produce eggs, respectively. The sperm fertilizes the egg, and a zygote is formed that develops into a sporophyte (2n) (Visch et al., 2019).

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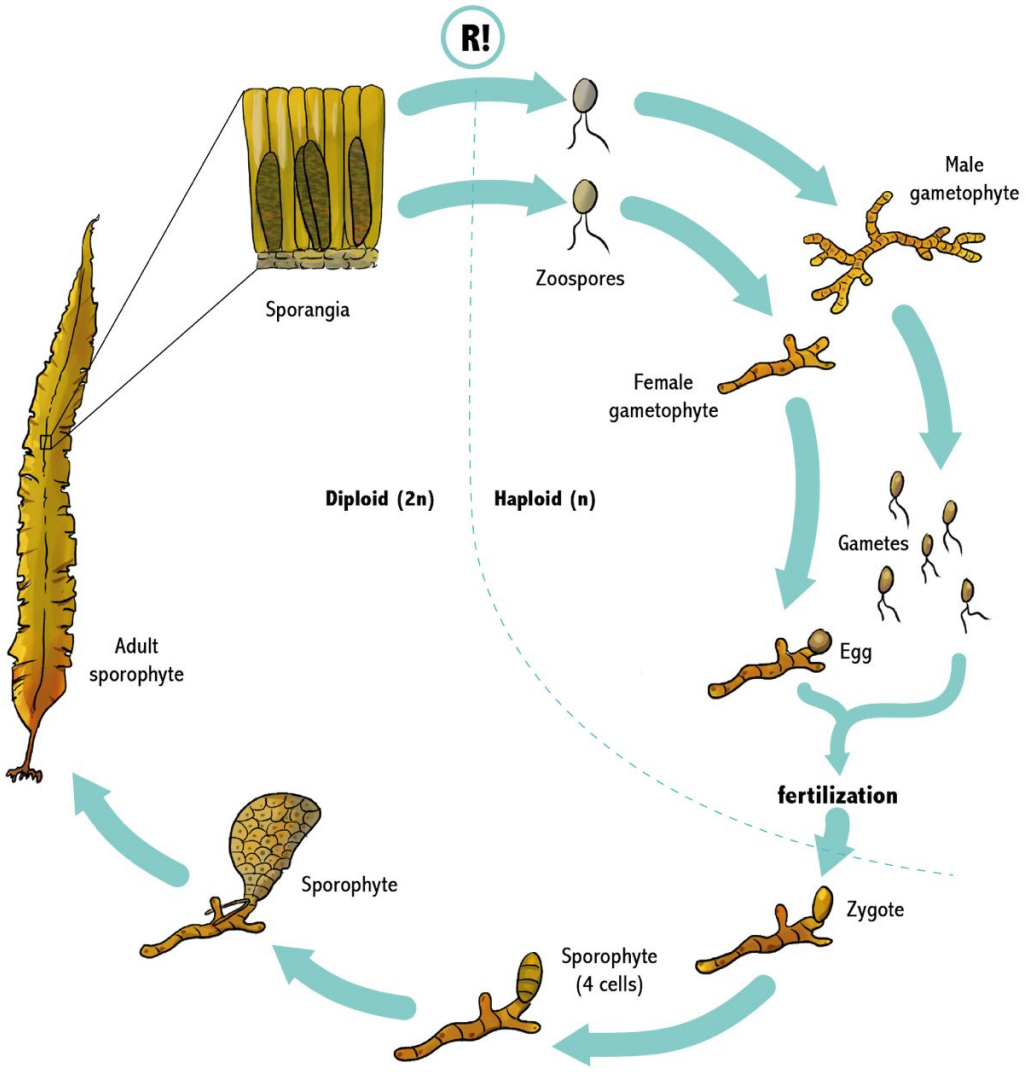

***Figure 14**. Life cycle of Saccharina latissima (*from *Visch et al., 2019).*

Understanding its life cycle is crucial for aquaculture, breeding, and environmental management, as various environmental factors and cellular processes influence its development and reproduction. The life cycle of *S. latissima* involves several stages, including hatchery (spore production and early growth), cultivation (growth on longlines in the sea), and harvesting. The process also includes preservation methods such as drying, ensiling, or freezing to maintain product quality after harvest (Thomas et al., 2020).

Hatchery techniques

Optimizing *Saccharina latissima* hatchery methods involves careful management of nutrient concentrations, sterilization, and seeding techniques. Twine seeding remains the most reliable

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method, while binder-seeding offers cost advantages in some contexts (i.e. may be lower than traditional twine seeding in more dynamic environments, (Umanzor et al., 2020)). The choice of nutrient source and twine material significantly affects early growth and yield. Sustainable practices and efficient hatchery operations are key to supporting the expanding kelp aquaculture industry. Kuralon twine is a standard, effective substrate for seeding *S. latissima*, supporting robust nursery growth and high yields, especially in sheltered sites. It remains a key material in traditional kelp farming practices (Boderskov et al. 2021).

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Saccharina latissima hatchery

	Start material	Spore released and seeding	Sporeling growth and yield	Out-growth
Propagules	**Meiospores** or zoospores, from mature sporophytes. Sorus induction achieved year-round by short-day treatments and removing the basal blade meristem (Forbord *et al.*, 2012).	**Settlement Conditions for meispores**: • Dark. • Nutrient enriched media. • Pre-treatment of surfaces with commercial yeast extract.		
Sporeling production		**Sporophyte** Seeding juvenile sporophytes onto textiles (Kuralon twine/textile) using a binder is highly effective and may reduce hatchery space requirements (Kerrison *et al.*, 2018).	**Nutrient:** Continued nutrient enrichment in hatchery crucial for sporophyte growth and survival (Kerrison *et al.*, 2016; 2015; 2019; Jevne et al., 2020). **Temperature:** Optimal temperature is 10°C Some southern populations of *S. latissima* can tolerate higher temperatures (up to 20°C) in land-based systems. (Jung *et al.*, 2024; Azevedo *et al.*, 2016; Krasnow *et al.*, 2024).	Juvenile sporophytes are used for outplanting, as they show better growth and survival compared to gametophytes or meiospores when seeded onto cultivation substrates (Kerrison et al., 2018).

Gametophytes can be kept free in liquid culture for propagation and storage, and then attached to a substrate to induce sporophyte formation and facilitate seeding. Both approaches are complementary and are used depending on the stage and purpose of cultivation (François et al., 2023; Forbord *et al.*, 2018).

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Palmaria palmata

Palmaria palmata (Linnaeus) F. Weber & D. Mohr, 1805 commonly known as dulse, is a red seaweed (Phylum Rhodophyta, class Florideophyceae, order Palmariales) valued for its nutritional content and commercial applications and has long been used as a food source. Due to increasing demand and limited availability in the wild, cultivation methods are being developed to support sustainable production.

This red macroalga thrives on rocky shores in cold-temperate regions and is easily recognized by its soft, edible, reddish fronds. It has traditionally been harvested for human consumption and as animal feed (Grote, 2019; Pang & Lüning, 2006; Stévant et al., 2023). Dulse is notable for its high content of proteins, minerals, and bioactive compounds, making it a sought-after ingredient in the food industry, dietary supplements, and livestock nutrition (Grote, 2019; Stévant et al., 2023; Liboureau & Pampanin, 2024). Although it was historically hand-harvested, it is now the focus of aquaculture initiatives aimed at meeting growing market demand while ensuring sustainable use (Grote, 2019; Stévant et al., 2023).

Palmaria palmata is primarily distributed along the North Atlantic coasts (Figure 15), within latitudes of approximately 40° to 80°N. It is found on the shores of Western Europe, Canada (notably New Brunswick and Nova Scotia), and the USA (Maine) (Stévant et al., 2023; Grote, 2019; Xu et al., 2024).

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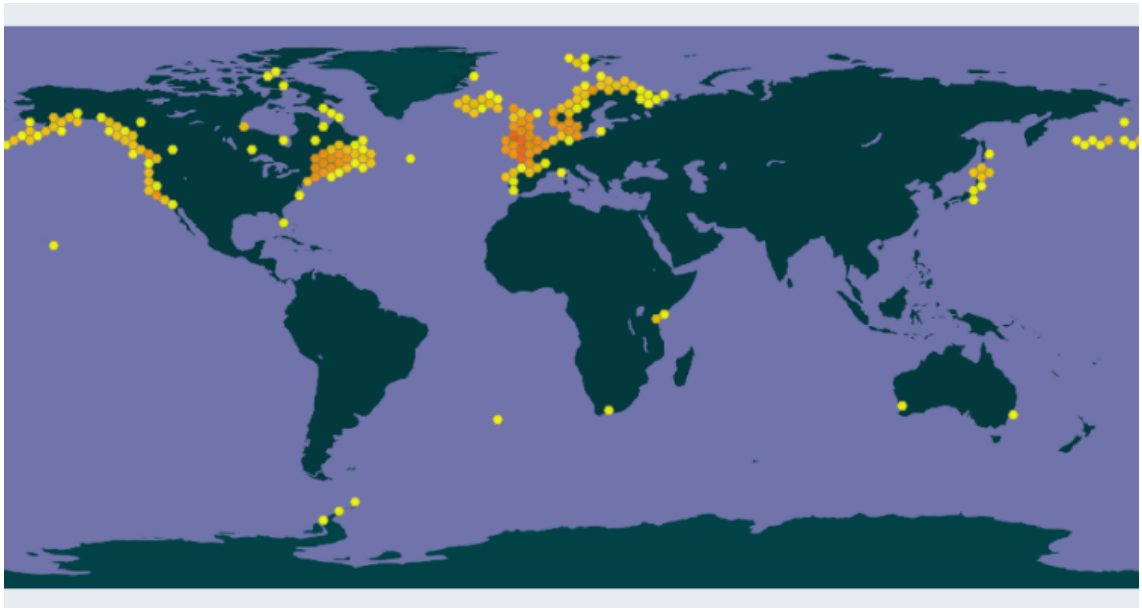

***Figure 15**. Worldwide distribution of Palmaria palmata. The points represent georeferenced occurrences of species: orange / reddish-orange: Data published as observations or specimen records (e.g., field observations, museum specimens); and, yellow: Literature-based records or other secondary sources; Light Green: Sensor-based data or camera trap records (GBIF Secretariat, 2023). Notice that morphologically similar species previously grouped under this species in the North Pacific are now recognised as genetically distinct, including Palmaria moniliformis and several species of the genus Devaleraea (Skriptsova & Kalita, 2020; Skriptsova et al., 2023).*

Life cycle

Palmaria palmata is considered pseudo-perennial since the fronds grow, reproduce and senesce from a holdfast that survives multiple years. It has a distinct life cycle among red seaweeds, involving both sexual and asexual stages (Figure 16). Haploid tetraspores develop within the sori (or sorus in plural, are reproductive structures) of the frond of diploid tetrasporophytes through meiosis. The haploid tetraspores germinate into either microscopic female or blade-like male gametophytes of a similar morphology to diploid tetrasporophytes. The female gametophyte develops oogonia with trichogynes (i.e. hair-like structures) to catch spermatia (i.e. non-motile male gametes) released from a mature male gametophyte (at least one-year-old). The zygote resulting from the fertilization of a female gamete by a spermatium grows into a diploid tetrasporophyte from the encrusting female gametophyte, which is overgrown at an early stage as the tetrasporophyte develops its own discoid holdfast.

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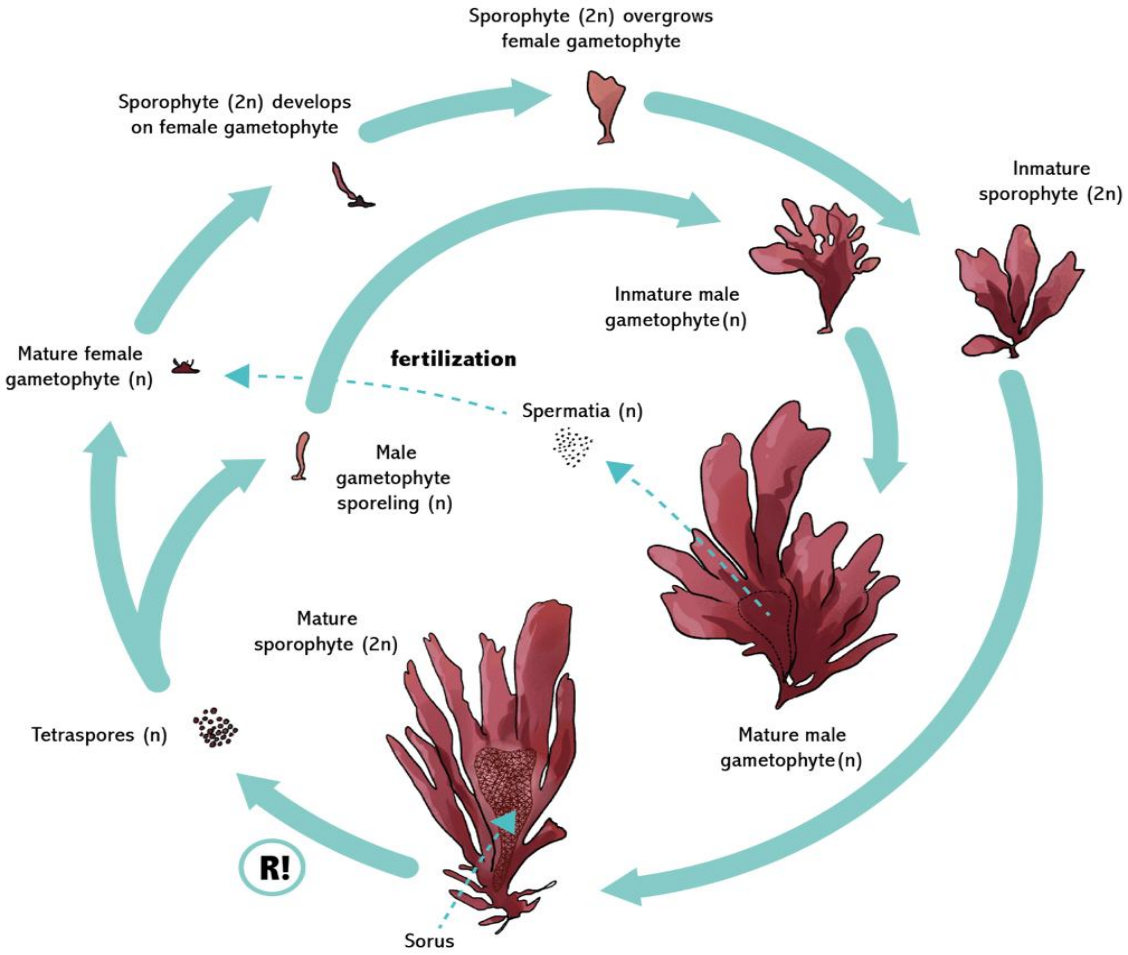

***Figure 16**. Life cycle of Palmaria palmata (Based on Visch et al., 2019).*

The species can reproduce from spores or vegetative fragments, and both approaches are currently being explored to support reliable and scalable cultivation (Grote, 2019; Pang & Lüning, 2006; Stévant et al., 2023; Liboureau & Pampanin, 2024).

Hatchery techniques

Hatchery and seeding methods to propagate *Palmaria palmata* have historically faced challenges such as low spore-to-seedling efficiency and high mortality. Recent research has led to significant advancements in hatchery techniques by optimizing the amount of sori tissue, boosting spore yield, promoting even spore settlement on substrates, enhancing seedling survival, and unlocking

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the potential for large-scale cultivation. Lately innovations in hatchery and seeding methods—especially those involving water agitation, propagule mixes, and vegetative propagation—have significantly improved the efficiency and scalability of *P. palmata* cultivation (Schmedes et al., 2019; Stévant et al., 2023; Titlyanov et al., 2006). The tetraspores constitute the initial propagules and it is the male gametophyte that is propagated and grown to tanks or in nature.

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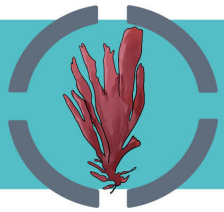

Palmaria palmata hatchery

	Start material	Spore released and seeding	Sporeling growth and yield	Out-growth
Propagules	**Tetraspores** Fertile fronds (sori) are placed in sporulation tanks with strong water agitation to induce spore release.	**Light intensity:** < 20 µmol photons m^2 s^{-1} is suggested for best results. **Photoperiod:** A 16:8 h light:dark. **Temperature:** The range of 8–12 °C. **Salinity:** 34–35 ppt **Nutrients and Water:** not critic.	**In-shore propagation** **Spore yield** (spores/g FW):5,000–67,906 (higher with agitation). **Spore density (cm^2):** ~500 (mean), up to 10 seedlings/ cm^2. **Sori tissue for seeding** 5–15 g FW per 3 nets over 9 days. **Seedling survival (3 months)** ~35% (Schmedes *et al.*, 2019; Gall *et al.*, 2004).	
Sporeling production	**Male gametophyte** Tetraspores are first released, within a few days, both male and female gametophytes germinate from these tetraspores, the mixture of germinated male and female gametophytes can be collected and used as a new inoculum for settlement on other substrates (GMA method (Grote, 2019; Pang & Lüning, 2006; Stévant *et al.*, 2023; Liboureau & Pampanin, 2024).	The conditions must be adjusted after tetraspore setlement, particularly **Higher light intensity** (>20 µmol photons m^2 s^{-1})and **Nutrients and Water:** Frequent seawater exchange and adequate nutrients (F/2 medium or urea (0.05–0.10 g/L) (Pang & Lüning, 2006; Grote, 2019; Schmedes & Nielsen, 2020; Liboureau & Pampanin, 2024).	After hatchery seeding, male gametophyte fronds can be further cultivated either in land-based tanks (inshore) or transferred to natural environments for continued growth.

Female gametophytes remain microscopic and are essential for sexual reproduction, but do not contribute to the visible crop.

Tetrasporophytes do not propagate or contribute to the main crop unless sexual reproduction is specifically induced, which is not typical in standard cultivation for biomass.

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5. INNOVATIONS AND FUTURE TRENDS

For the sector to be considered feasible and strong, several EU standards must be adopted, such as nutritional control, health issues, and sustainability, environmental of course, but also economical, all along the value chain. Concerning aquaculture, the industry has to overcome the rather scarce and sometimes random availability of raw material and substitute for a strong basement of farmer supplier, aquaculture is in the base of the EU seaweed industry.

As revealed by Ebbing et al. (2021) in the culture of *Saccharina latissima* there are two ways to feed field cultures, the more pragmatic but uncontrolled way of hatchery conditions and the more efficient but costly way of controlled culture. Being the first one the predominant one, we understand however, that European standards force us to ensure the provision of culture material from fully controlled hatchery conditions. We propose in this document six innovations aimed precisely at increasing our possibilities to control the quantity and quality of the material that finally ends up in the culture sites.

The expected intensive cultivation work requires a support of quality material to nurture the cultivars. European industry standards require control and sustainability of operations throughout the entire life cycle of the product. For many European species of interest these methods are very poor developed or non-existent.

The following six innovations are recommended for exploration within the context of a hatchery concept executed under controlled conditions:

- In vitro culture for micropropagation and germplasm conservation.
- Spore induction and culture with plant growth regulators.
- Genetic characterization of species. The first step to breeding
- Cryopreservation for germplasm conservation
- Seaweed microbiome and aquaculture
- Seedling materials to increase seeding efficiency and sustainability.

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In vitro culture for micropropagation and germplasm conservation.

Plant tissue culture includes a set of biotechnological tools that allow for the controlled growth and multiplication of plant material outside the natural environment, supporting both basic research and a wide range of practical applications in agriculture, industry, and conservation. It refers to the methods used to grow and maintain plant cells, tissues, or organs under sterile (in vitro) conditions on a nutrient culture medium. These techniques enable the propagation, regeneration, and genetic manipulation of plants by culturing isolated plant parts such as cells, tissues, or organs in a controlled environment. Applications include plant propagation, production of disease-free plants, genetic improvement, conservation of rare species, and the production of valuable bioactive compounds (Compost & Compost, 2018; Loyola-Vargas & Ochoa-Alejo, 2018; Shinde et al., 2020).

Plant tissue culture has been an area that has always held high expectations for incorporation into the field of algal biotechnology. This can be seen in the periodic reviews that have been published on the subject, among the most recent ones: Chandimali et al., (2023) provides an up-to-date and thorough overview of seaweed callus culture, a key tissue culture technique. The review explains the principles of callus culture, its advantages for rapid and efficient metabolite production, and the current limitations compared to terrestrial plant tissue culture. For example, cell suspension cultures from protoplast-derived cells are rare in seaweeds, limiting the ability to produce homogeneous cell lines for research and industrial applications. In summary, there is a lack of comprehensive understanding of the physiological and developmental processes in seaweed tissue culture, which hinders the optimization and scaling of these techniques.

Science mapping seaweed tissue culture

Certainly, scientific mapping offers us a rather disjointed panorama of scientific production, which is impossible to constitute into concepts. Different groups of algae (red, brown and green) have been worked on for very different purposes, which makes it impossible to generate a common body of doctrine (Table 2.).

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Table 2. Essentials on Science mapping of the field seaweed tissue culture.

Data	Description	Comments
Period	1984-2025	
Documents	71	(see references in Annex II)
Keywords	401	
Groups	10	(See groups and associated key words in Annex II)

Minimal Growth as a Viable Strategy for In Vitro Seaweed Germplasm Preservation

Admittedly, it may not yet be useful for the production of secondary metabolites from free cells, however cultivation of seaweeds in vitro has been suggested as useful for seaweed aquaculture in its present status because it enables clonal propagation of seed material for mariculture, allowing for the selection and cultivation of desirable seaweed strains. The technique allows explants to be cultivated axenically in enriched or artificial seawater culture media, achieving regeneration and even callus formation, which can be exploited for marine agronomy and the propagation of seaweed strains for mariculture (Baweja et al. 2009). In other words, it is an innovative method for the necessary control of operations and plant material needed in the hatchery phase.

In the context of cells fully differentiated into mature thallus, it is not surprising that on some occasions no response has been found when testing the effect of plant hormones, whose action, as we know, is based on cellular competence for growth and differentiation (Pulianmackal et al., 2014).

The preservation of seaweed germplasm in vitro does not necessarily require active proliferation; minimal growth may be sufficient, provided that the primary objective is long-term conservation rather than rapid biomass production. A growing body of research demonstrates that seaweed explants can survive for extended periods under basic or suboptimal culture conditions, even in the absence of plant growth regulators (PGRs), thereby supporting the viability of minimal-growth protocols for germplasm maintenance.

Xu et al. (2024) reported that *Sargassum fusiforme* holdfasts remained viable in vitro for up to 120 days when cultured under controlled temperature (8°C) and salinity (19‰), without the application of PGRs. During this period, explants maintained photosynthetic activity, exhibited low

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levels of stress biomarkers, and retained morphological integrity, indicating that basal metabolic activity is sufficient to sustain viability and structural stability over time. Similarly, Liboureau and Pampanin (2024) observed that explants of *Palmaria palmata* demonstrated sustained but modest growth (~5% daily) under laboratory conditions. Although not aimed at propagation, such slow proliferation was adequate to preserve and gradually increase germplasm biomass, highlighting its relevance for long-term storage with minimal input.

Investigations into species such as *Kappaphycus alvarezii* further emphasize the importance of physical factors—particularly salinity and temperature—in maintaining explant viability under PGR-free conditions. Studies by Luhan and Mateo (2017) and Aris et al. (2021) confirmed that even in the absence of chemical stimulants, precise environmental control can promote low yet stable growth sufficient for conservation purposes.

In contrast to micropropagation techniques, germplasm conservation prioritizes genetic integrity and viability over time. Minimal or slow growth is often preferred, as it reduces the likelihood of somaclonal variation and lowers nutrient and energy demands. Fine-tuning parameters such as temperature, salinity, and photoperiod is thus critical for maintaining explant stability and function without inducing excessive metabolic activity. This approach offers a cost-effective, biologically sound, and scalable strategy for the long-term in vitro conservation of seaweed germplasm.

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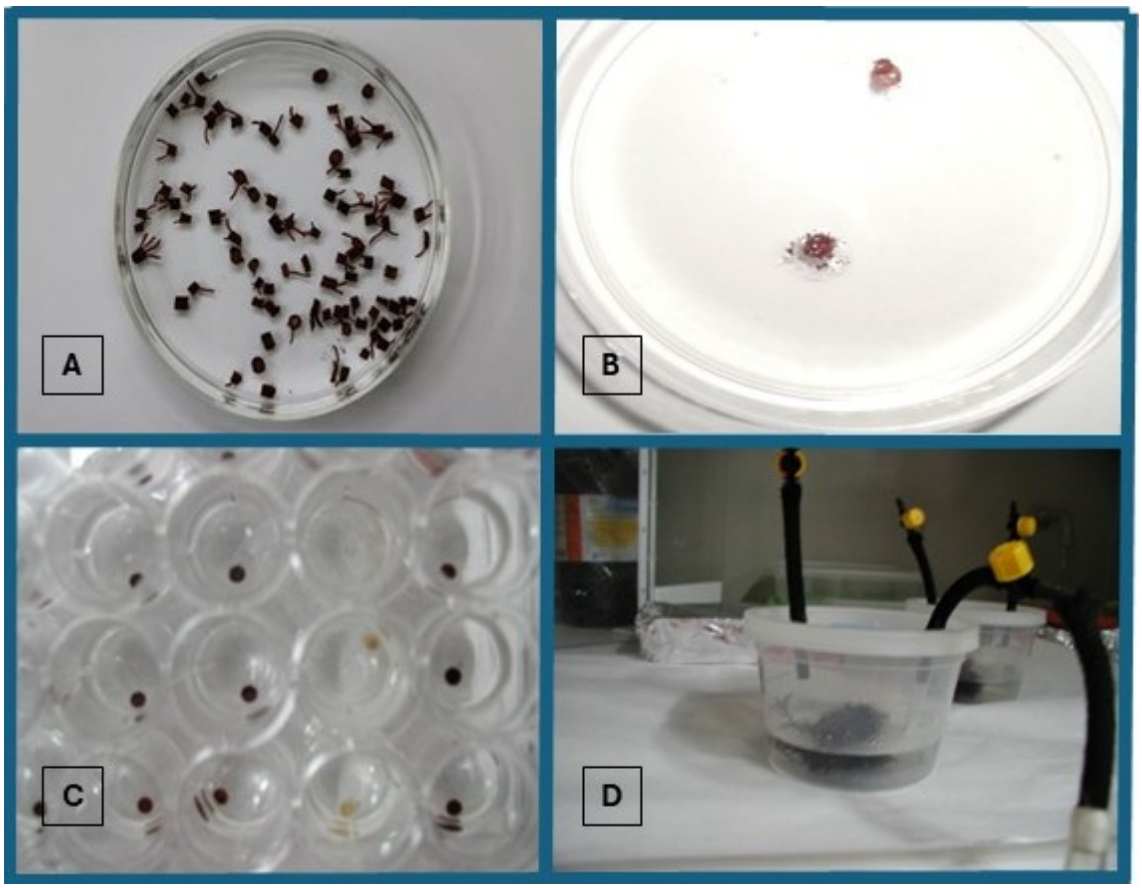

Figure 17. *In vitro culture of explants and spores of the red seaweeds Grateloupia imbricata. The cultures lasted for months in Provasoli Enriched Seawater media (PES, Provasoli 1968), particularly the cultures of carpospores* ***(A, B)****. Multiwells for antibiotic treatments to establish aseptic cultures* ***(C),*** *Bottelgario for ethylene treatments to induce sporulation* ***(D)***.Source: Physiology and Biotechnology Research Group own records

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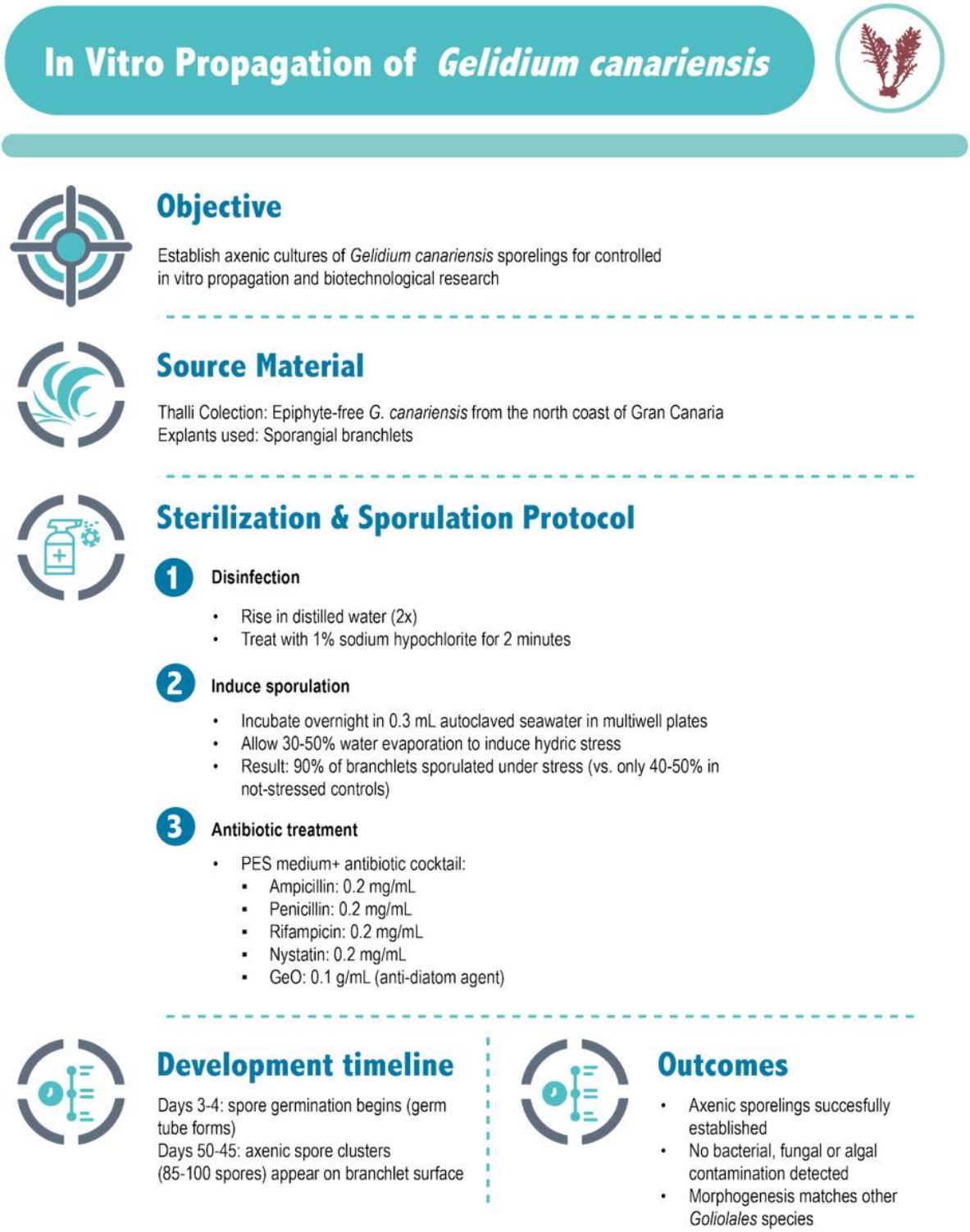

***Figure 18**. Factsheet outlining the in vitro propagation of red seaweeds without plant hormones (the case of Gelidium canariensis) under sustained growth conditions.*

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Spore induction and culture with plant growth regulators.

Plant growth regulators (PGRs) are natural or synthetic compounds that play a critical role in modulating the growth, development, and physiological responses of plants, including marine macroalgae. Various studies have confirmed the natural occurrence of PGRs in numerous seaweed species, often at concentrations comparable to those found in terrestrial plants. The major classes of PGRs identified in seaweeds include auxins, cytokinins, gibberellins, abscisic acid, polyamines, and ethylene, along with more recently characterized groups such as jasmonates and brassinosteroids (Spagnuolo et al., 2022; Stirk & Staden, 2014; Prasad et al., 2010; Panda et al., 2012).

The application of auxins and cytokinins, either individually or in combination, has been shown to enhance cell division and tissue growth in seaweed cultures, although excessively high concentrations can inhibit regeneration (Bradley & Cheney, 1990). Gibberellins promote cell elongation and biomass accumulation, while abscisic acid and ethylene are involved in stress responses and developmental regulation (Spagnuolo et al., 2022).

In agricultural applications, the effectiveness of seaweed-based biostimulants is largely attributed to their PGR content rather than merely their mineral composition (Crouch & Staden, 1993; Panda et al., 2012).

Consequently, the study and utilization of PGRs in seaweeds represent a key area for advancing both ecological understanding and the development of commercial biotechnological applications.

PGRs have been shown to be particularly effective when tested on competent tissues, i.e. cells in a hormone-receptive state due to their high multiplicative activity, e.g. spores. PGRs have been shown to be particularly effective when tested on competent tissues, i.e. cells in a hormone-receptive state due to their high multiplicative activity, e.g. spores or sporangium.

Research shows that polyamines, especially spermine, can induce and promote sporulation in seaweeds, thus Polyamines, particularly spermine, induce the maturation of the cystocarp in several species of this group (Guzmán-Urióstegui et al., 2002; Sacramento et al., 2004, 2007, Kumar et al. 2015).

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There is a wide variety of volatile organic compounds in marine macroalgae (Garcia-Jimenez et al., 2013; Garcia-Jimenez & Robaina 2017, 2019) and among them, two especially active also described in higher plants: ethylene and methyljasmonate (Garcia-Jimenez et al., 2012, 2016; 2017, 2018, Garcia-Jimenez & Robaina 2017, 2019).

Both methyljasmonate (MeJa) and ethylene cause drastic changes in the reproductive status of red algae species, such as *Pterocladiella capillacea* and *Grateloupia imbricata* in the short term, seven days for ethylene and only 2 days for MeJa. Ethylene induced the maturation of tetrasporangia of the sporophytic phase (2n) of *P. capillacea* (Garcia-Jimenez et al., 2012); in the case of MeJa, its action with effects as sudden as the reduction of the maturation period and the dehiscence of the cystocarp, makes us suspect a parthenogenetic induction of the formation of carpoespores in *G. imbricata* (Garcia-Jimenez et al., 2016; Garcia-Jimenez & Robaina 2017, 2019). The effects of these two volatile hormones are translated at the molecular level into a symphony of activation, deactivation and / or gene coordination according to the reproductive events and / or synthesis of these regulators (Garcia-Jimenez et al., 2016, 2017, 2018).

Although their action on differentiated tissues remains controversial, there is evidence of the usefulness of growth regulators in inducing the development of reproductive structures and the growth of the propagules, which may prove to be an innovation for the future development of efficient hatcheries. Inducing sporulation/reproductive structure with PGRs in hatchery work is to overcome reliance on seasonal collections of wild material.

Science-mapping PGR´s and seaweeds sporulation

The scientific mapping of the field seaweed or alga and spore and hormone or plant regulator returns 85 papers between 1989 and 2025, of which the keyword analysis (n =613) with a preponderance of studies on red algae (Figure 19).

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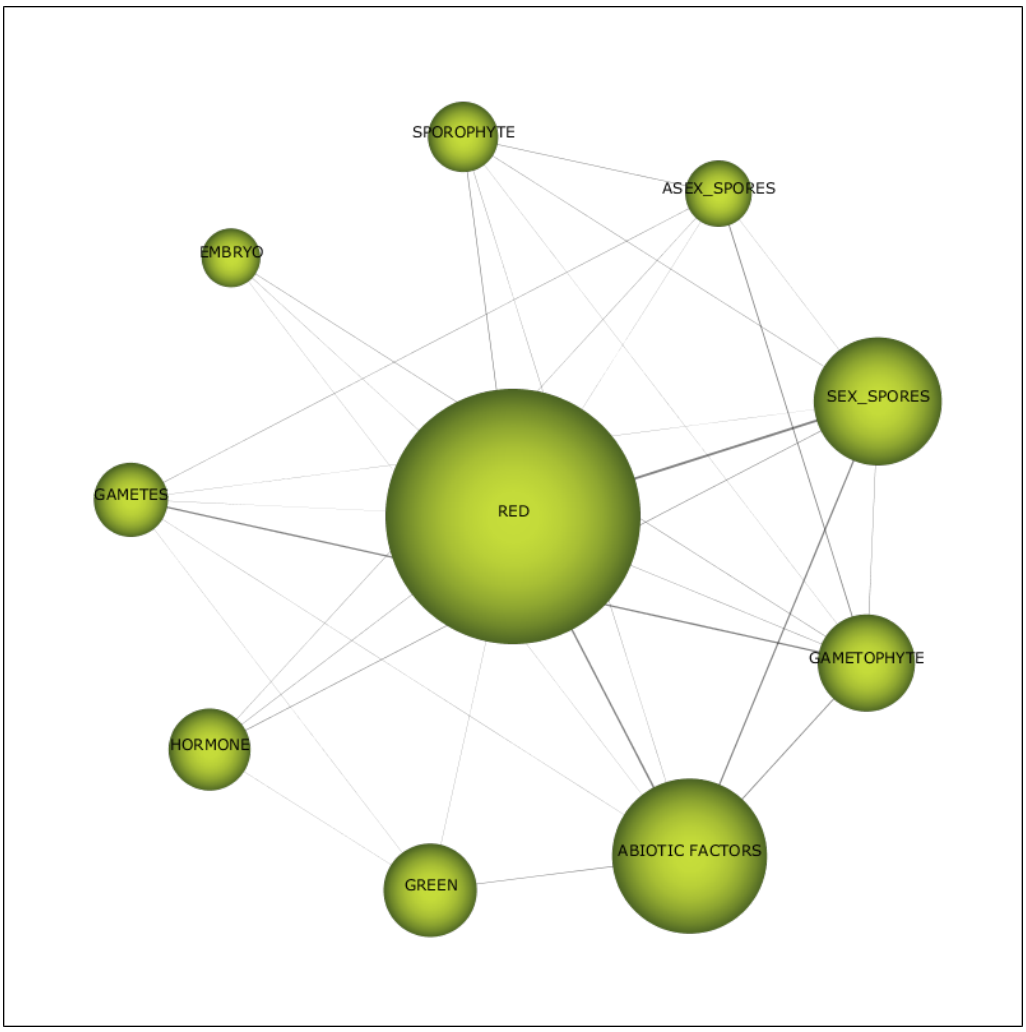

Figure 19. Concept network as a result of science mapping of seaweed or alga and spore and hormone or plant regulator field

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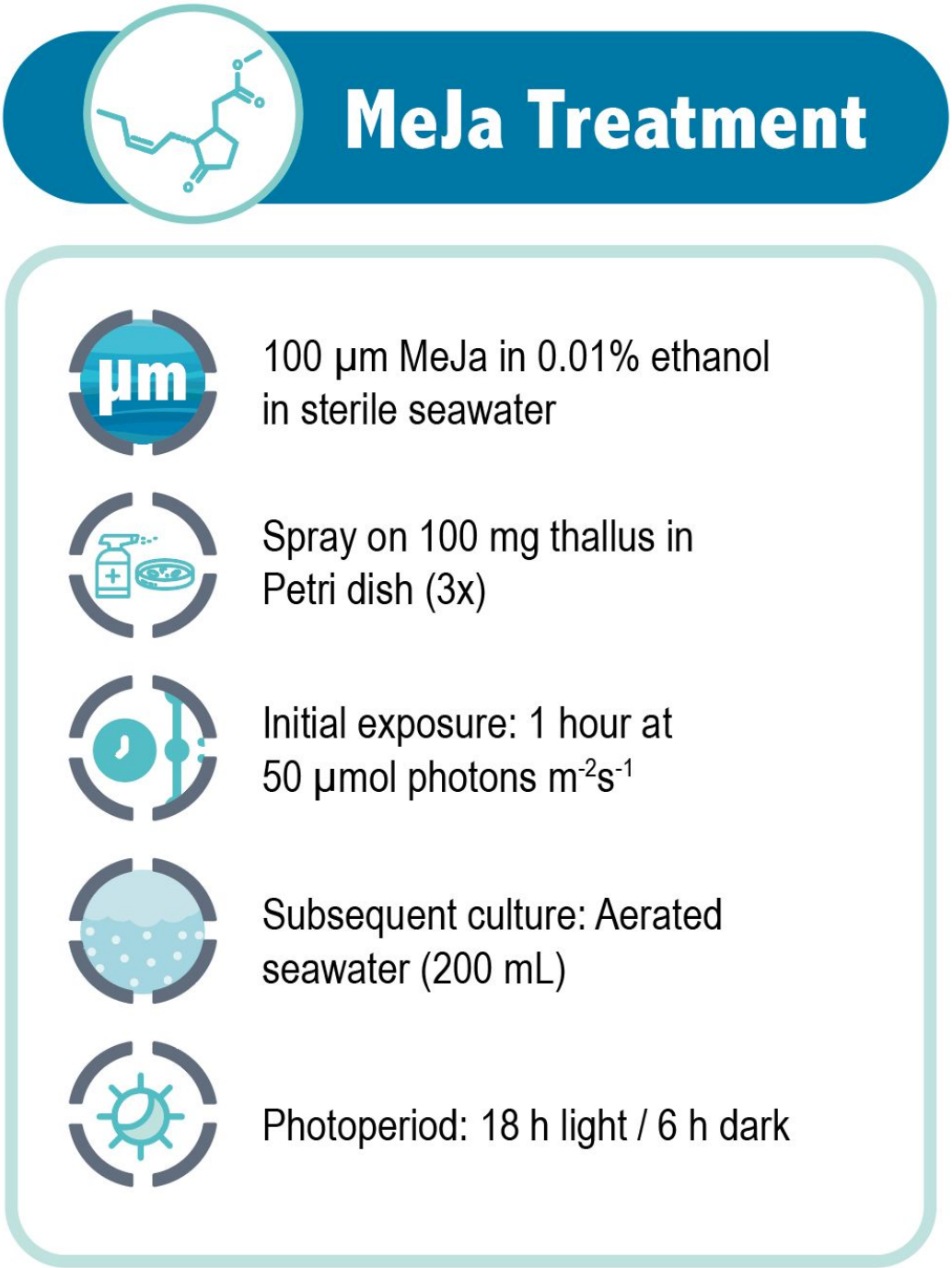

Figure 20. *The effects of the plant growth regulator Methyljasmonate (MeJa) on the induction of sporulation in red seaweeds. A simple procedure to induce sporulation is outlined*

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Genetic characterization of species. The first step to breeding, disease combat and genome editing.

Seaweed aquaculture under European standards requires precise control over the species being cultivated, even at the strain level. This is particularly important if breeding programs are to be implemented, given the high phenotypic plasticity of these organisms (Figure 21).

***Figure 21**. Specimens of the genus Enteromorpha (filamentous, left) and Ulva (blade, right), formerly separated into two genera and to date reassigned as Ulva genus after Hayden et al. 2012*

Various genetic approaches have been employed to investigate the diversity, population structure, and adaptive potential of marine macroalgae. Population genetics studies have utilized tools such as microsatellites, RAPDs, SSCPs, RFLPs, isoenzymes, and DNA sequencing, particularly in red and brown algal species, to assess genetic structure and variability among populations; genetic barcoding using the COI (cytochrome oxidase I) marker has proven effective in distinguishing closely related species due to its higher interspecific divergence compared to other markers like rbcL; while Genome-Wide Association Studies (GWAS) have become a powerful tool in the genetic characterization of cultivars and the selection of high-performing varieties, particularly in major agricultural crops such as rice, maize, wheat, and soybean.

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Science mapping genetic characterization of cultivated seaweed species

Improvements in our methods for sequencing genetic material have recently allowed us to access the fine structure of the genome of complex organisms such as seaweeds, so that more and more data are accumulating from areas of the genome with sufficient variability to characterise at the cultivar level, or to associate that variability with traits of interest. The novelty and innovation of the field means that the data are concentrated on one type of seaweed or marker, but we estimate that it will soon be possible to find markers of variability useful for the selection and genetic improvement of all interesting seaweeds. In this sense, the most progress has been made in brown seaweed (Figure 22) and among the markers found, the bibliography found points to those described in Table 3.

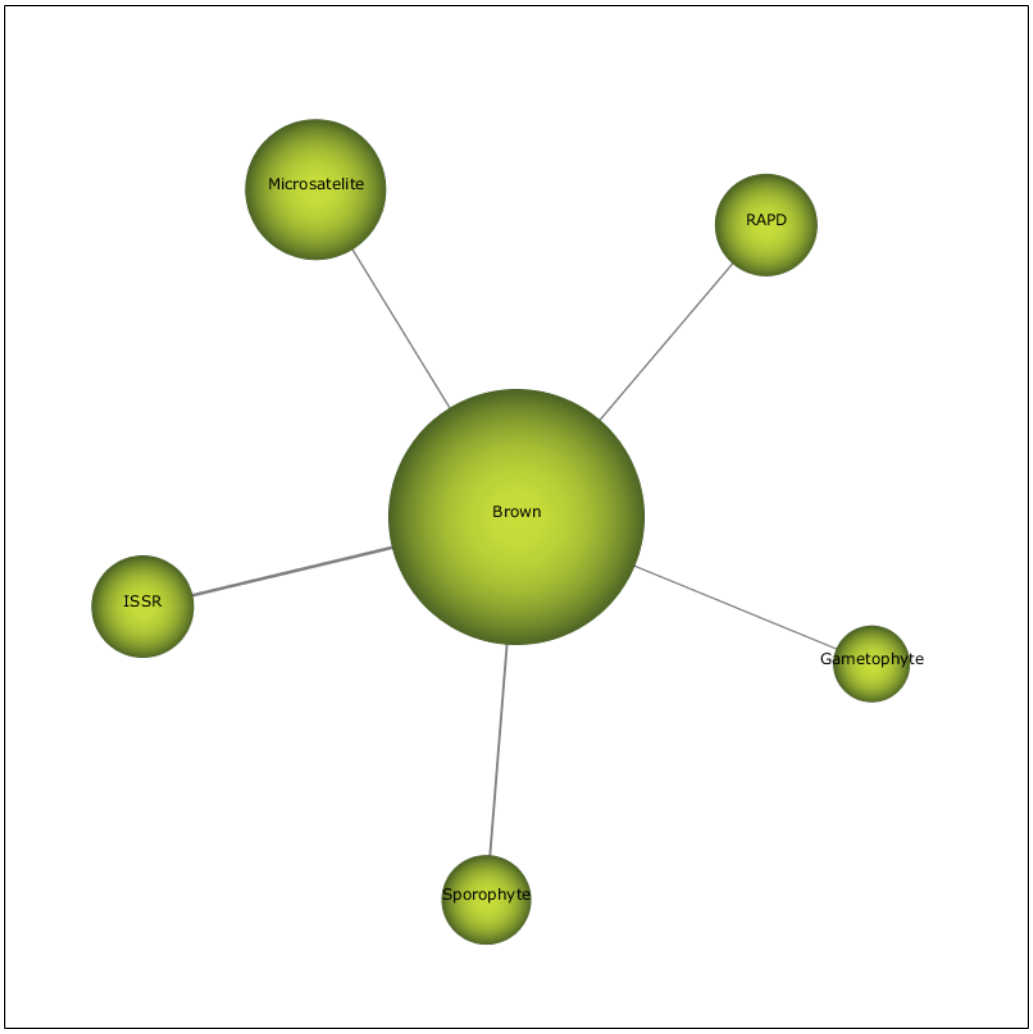

***Figure 22**. Concept network as a result of science mapping field **genetic markers and seaweed and cultivated** (32 papers since 2004, 246 keywords analysis)*

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Table 3. Genetic markers found when mapping the field ***genetic markers and seaweed and cultivated***

Full Name	Acronym	Description	Examples / Notes
Inter-Simple Sequence Repeat	ISSR	A marker technique that amplifies regions between microsatellites using primers designed for SSRs. It detects polymorphisms in multiple loci.	Used in genetic diversity studies in plants (e.g., Oryza sativa, Zea mays).
Single Nucleotide Polymorphism	SNP	A variation at a single base pair in the DNA sequence among individuals. Highly abundant and stable.	
Microsatellite Repeats	SSR	Short tandem repeats of 1–6 base pairs. Highly polymorphic and codominant. Also known as SSRs (Simple Sequence Repeats).	Forensic DNA profiling, parentage testing. Example: (CA)n repeats.
Random Amplified Polymorphic DNA	RAPD	PCR-based method that amplifies random DNA segments with single primers of arbitrary sequence.	Used in genetic fingerprinting and biodiversity analysis.
Gene Sequence Marker	–	Specific gene or sequence known to be associated with a trait or phenotype.	rbcL, Cox genes
Genome-Wide Association Study	GWAS	A method to associate specific genetic variants (mainly SNPs) with traits across the genome in large populations.	GWAS identifying loci linked to Type 2 Diabetes, height, or Alzheimer's.

It follows an overview of all these techniques, highlighting how to approach them experimentally and key application in seaweed aquaculture.

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DNA barcoding for molecular species of species

DNA barcoding is a taxonomic technique that uses a short, standardised genetic fragments to identify species by comparison with a database of known sequences. For example, universal markers such as mitochondrial or chloroplastic genes (COI, rbcL) and ribosomal regions (ITS) are used depending on the algal group. In green macroalgae of the genus *Ulva*, the ITS (internal transcribed spacer) region of ribosomal DNA has been successfully used to distinguish species, given its high variability between closely related taxa (Favot et al., 2019). This methodology is based on PCR amplification and sequencing of the genetic marker, followed by comparison with references to determine the identity of the sample.

Key Applications of DNA Barcoding in Seaweed Aquaculture

Species verification: Confirms the identity of cultivated species and detects unwanted or wild-growing species (e.g., *Ulva flexuosa* in Portugal) (Favot et al., 2019).

Quality control & traceability: Prevents fraud and ensures the processed product matches the declared species (e.g., *Porphyra/Pyropia*, *Kappaphycus, Eucheuma*) (Tan et al., 2012).

Hidden diversity revealed: Detects cryptic species or lineages, aiding in selecting high-performance strains for cultivation.

Environmental monitoring: Early detection of invasive or contaminant species via eDNA and metabarcoding enhances biosecurity.

Business and production impact: Reduces risk of misidentification, improves yield and product consistency, and ensures market confidence.

Support for innovation: Facilitates the creation of genetic databases, discovery of bioactive compounds, and protection of commercial strains.

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Microsatellites, SNPs and molecular fingerprinting to distinguish genotypes

Molecular tools make it possible to **distinguish genotypes within species** and to quantify genetic variability. Polymorphic DNA markers are used for this purpose, including **microsatellites (SSRs)** and **SNPs** (single nucleotide polymorphisms). *Microsatellites* are highly variable short repetitive sequences that act as genetic "fingerprints" of each individual, while *SNPs* are point changes in the genomic sequence that can be detected in large numbers by sequencing. Historically, techniques such as RAPD, AFLP or RFLP were also used, but in the last decade, SSRs and especially SNPs have gained prominence thanks to massive sequencing. In macroalgae, developing these markers used to be a challenge, but today there are efficient methods such as **RAD-seq** (restriction enzyme-associated DNA sequencing) or **GBS** (*genotyping-by-sequencing*) to discover thousands of SNPs and microsatellites quickly. A recent study (Mauger et al. 2023) showed that *ddRAD-seq* could identify **thousands of** novel **microsatellite loci** in several macroalgae **quickly and affordably**, yielding 105 useful polymorphic markers in 6 different species. In contrast to traditional marker development methods, which were slow and expensive - next-generation sequencing has greatly accelerated the availability of genetic tools for macroalgae.such as **RAD-seq** (restriction enzyme-associated DNA sequencing) or **GBS** (*genotyping-by-sequencing*) to discover thousands of SNPs and microsatellites quickly. A recent study (Mauger et al. 2023) showed that *ddRAD-seq* could identify **thousands of** novel **microsatellite loci** in several macroalgae **quickly and affordably**, yielding 105 useful polymorphic markers in 6 different species. In contrast to traditional marker development methods, which were slow and expensive - next-generation sequencing has greatly accelerated the availability of genetic tools for macroalgae.

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Key Applications of Seaweed Microsatellites, SNPs and molecular fingerprinting in seaweed Aquaculture

Assessment of genetic diversity: SSRs and SNPs reveal narrow genetic bases in cultivated lines (e.g., few clonal genotypes in *Kappaphycus* and *Eucheuma*; Teasdale et al., 2021). In Malaysia, limited mitochondrial haplotype variation has been observed (Satriani et al., 2023; Lim et al., 2021; Zuccarello et al., 2006).

Strain identification and traceability: Molecular markers verify clonal identity and differentiate elite lines, as shown in *Kappaphycus alvarezii* through genetic fingerprinting tools (e.g., MARINER Sugar Kelp Selective breeding project, Seamark project, BlueBioBoost project)

Parent stock selection: In breeding systems like kelp (*Saccharina*), markers confirm parentality and identify superior hybrid crosses (Bråtelund et al., 2024).

Monitoring genetic changes: Markers track genetic erosion in vegetatively propagated crops and detect gene flow between wild and cultivated populations.

Identifying genes of interest: Neutral markers (e.g., SSRs, SNPs) support the discovery of genes linked to desirable traits (see QTL/GWAS studies).

Business impact: Marker use accelerates cultivar development (e.g., elite *Saccharina* lines in China) and enhances product traceability, resilience, and competitiveness.

Bioprospecting and innovation: Genetically profiled collections help identify strains with valuable biochemical properties, supporting targeted product development and R&D.

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Next-generation sequencing and genomic resources in macroalgae

The last decade has seen a significant increase in the availability of macroalgal genomic data, largely due to the development and application of high-throughput next-generation sequencing (NGS) technologies. Advances in mass sequencing (Illumina, PacBio, Oxford Nanopore, etc.) have led to significant developments in this field, as it made possible to decipher the **complete genomes** of numerous macroalgae and to construct **transcriptomic libraries** to understand gene expression. Since the first nuclear genome of a macroalga, *Ectocarpus* sp., a model brown alga, was published in 2010 (Cock et al., 2010), **genomes of representatives of all major groups** (red, brown and green algae) have been **sequenced**.

Some milestones include the genome of the Laminariales *Saccharina japonica*, nori (*Pyropia yezoensis/Neopyropia*), the red alga *Chondrus crispus*, the green alga *Ulva mutabilis*, and more recently that of macroalgae of commercial interest such as *Sargassum fusiforme* or *Macrocystis pyrifera*. In parallel, transcriptomes (with RNA-seq) have been generated for dozens of species under different conditions, providing catalogues of active genes and metabolic pathways. These initiatives have given rise to **genomic resources** (sequences, gene annotations, genome-scale SNP-type markers, etc.) that are the basis for advanced association studies and genetic manipulation. However, it is important to note that many macroalgal genomes remain partially uninterpreted: assessments indicate that more than 50% of predicted genes in algae still lack known function, reflecting how much remains to be investigated in the molecular biology of these organisms (Liang et al., 2014; Xu et al., 2016; Li et al., 2021; Liu et al., 2023, Root, 2022; Poo et al., 2018).

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Key applications of whole genomics in seaweed aquaculture

Gene and metabolic pathway discovery: Genomes and transcriptomes help identify genes linked to growth, stress tolerance, and biosynthesis of key compounds (e.g., agar, carrageenan).

Genome-wide SNP databases: Genomic references enable SNP mapping for GWAS and genomic selection, e.g., SNP chips in Saccharina (Zhang et al., 2015).

Reproductive cycle insights: Genomics clarifies life cycle regulation (e.g., sex markers, phase transition), supporting breeding of improved sporophytes.

Transcriptomics for stress resilience: Comparative expression studies reveal resistance pathways (e.g., in *Saccharina japonica*; Zhuang et al., 2024), guiding selection and treatments.

Metagenomics of algal microbiomes: Microbiome analysis identifies beneficial or harmful microbes, enabling probiotic applications in seaweed culture.

Business impact: Accelerates elite variety development, reduces losses, and allows trait-specific breeding (e.g., agar yield, color, texture).

Bioproduct development: Genomic data enable biotechnological innovations in biofuels, pharmaceuticals, and materials; supporting biotech diversification and R&D partnerships.

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Marker-assisted selection, QTL mapping and GWAS studies

Once abundant genetic markers and genomic data are available, advanced breeding strategies such as **marker-assisted selection (MAS)** and **genome-wide association studies (GWAS)** can be undertaken. These techniques seek to correlate molecular variants with important quantitative phenotypic traits (growth, metabolite content, disease resistance, etc.). There are two main approaches:

- **QTL (Quantitative Trait Loci) mapping:** this consists of obtaining a mapping population (e.g. offspring from a cross between contrasting parents, or haploid/diploid lines in species with alternating cycles) and genotyping it with markers and then associating regions of the genome with variations in the trait of interest. The result is QTL loci at certain markers that explain part of the phenotypic variation. In macroalgae, this approach has been applied to algae with manageable sexual reproduction. A pioneering example is *Pyropia yezoensis*, where a genetic linkage map was constructed using SRAP markers and QTL were identified for several economic traits of the algae such as stem width and length (Huang & Yan, 2019). Similarly, in *Saccharina japonica* mapping studies have detected QTL for yield traits such as frond length and frond width (Wang et al., 2023).
- **GWAS (Genome-Wide Association Studies):** This approach exploits genetic variation in broad populations (whether wild, crop collections or varieties) to find statistical associations between SNPs distributed across the genome and the trait of interest. It requires genotyping many closely unrelated individuals with sufficient historical recombination events. Although more common in terrestrial plants, it is recently spreading to macroalgae as genomically characterised populations become available. For example, in 2024 Wang et al. published a GWAS in *Neopyropia yezoensis* (nori seaweed) that analysed 124 genomes from cultivated and wild populations, identifying specific SNPs associated with **thallus length traits** and detecting traces of domestication selection in certain candidate genes (e.g., growth-related). This study combined GWAS with *selective sweep* analysis, marking a milestone in the application of association methods in cultivable red algae.

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Key applications of Marker-Assisted Selection and QTL/GWAS in Seaweed Breeding

Development of improved varieties: SNP markers linked to traits like growth or disease resistance enable early selection (e.g., *Saccharina japonica, Pyropia haitanensis*; Wang et al., 2018; Liu et al., 2024).

Improvement of quality traits: GWAS can identify SNPs for traits like carrageenan yield or protein content, aiding selection of superior *Kappaphycus* or *Ulva* strains.

Disease and stress resistance: MAS facilitates the introgression of resistance QTL (e.g., ice-ice resistance in Kappaphycus; Azizi et al., 2018) into cultivated stocks.

Optimised breeding programmes: Knowing favourable alleles enables strategic crosses and gene stacking to create multi-trait elite varieties.

Foundation for genomic selection (GS): Although not yet widely applied in macroalgae, GS promises even more accurate selection using thousands of SNPs.

Business impact: Elite strains with improved growth, resistance, or quality traits increase profitability, reduce losses, and open new product markets.

Innovation and competitiveness: MAS/GWAS support proprietary cultivar development, IP protection, and targeted bioproduct research (e.g., high-ulvan *Ulva*, pharmaceutical-grade Sargassum).

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Molecular diagnosis of diseases in seaweeds

Seaweed diseases (caused by fungi, oomycete-like protists, bacteria or viruses) represent a significant risk to intensive farming, and molecular tools are transforming their diagnosis and control. Traditionally, pathogen detection in algae was late (when symptoms were already evident, e.g. spots, rots) and relied on microscopic observation or microbiological culture, slow and sometimes inconclusive methods.

Rapid techniques such as pathogen-specific **PCR**, **real-time quantitative PCR (qPCR)** to estimate infectious loads, and even metagenomic approaches to discover unknown aetiological agents are now available. The basic principle is to amplify DNA/RNA sequences characteristic of the pathogen (e.g. fungal ITS, bacterial 16S genes, viral genes) from samples of algal tissue or culture water, and to detect their presence even at early stages of infection.

These techniques offer **very high sensitivity** - they can detect minute amounts of pathogenic material before it spreads widely. For example, researchers in China developed a qPCR assay capable of detecting in seawater concentrations as low as **10 zoospores per mL** of the oomycete *Pythium porphyrae* (the pathogen causing the "stripe rust" disease of *nori*), and 100 zoospores/mL of *P. chondricola* (another similar oomycete) (Liu et al., 2024). Furthermore, molecular biology allows differentiation between very similar pathogens: using specific markers or enzymatic digests (PCR-RFLP), the same study was able to unequivocally distinguish between *P. porphyrae* and *P. chondricola*, which is crucial given that both species cause similar symptoms but may have different epidemiology (Lee et al., 2021).

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Key application of molecular techniques to early disease detection and combat

Accurate identification of causative agents: DNA tools reveal pathogens behind syndromes like ice-ice in Kappaphycus (e.g., *Vibrio*, *Cytophaga* spp.).

Strain-specific diagnostics: PCR can distinguish virulent strains (e.g., green spot virus in *Pyropia*), guiding targeted responses.

Quantification of infection: qPCR measures pathogen load, helping define action thresholds (e.g., Pythium abundance correlates with red disease risk).

Resistance breeding support: Identifying specific pathogens (e.g., *Pythium porphyrae* in *Pyropia*) enables selection of resistant lines using molecular markers.

Business impact: Early detection prevents harvest losses, enables better planning, reduces treatment costs, and allows certified pathogen-free seed production.

Innovation and product quality: Disease-free cultures ensure reliable bioproduct yields; understanding pathogen-host interaction supports new health strategies (e.g., probiotics, immunity markers).

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Genome editing and advanced biotechnology in macroalgae

The latest frontier of molecular tools in macroalgae is **genome editing and genetic engineering**, which allows direct modification of the DNA of algae to give them desired characteristics.

For a long time, genetic manipulation in macroalgae lagged behind due to the difficulty of transforming their cells (resistant cell walls, complex life cycles, etc.). However, recent advances show that **CRISPR/Cas9** and other editing technologies can work in some macroalgae, at least under laboratory conditions. In fact, **proof-of-concept CRISPR editing** has already been achieved in two brown algae (including *Saccharina japonica* itself) and in a green alga (*Ulva prolifera*), marking the first cases of gene editing in macroalgae (De Saeger et al., 2024). In these initial studies, to circumvent the low editing efficiency, researchers co-introduced constructs targeting the *adenine phosphoribosyl transferase* (APT) gene, so that they could select edited cells (mutating APT confers resistance to certain adenine analogues, making it easier to isolate mutants).

Even with these advances, the percentages of edited cells obtained have been low, and **the field faces challenges** such as the need to improve stable transformation of macroalgae and to better understand how these organisms repair DNA (repair is key to increasing CRISPR's efficacy). In addition to CRISPR, classical random mutagenesis techniques (radiation, chemicals) combined with molecular selection are being explored to generate improved varieties.

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It should be recalled that even before CRISPR, **spontaneous or induced mutant breeding had already produced** in macroalgae: for example, strains of red algae with faster growth, different pigmentation (pale green vs. deep red) or high spore production were isolated, which then served as the basis for commercial strains (De Saeger et al., 2024). Genome editing takes this to the next level by allowing precise alterations in specific genes.

Key applications of gene editing in seaweed aquaculture

Trait enhancement: Editing can deactivate growth-limiting genes or overexpress biosynthetic genes to boost production (e.g., Tic20 for leaf size in *S. japonica*).

Disease/stress resistance: Introducing resistance genes or removing pathogen entry points can enhance algal resilience (e.g., antifungal pathways in Porphyra).

Reproductive cycle control: Editing may block sexual phases, induce sterile lines for biosafety, or synchronize spore production.

Bioproduct synthesis: Macroalgae could become biofactories for pharmaceuticals, enzymes, or bioplastics via engineered biosynthetic pathways.

Functional gene studies: Knockout mutants help understand gene roles, improving target identification for future breeding.

Business impact: Edited strains may dominate high-value markets (e.g., faster-growing *Kappaphycus* or carrageenan-enhanced lines); increases yield and adaptability. The use of these techniques will position companies at the biotech frontier, attracting R&D collaborations in pharma, materials, and marine bioenergy.

Future outlook: CRISPR editing in *Saccharina japonica* (Shen et al., 2023) and *Ulva prolifera* (Ichihara et al., 2021) mark early successes. First edited commercial strains could emerge within 5–10 years; transformative R&D potential supports sustained industry investment (De Saeger et al., 2024).

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Cryopreservation for germplasm conservation

Cryopreservation is the process of cooling and storing biological materials—such as cells, tissues, or organelles—at very low (subzero) temperatures to halt all biological activity and preserve their viability and physiological functions for future use. This technique is essential for long-term preservation, as it prevents cellular damage and death that would occur with simple freezing due to ice crystal formation, osmotic shock, and membrane damage (Iussig et al., 2019; Jang et al., 2017; Parihar et al., 2023; Elliott et al., 2017; Rajan & Matsumura, 2018).

The origins of cryopreservation can be traced back to early observations of freezing tolerance, but the field began to advance significantly with the accidental discovery of glycerol's protective effects on cells in the mid-20th century. The first major successes in cryopreservation, particularly for reproductive cells, were achieved in the 1980s. Since then, the development of new cryoprotectants and techniques, such as vitrification, has greatly improved outcomes and expanded applications in medicine, biotechnology, and conservation (Iussig et al., 2019; Carr et al., 2002; Vaishnav et al., 2022; Elliott et al., 2017; Marcantonini et al., 2022; Murray & Gibson, 2022).

Key Elements of cryopreservation are cryoprotectants, cooling and thawing rates and storage conditions

Cryoprotectants are chemical compounds added to biological samples before freezing to prevent damage from ice formation and osmotic stress. Common cryoprotectants include glycerol, dimethyl sulfoxide (DMSO), and sugars. They work by reducing ice formation, stabilizing cell membranes, and sometimes enabling vitrification (the formation of a glass-like state without ice crystals). However, their use must be carefully balanced, as high concentrations can be toxic to cells (Carr et al., 2002; Parihar et al., 2023; Vaishnav et al., 2022; Elliott et al., 2017; Rajan & Matsumura, 2018; Marcantonini et al., 2022; Murray & Gibson, 2022).

The rate at which samples are cooled and thawed is critical. Slow cooling can help prevent intracellular ice formation, while rapid cooling (vitrification) can avoid ice altogether but requires higher concentrations of cryoprotectants. Both approaches have their own advantages and challenges, and the optimal method depends on the type of biological material being preserved (Iussig et al., 2019; Jang et al., 2017; Carr et al., 2002; Bai et al., 2023; Parihar et al., 2023).

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Maintaining ultra-low temperatures (typically in liquid nitrogen at -196°C) is essential for long-term storage, as it ensures that all metabolic and biological processes are effectively stopped (Jang et al., 2017; Parihar et al., 2023; Rajan & Matsumura, 2018).

Science-mapping cryopreservation of seaweeds

Scientific mapping offers us a panorama of scientific production since 1990, discrete in terms of productivity, but important in terms of the consideration of the phycology community for having these techniques. Work has been carried out with the different groups of algae (red, brown and green), particularly with brown algae, focusing on obtaining a good cryoprotectant (Figure 23).

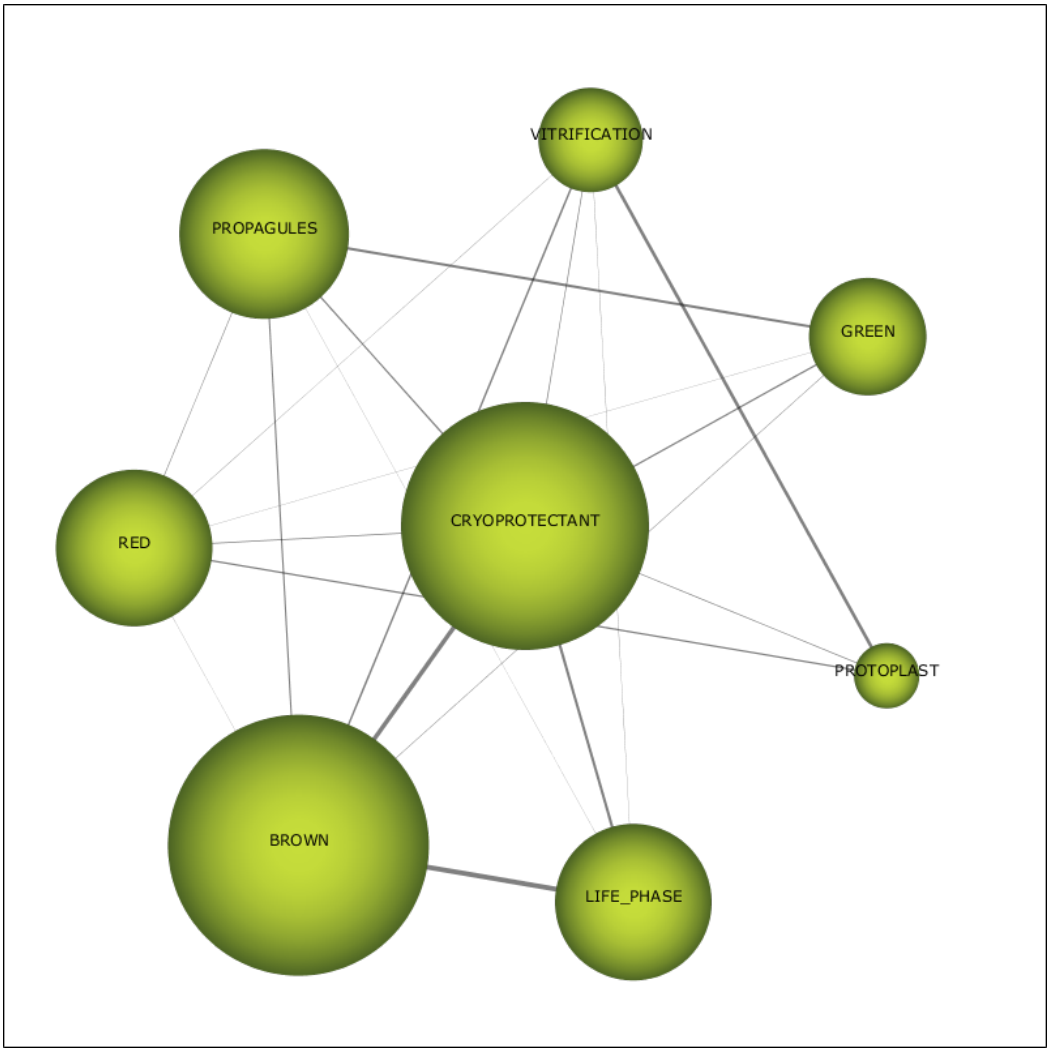

Figure 23. *Concept network as a result of science mapping of seaweed/alga cryopreservation scientific field.*

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Effectiveness of Seaweed Cryopreservation

Cryopreservation has been shown to maintain high viability in various seaweed species, including both model and economically important algae. Post-thaw viability rates can reach 64–87% depending on the species and protocol used, indicating that cryopreservation is a reliable preservation method for seaweeds (Avila-Peltroche et al., 2023; Visch et al., 2019; Taylor & Fletcher, 1998).

Concerning cryoprotectant substances, glycerol and proline (10% :10%) proline has been particularly effective, yielding the highest post-thaw viability in *Ectocarpus siliculosus* and *Acinetospora asiatica* (Avila-Peltroche et al., 2023). For *Saccharina latissima* gametophytes, 10% DMSO used with controlled-rate cooling produced the best results for both male and female gametophytes (Visch et al., 2019).

The following tables summarize the protocols used for different authors in different seaweeds *Ectocarpus* sp. and *Laminaria digitata*, and in the marine plant *Posidonia oceanica* by two authors of this report (**PGJ, MCA**).

The conventional colligative **cryopreservation protocol** developed by Heesch et al. 2012 for the filamentous brown alga *Ectocarpus* sp. involves the following materials and steps:

Material

• A programmable, controlled rate cooler, or alternatively a passive cooling unit and a −80°C freezer.

• Cryoprotectant solutions: 10% (v/v) DMSO and 9% (v/v) d-sorbitol in an appropriate culture medium.

• Plasticware: membrane filters (0.5 µm pore size).

• Petri dishes (5 cm diameter).

• Universal tubes (20 mL).

• Modified Provasoli (MP) medium (West JA & McBride DL, 1999).

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Experimental procedures

Cryopreservation of cultures

1. One to two weeks before cryopreservation separate thalli into explants (approximately 1–2 mm in length). Then transfer to Erlenmeyer flasks containing 100 mL of culture medium under the same culture conditions.

2. Prepare 10 mL aliquots of cryoprotectant solution (10% [v/v] DMSO and 9% [v/v] d-sorbitol in the appropriate culture medium) and filter-sterilize into a sterile universal tube.

3. Aseptically transfer 1 mL aliquots of sterilized cryoprotectant solution into 2 mL cryovials.

4. Aseptically transfer intact sections of thalli to each cryovial, seal the cryovials, and incubate for 15–30 min at room temperature.

5. Program the controlled cooler:

- Start temperature 20°C;
- ramp, cool at −1°C min to −40°C;
- dwell, hold at −40°C for 10 min.

6. Start the program to purge the system with nitrogen vapor and to allow the system to stabilize at the start temperature.

7. On reaching the start temperature (most systems have an audible alarm), transfer the cryovials to the cooling chamber of the programmable cooler and initiate the cooling ramp.

8. After the end of the program, an alarm will sound; rapidly transfer the cryovials to a small dewar containing liquid nitrogen using long forceps.

9. Samples for storage should be transferred to the cryostat (ultra-cold freezer) in the liquid nitrogen containing dewar. Transfer of cryovials to the storage system should be performed rapidly using long forceps.

Recovery of cultures

10. To recover cultures, vials are thawed by placing in a preheated water bath (40°C) and agitated until the last ice crystal has just melted.

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11. On thawing, rapidly transfer to a laminar flow/biological safety cabinet and wipe the outside of the vial with 70% (v/v) ethanol.

12. By using a disposable plastic pipette (Pastette), the cryoprotectant solution is aseptically removed, discarded, and replaced by 1 mL of fresh sterile medium. The thallus is then aseptically transferred to a labeled Petri dish containing 10 mL of an appropriate medium. Then cover in aluminum foil and relabel with the strain designation and date.

13. Incubate at the standard culturing temperature for the cryopreserved organism; after 24 h, partially remove the foil and after a further 24–96 h, remove all the foil covering.

14. After one week, by using standard aseptic techniques, replace the medium.

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The **vitrification-based protocol** developed is based on Harding et al. 2008 and successfully employed for *Laminaria digitata* gametophytes, involves the following materials and steps:

Material

- Alginate (5% w/v) encapsulation solution is made from low viscosity (3%) sodium salt. The alginate solution is prepared in preheated (60°C) culture medium in a 250 mL Schott bottle; 5 g of sodium alginate is directly added to the bottle containing deionized water (which should contain a magnetic stirring rod). The bottle contents are vigorously shaken (not stirred) until the alginate is wet (it will not completely dissolve) and thoroughly dispersed in the solution. Sterilize by autoclave the alginate at 121°C for 15 min. Remove the bottle between 80°C and 100°C and place it on a magnetic stirrer until the alginate dissolves (this can be overnight).
- Calcium chloride (100 mM) solution is prepared in deionized water.
- Sucrose (0.5 and 0.75 M) dehydration medium is made in the appropriate culture medium.
- Sterile 9 cm filter papers.
- Sterile 9 cm Petri dishes.
- Multiwell recovery plates (Biddy Sterilin Ltd., 100 mm square Petri dish, or equivalent).
- Sterile forceps.
- Heated magnetic stirrer.
- Thermometer and humidity meter (optional).
- ESP culture medium.

Experimental procedures

Preparation of encapsulated beads

1. One to two weeks before cryopreservation, separate thalli into explants (approximately 1 mm in length). Then transfer to Erlenmeyer flasks containing 100 mL of ESP culture medium, under the same culture conditions.

2. Remove the supernatant and add ~10 mL of 5% (w/v) alginate.

3. Gently swirl the mixture of algae and alginate to evenly distribute the sections of thalli, but ensure that air bubbles are not formed.

4. By using a disposable sterile plastic Pastette and holding it in a vertical position, slowly dispense the alginate/algal solution dropwise into a 150 mL of 100 mM $CaCl_2$ and allow the encapsulated beads (henceforth beads) to equilibrate for 60 min.

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5. Carefully, decant off the calcium solution and transfer the beads to 0.5 M sucrose in culture medium to osmotically dehydrate the cells for 24 h (under standard light and temperature conditions).

6. Decant this medium and replace with 0.75 M sucrose in culture medium for another 24 h (under standard light and temperature conditions).

7. Remove the beads from the pre-culture sucrose solution and remove excess liquid sucrose medium by blotting the surface of the beads on sterile filter (7–8 cm) papers placed on Petri dishes.

8. Transfer the beads to sterile Petri dishes (9 cm) ensuring that they are not touching each other and that they are evenly distributed throughout the dish.

9. Place the open Petri dishes with the beads in a horizontal flow laminar airflow cabinet. Note and monitor the temperature (~25°C optimum) and laboratory relative humidity.

10. Air-dry the beads in the airflow (~1 m s^{-1}) for 3 to 4 h. This normally results in beads with a residual moisture content of ~25%–30% (w/w).

Cryopreservation of cultures

11. Transfer the desiccated beads into cryovials (10 beads per cryovials) and plunge directly into liquid nitrogen in a 1 L dewar.

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The conventional colligative cryopreservation protocol developed by Carrasco-Acosta and Garcia-Jimenez (2021) for free cells of the seagrass *Posidonia oceanica* consists of the following materials and steps:

Material

- Liquid Murashige and Skoog (MS) medium (pH 5.7) + 30 g/L sucrose
- Rotary shaker
- Solution of 1.3 M DMSO
- Solution of 60% glycerol
- Sterile filter paper
- Laminar air flow hood (work entirely under laminar air flow using autoclave-sterilized equipment).

Experimental procedures

Cryopreservation of cells

1. Cells were suspended at a concentration of 10^6 cells/mL in a cryoprotectant mixture of 1.3 M DMSO with 60% glycerol.

2. The cell suspension was transferred into sterile cryovials.

3. Cryovials were first placed at −20°C for 5 minutes to initiate freezing.

4. Subsequently, the cryovials were stored at −80°C for 24 hours for long-term freezing.

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Seaweed microbiome and aquaculture

Seaweeds host complex communities of microorganisms—known as the seaweed microbiome or holobiont—that play essential roles in their health, development, and ecological function. The seaweed microbiome is highly dynamic, shaped by both the host and environmental factors, and includes bacteria, fungi, viruses, and other microbes that can be beneficial, neutral, or harmful.

Ongoing research is expanding understanding of these complex relationships, with promising applications in aquaculture, biotechnology, and ecosystem management (Ren et al., 2022; Marzinelli et al., 2024; Saha & Weinberger, 2019; Li et al., 2022).

Science-mapping seaweed/algae microbiome and aquaculture

The scientific mapping provides an overview of scientific production since 2015. Work has been carried out with the different groups of algae (red, brown and green algae), particularly with brown algae, focusing on the bacterial characterisation of the microbiome using state-of-the-art genetic techniques. This is confirmed to be an emerging field of research of great interest, as described below (Figure 24).

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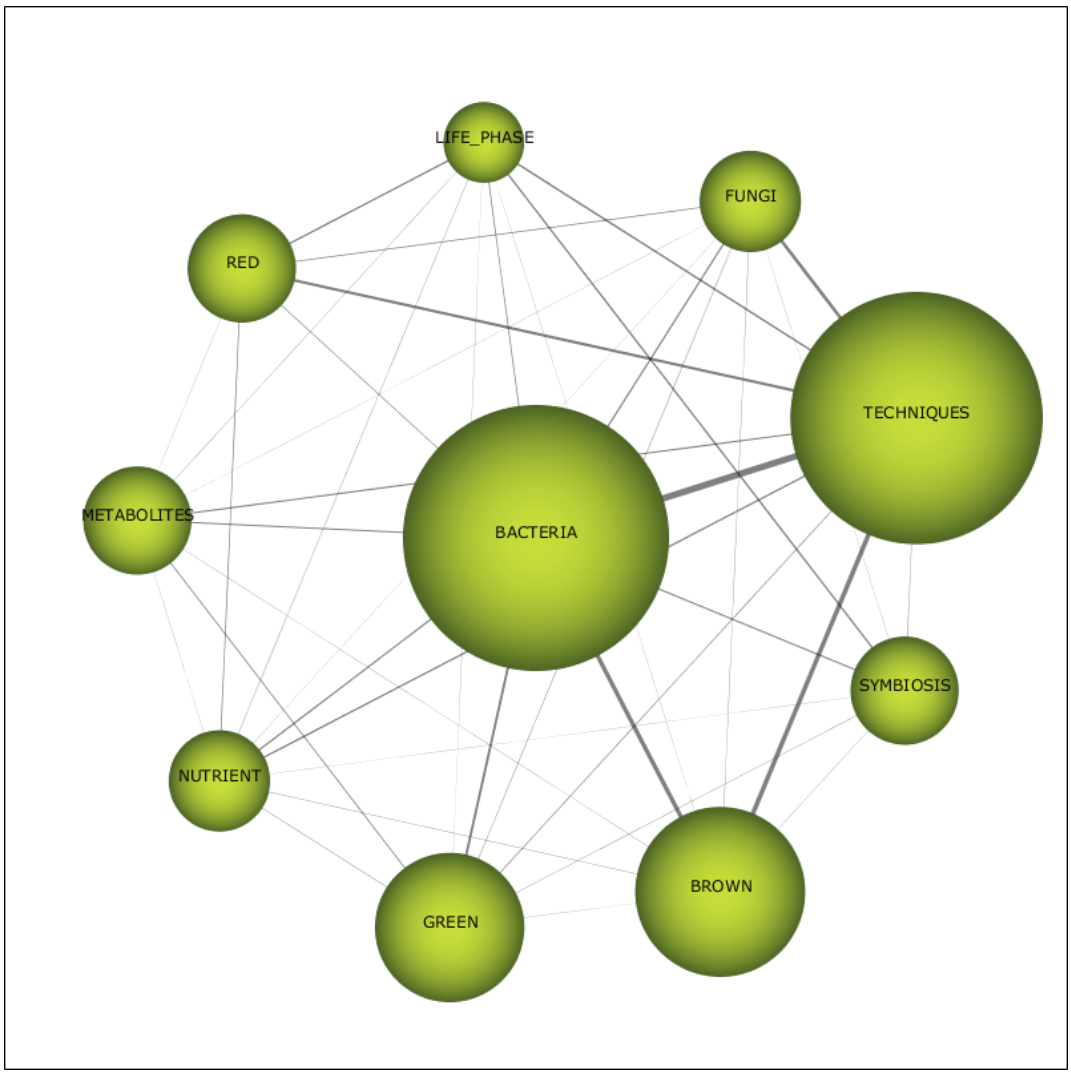

Figure 24. *Scientific-mapping Seaweed and Microbiome. The works have focus in the characterization of microorganism, particularly bacteria, using modern techniques in red, green and brown seaweeds.*

Microbiomes enhance algal growth and disease resistance

The microbiome facilitates seaweed adaptation to conditions of environmental stress as the release of bacterial promoting factors for algal growth and morphogenesis is crucial for the healthy development of macroalgae. Seaweed beneficial microorganisms (SBMs) can promote seaweed growth and improve disease resistance, offering a pathway to enhance commercial seaweed cultivation (Zhang et al., 2022). Also, biosynthesis of secondary metabolites and degradation of complex polysaccharides by microbial communities enhance nutrient availability for host (Mohapatra 2023). Examples of synergy between seaweed and microbiome are reported for green seaweeds such as *Ulva* species, and for brown seaweeds, such as *Saccharina japonica*

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and *Macrocystis pyrifera*, because their microbiomes are linked to rapid growth rates, stress tolerance, disease resistance and bioremediation potential.

Enhancing algal development has been reported for the green seaweed *Ulva rigida* in presence of phyla Cyanobacteria, Planctomycetes, Verrucomicrobia, and Proteobacteria and genus *Glaciecola* (Califano et al., 2020). Specific bacteria can restore normal morphogenesis in *Ulva mutabilis*, which otherwise develops abnormally in their absence (Wichard 2022; Alsufyani et al., 2020). These bacteria release morphogenetic compounds that are crucial for the development of seaweed structures (Alsufyani et al., 2020). Moreover, key bacterial genera such as *Sulfitobacter* and *Roseobacter*, are also associated with growth promotion in cultivated *Ulva* (van der Loos et al., 2021, 2024).

Additionally green seaweeds are used in integrated multitrophic aquaculture as *Ulva* species can reduce the bacteria load through decreasing the abundance of *Vibrio* (de Jager et al., 2024). Otherwise, *Ulva lactuca* (sea lettuce) and *Rhizobia* are associated for fixing nitrogen by bacteria and making it available to *Ulva*, which in turn provides carbohydrates to the bacteria (Kong et al., 2023).

In the brown seaweed *Saccharina latissima*, the core microbiome which includes taxa *Blastopirellula* and *Pseudoalteromonas*, is essential for nutrient cycling and immune regulation (Park et al., 2023; Zhuang et al., 2024). Also, it has been reported that the microbiome of the giant kelp *Macrocystis pyrifera* affected to blade development. Thus, mature blades mainly show Bacteroidia and Gammaproteobacteria (Esaian et al., 2024) that is associated with an increase of exudation of dissolved organic carbon and, in turn, supported microbial growth.

Likewise, the red seaweeds such as *Porphyridium purpureum* get benefits from nitrogen-fixing bacteria, such as *Rosembaum*, which produce vitamins and secondary metabolites that enhance algal growth and reduce oxidative stress (Kim et al., 2024). Furthermore, other red seaweeds such as *Neoporphyra haitanensis* have been reported as recruitment of beneficial bacteria which contribute to nutrient (C, N and S) cycling during early stages of culture and reduce environmental pollutants (Liu et al., 2024).

Regarding disease resistance, it has been reported that microbiome enhances disease resistance as microorganisms can mitigate disease and deter pathogens as well as produce antimicrobial compounds. In this sense, beneficial microorganisms associated with seaweeds play crucial roles in enhancing the health and defence of their host. For example, certain bacteria exhibit

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antiviral, antimicrobial, and antioxidant properties, which can protect seaweeds from pathogens. It has been reported that, early successional bacterial strains can protect seaweeds from pathogenic strains, highlighting the importance of microbiome composition in disease prevention (Longford et al., 2019).

Moreover, introduction of bacteria endophytes into *Ulva* sp. reveals bioactivity against the aquaculture pathogen *Streptococcis iniae* (Deutsch et al., 2023). Likewise beneficial bacteria such as *Vibrio alginolyticus* X-2 can protect seaweeds like *Saccharina japonica* from diseases such as bleaching disease by maintaining healthy microbial communities and enhancing the host's immune responses (Zhuang et al., 2023; Wang et al., 2014). Also, *Vibrio* produce biofilms that help red seaweed *Gracilaria vermiculophylla* to attach to surfaces and resist environmental stressors (Düsedau et al., 2023).

Otherwise *Proteobacteria* and *Firmicutes* produce bioactive compounds that help protect seaweed from harmful microorganisms (Ravindra & Reddy 2014). Seaweeds can chemically attract beneficial microbes while deterring pathogens, a process observed in *Agarophyton vermiculophyllum*. This selective recruitment helps in forming protective microbial communities that prevent diseases (Saha & Weinberger, 2019).

Also, *Laminaria digitata* and *Pseudoalteromonas* work in synergy in a manner such as *Pseudoalteromonas* produce antibiotics and other secondary metabolites that help protect *Laminaria* from pathogens (Handayani et al., 2024). On the other side, *Roseobacter* spp. produce secondary metabolites that help protect *Fucus vesiculosus* (bladder wrack) from oxidative stress (Martens et al., 2007).

Ultimately, such beneficial microorganisms can be used in aquaculture to improve the health and resilience of seaweed crops, thereby ensuring a reliable supply of healthy sporelings. Therefore, manipulation of the microbiome can work in favour of seaweed aquaculture practices, as the use of antibiotics in cultures could be reduced.

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***Table 4**. Summarised information on seaweeds and main features of their microbiome with implications for aquaculture*

Seaweed type	*Seaweed name*	Key Microbiome Features	Implications for Aquaculture
BROWN	*Ascophyllum, Fucus, Laminaria saccharina*	Host *Roseobacter*, *Vibrio*, *Aeromonas*, etc.	Source of biotechnological compounds like antibiotics, antioxidants
	Fucus vesiculosus	Associated with *Roseobacter* producing antioxidants and secondary metabolites	Enhances disease resistance; reduces oxidative stress
	Laminaria digitata	Synergy with *Pseudoalteromonas* producing antibiotics	Disease control through natural microbial defense
	Saccharina japonica	Vibrio alginolyticus protects from bleaching; core microbiome includes *Blastopirellula*	Improves immune response and resilience
	Macrocystis pyrifera	Mature blades host Bacteroidia, Gammaproteobacteria	Supports microbial growth, enhances nutrient cycling
	Saccharina latissima	Core microbiome includes *Pseudoalteromonas*, *Blastopirellula*	Supports immune regulation and nutrient exchange

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GREEN	*Ulva spp*	Hosts Sulfitobacter, Roseobacter, Glaciecola, and phyla Proteobacteria, Verrucomicrobia, Cyanobacteria	Promotes morphogenesis, growth, and pathogen resistance; key in IMTA system
	Ulva rigida / Ulva mutabilis	Dependent on bacteria for proper morphogenesis	Essential bacterial interaction for cultivation success
	Ulva lactuca	Associated with *Rhizobia* (N-fixation)	Enhances nutrient availability, supports bacteria–alga mutualism
RED	*Porphyridium purpureum*	Associated with *Rosembaum* (produces vitamins, secondary metabolites)	Enhances growth, stress resistance
	Neoporphyra haitanensis	Recruits bacteria for C, N, S cycling	Nutrient cycling and early-stage pollution mitigation
	Gracilaria vermiculophylla	*Vibrio* helps with surface attachment, biofilm formation	Increased environmental resilience and anchorage

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Implications of microbiome studies for hatchery management

The integration of microbiomes into algal hatchery systems is a growing field of interest due to its potential to enhance production efficiency and sustainability. However, practical implementation remains limited due to an incomplete understanding of how microbial communities function in artificial systems, ranging from laboratory setups to industrial-scale ponds (Lian et al., 2018).

The success of algal cultivation depends not only on physical and chemical conditions but also on the complex interactions between algae and their associated microorganisms. These interactions can be mutualistic or antagonistic and change throughout the algal life cycle. Understanding the influence of environmental factors on these microbial communities, and their functions, is key to designing strategies that manipulate the microbiome to improve algal health and productivity (Bossier et al., 2016; van der Loos et al., 2024).

In green algae such as *Ulva* spp., bacterial symbionts play an essential role in morphological development. *Ulva mutabilis*, for instance, depends on *Roseovarius* sp. and *Maribacter* sp. to produce morphogenetic compounds such as thallusin, which is critical for rhizoid and cell wall formation (Alsufyani et al., 2020). Additionally, Gram-negative bacteria can regulate zoospore settlement via quorum sensing (Joint et al., 2007), and cross-domain signalling mechanisms have been reported to trigger carpospore release in red algae such as *Acrochaetium* and *Gracilaria* (Weinberger et al., 2007; Singh, 2013).

Bacterial consortia are also fundamental for maintaining healthy algal cultures. In *Saccharina latissima*, the brown endophyte *Laminarionema elsbetiae* interacts with bacterial communities that help protect against disease (Bernard et al., 2018). In coculture, *Ulva mutabilis* shows dramatic improvements in growth, increasing from 0.04 to 3.79 mm/day, and accumulates significantly more glucose and glycerol (Polikovsky et al., 2020).

Effective microbiome management in hatcheries involves several strategies. First, maintaining high microbial diversity ensures ecosystem stability and resilience (Bush, 2015). This can be encouraged by providing a variety of environmental conditions (temperature, pH, nutrient levels) to create diverse ecological niches.

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Second, microbial interactions can be manipulated by introducing beneficial strains, such as nitrogen-fixing or antimicrobial-producing bacteria, to displace harmful microbes and enhance the functional capacity of the holobiont.

Third, optimizing nutrient cycling involves monitoring and controlling the availability of key nutrients such as nitrogen, carbon, and sulfur. Ensuring proper nutrient balance supports both microbial functionality and algal productivity.

To implement these strategies, the isolation and selection of functional bacteria is essential. This requires the collection and cultivation of epiphytic and endophytic bacteria from either wild or cultivated algae. Selected bacterial strains are then identified using 16S rRNA sequencing and biochemical characterization.

For endophytic bacteria, small seaweed fragments are incubated in seawater with an antibiotic solution (penicillin, ampicillin, nystatin, GeO_2). After one week, the fragments are transferred to nutrient agar plates, incubated, and colonies are isolated and purified.

For epiphytic bacteria, algae fragments are sonicated in sterilized seawater. The resulting suspension is plated on nutrient agar and incubated. Bacterial colonies are then isolated and purified through successive subcultures.

Tailoring the microbiome to specific algal species remains challenging due to species-specific associations and environmental variability. The ratio of bacteria to algal biomass must be carefully adjusted depending on the desired outcomes.

Case studies demonstrate the impact of microbiome manipulation. *Enteromorpha* and *Hypnea* host diverse bacterial communities that enhance algal morphology and disease resistance (Lakshmanaperumalsamy & Purushothaman, 1982; Egan et al., 2013). Cocultures of *Maribacter* sp., *Roseovarius* sp., and *Ulva mutabilis* improve not only growth but also carbohydrate and amino acid profiles (Polikovsky et al., 2020). Furthermore, bacteria such as *Vibrio parahaemolyticus* and *Bacillus amyloliquefaciens* have shown carbon conversion efficiencies of 22–25% from algal biomass (Kooren et al., 2023).

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***Table 5**. Basic procedures for the integration of the microbiome in the hatchery operations*

Procedure	Description	Purpose
Endophyte Isolation	Incubation of seaweed fragments in antibiotic solution, followed by culturing	Access internal microbes and remove surface contaminants
Epiphyte Isolation	Sonication in sterile seawater and plating of supernatant	Isolate bacteria from algal surfaces
Antibiotic Treatment	Penicillin, Ampicillin, Nystatin, GeO_2	Selectively eliminate unwanted microbes
Culture on Nutrient Agar	Growth and isolation of colonies	Obtain pure bacterial strains
Molecular Identification	16S rRNA sequencing and biochemical testing	Identify functional strains
Screening for Functions	Test for growth promotion, morphogenesis, nutrient cycling, pathogen resistance	Select strains for hatchery application
Reintroduction to Culture	Inoculation into algal hatchery systems	Enhance algal development and resilience

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Seedling materials to increase seeding efficiency and sustainability

Seaweed seedling operations require specific materials to ensure successful cultivation, attachment, and growth of young seaweed plants. The most commonly used materials are ropes (often synthetic or biodegradable), frames, and various culture media for laboratory propagation. Concerns about plastic pollution have led to the development of biodegradable ropes made from seaweed extracts, which offer similar or better durability and strength compared to synthetic options and are environmentally friendly. New materials, such as ropes made from polysaccharides extracted from seaweed species (e.g., *Gracilaria dura, Gelidiella acerosa, Kappaphycus alvarezi*), are being developed to replace synthetic ropes, offering both durability and eco-friendliness (Herlekar, 2015).

Scientific mapping seaweed/algae seeding materials

The concern to replace current seeding materials with materials that increase efficiency while ensuring that their chemical constitution ensures degradation is a relatively recent concern, hence only 6 articles appear in a search for SEAWEED OR ALGA AND SEEDING AND MATERIALS + AQUACULTURE. It is therefore not possible to construct a network of concepts, but it is possible to describe what materials are being proposed and what their properties are.

New biodegradable materials for seaweed seeding. Banana fiber.

Biodegradable ropes made from polysaccharides extracted from seaweeds such as *Gracilaria dura*, *Gelidiella acerosa*, and *Kappaphycus alvarezii* have demonstrated excellent mechanical properties and seawater durability. These ropes remained intact for over 45 days in field conditions and over six months in laboratory-controlled seawater. With a tensile strength of 65 MPa—higher than that of many synthetic counterparts—they present a viable replacement for conventional plastic ropes in marine environments (Herlekar, 2015).

Seaweed waste, particularly from *Eucheuma cottonii*, can be transformed into biodegradable films with tensile strengths ranging from 23 to 39 MPa. These values are comparable to those of common plastics such as PTFE and polypropylene. Notably, these films decompose completely within 14 days, emphasizing their potential for rapid biodegradability (Hidayati et al., 2021).

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Incorporating microcrystalline cellulose from bamboo or calcium carbonate fillers into seaweed-based films significantly enhances their tensile strength, water resistance, and overall durability. These composites are even more suitable for demanding marine applications, such as packaging and structural support in aquaculture (Hasan et al., 2019; Khalil et al., 2018).

Several findings suggest that banana fiber is a promising biodegradable material with properties that could make it suitable for aquatic plant cultivation, including seaweed seeding.

Banana fiber, derived from the banana plant's pseudostem, is highly biodegradable, renewable, and possesses good mechanical strength. It has been successfully used in eco-friendly applications such as biodegradable pots, bioplastics, and composite materials for horticulture, demonstrating its ability to support healthy seedling growth and degrade naturally in the environment (Balda et al., 2021; Bordon et al. 2021; Anirudh et al., 2024; Pongsuwan et al., 2022; Akatwijuka et al., 2023).

Banana fibers can be extracted using seawater-based processes, which enhances their environmental compatibility for marine applications and reduces the freshwater footprint (Akatwijuka et al., 2023).

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6. INNOVATIONS ALREADY TESTED ON THE MOST WIDELY CULTIVATED SPECIES IN THE EU

Some of the innovations described in the previous section have already been tested on the most cultivated species, and although they cannot be considered fully established methods given the occasional, non-systematic nature of the studies, they do show that their application is possible, so that expectations of their contribution to the European seaweed industry increase with the results obtained. In table 6, main results obtained with the different species are summarized.

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***Table 6**. Innovations introduced so far in hatchery/seeding operations for the most popular species in Europe.*

Innovation / Species	In vitro tissue culture	PGR induction of spores or Sporulation
Porphyra/Pyropia	Axenic Tissue Culture Established: *Porphyra yezoensis* was successfully cultured aseptically in defined synthetic media, enabling controlled studies of its development. Sporophyte (Conchocelis) Phase: Filamentous thalli retained their normal, densely tufted, uniseriate filament structure under axenic conditions, showing no major differences from standard cultures. Gametophyte (Foliose) Phase: Under axenic conditions, conchospores that would typically form foliose blades instead developed into callus-like masses. Most gametophytes lost their typical morphology after the first cell division. Callus and Rhizoid Formation: Some callus-like masses formed rhizoid-like structures, either in specific areas or along the entire mass. Research Applications: The axenic tissue culture system is highlighted as a promising tool for identifying growth and morphogenetic factors in *Porphyra yezoensis*	Ethylene (via ACC) Promotes sexual spore formation *Pyropia yezoensis* Methyl jasmonic acid Enhances conchosporangia maturation *Pyropia haitanensis*
Alaria	No evidences to date	No evidences to date
Saccharina	No evidences to date	No evidences to date
Palmaria	Plantlets and tetraspores were produced from meristematic tissue within 6 weeks using a freezing–thawing method.	No evidences to date
Ulva	*U. mutabilis* Axenic culture, full life cycle in vitro *U. linza* Axenic culture, induced sporulation *U. lactuca* Morphology controlled by bacteria in vitro *U. rigida* Reproduction induced by fragmentation	No evidences to date

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Table 6 *(cont.)*

Innovations / Species	Genetics	Cryopreservation
Porphyra/Pyropia	SSR/microsatellites Identification and genetic diversity (Wi et al., 2021; Varela-Álvarez et al., 2016) Genomic sequencing cultivar differentiation (Hwang et al., 2014; Ge et al., 2019) Trait-specific genes Marker-assisted selection (Xie et al., 2024; Chen et al., 2021)	Gametophytic thalli in DMSO + polymers, Liquid N_2 storage >95% survival, clonal maintenance Conchocelis by Prefreezing, encapsulation 65–90% survival, colony formation Protoplasts Vitrification 66.5% survival, plant regeneration Spores/gametes Controlled cooling/vitrification successful cryopreservation
Alaria esculenta	SNPs Identification of origin, traceability, selection (Ghriofa et al., 2022) Microsatellites (SSRs) Genetic diversity, population structure, breeding (Creis et al., 2023)	No evidences to date
Saccharina latissima	Genomic selection (GS) Prediction and selection of superior cultivars (Yarish et al., 2023; Huang et al., 2022)	Male gametophyte Controlled-rate cooling + 10%

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	Reference genomes Gene identification, marker development (Plott et al., 2025; Serrão et al., 2016) Microsatellites and SNPs Diversity, structure, traceability, selection (Cock et al., 2025; Goecke et al., 2024; Zhan et al., 2022; Serrão et al., 2016; Riddell et al., 2018)	DMSO High viability, normal development Female gametophyte Controlled-rate cooling + 10% DMSO High viability, normal development
Palmaria palmata	Reference genome Gene analysis, assisted selection (Schmid et al., 2024) Diversity analysis Identification of groups and crosses (Schmid et al., 2024)	No evidences to date
Ulva spp.	Comparative genomics Species and strain differentiation (Cascella et al., 2020; Lebrault et al., 2019; Lopez et al., 2019) High-throughput phenotyping Selection of strains with better traits (Lebrault et al., 2019; Sawicki et al., 2023) Gene editing (CRISPR) Targeted breeding (Ribera et al., 2025; Yamazaki et al., 2024) Selection of asexual variants Stable and productive cultivars (Sato et al., 2021)	Gametophytic thalli Two-step cooling, 20% glycerol 91% viability, normal development Vegetative thalli Liquid nitrogen storage (up to 120 days) 82% average survival, regrowth
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7. CONCLUSIONS

This toolkit outlines the essential knowledge and innovations required for advancing seaweed hatchery operations in Europe. As seaweed aquaculture expands, the development of efficient and sustainable hatchery practices becomes critical for supporting the industry's growth. Traditional methods, while foundational, often lack the control and scalability needed to meet modern demands.

This report has highlighted six key innovations—ranging from in vitro culture and spore induction with plant growth regulators, to genetic characterization, cryopreservation, microbiome integration, and biodegradable seedling materials—that together create a pathway toward fully controlled hatchery systems.

The integration of these innovations enhances the quality, traceability, and resilience of seedstock, contributing to a more robust value chain and aligning with EU standards for bioeconomy and environmental sustainability. Furthermore, the compilation of species-specific case studies and practical hatchery techniques offers valuable guidance for farmers, researchers, and entrepreneurs aiming to scale operations effectively. The cases studied can be expanded following the same structure as new species are consolidated.

Investing in hatchery innovation is not just a technical upgrade—it is a strategic necessity to ensure long-term productivity, environmental compatibility, and competitiveness of the European seaweed sector in the global blue economy. However, a lot of research is still needed to consolidate controlled methods of hatchery, in view of the difficulty for SME's to address major R&D activities, the alternative approach is to define European reference laboratories that work for the sector.

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8. SCIENCE MAPPING METHODS

The scientific mapping of an area of knowledge is a methodology recently imported into the experimental sciences from the social sciences, where it has been widely used (Small, 1973). It is about giving an overview of the dimensions of knowledge in an area of science, but with an objective treatment of the bibliographic records because the records are not chosen on the basis of a previously conceived idea, but it is the processing that gives us the dimensions that the area objectively contains. These dimensions are translated into circles of a network of interactions (Figure 2), in which the relative size of the circle expresses its relative importance and the connection expresses the degree of interaction, the thicker the connection. Behind all this is a mathematical operationalisation that is solved with analysis models, for which various software possibilities are available (Table 7).

Scientific mapping (SM) is an ideal tool when an overview of a particular topic is required, but a standard scientific thematic review cannot be undertaken for reasons of time or efficiency and operationality. SM is more objective and automated, based on large volumes of data extracted from databases such as Web of Science or Scopus, the more interpretative and critical review can include the author's view of the state of the art.

***Table 7**. Tools available to perform science mapping analysis*

Tool	Description
VOSviewer	Software for constructing and visualizing bibliometric networks, such as co-citation or co-authorship.
CiteSpace	Tool for detecting emerging trends and transient patterns in scientific literature.
CitNetExplorer	Tool for visualizing and analyzing citation networks of scientific publications.
Bibliometrix / Biblioshiny	R package for comprehensive bibliometric analysis, with a web interface for ease of use.
BibExcel	Tool to assist in bibliometric data analysis and prepare data for external visualization.

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HistCite	Software for generating historiographs and identifying key papers in a research area.
Science of Science (Sci2) Tool	Modular tool for scientific study supporting geospatial, temporal, and network analyses.
pyBibX	Python library for bibliometric and scientometric analysis with AI-powered topic modeling.
Connected Papers	Visual tool for exploring papers related to a seed article via similarity maps.
Inciteful	Generates literature maps from multiple seed articles to find connected research.
ResearchRabbit	AI-based tool for exploring and visualizing academic paper networks.
Open Knowledge Maps	Web platform for creating visual maps of research fields from academic databases.
Citation Gecko	Discover relevant academic literature based on known papers and visualize their links.
ScholarGPS	AI-powered platform that analyzes and ranks researchers and institutions globally.
scanR	French government-developed platform for large-scale mapping of scientific communities.

SCIMAT (Cobos et al. 2012) is an open-source software designed for scientific mapping and bibliometric analysis, enabling the identification and visualization of the intellectual, social, and conceptual structures of a research field based on bibliographic data. It allows researchers to analyze scientific production, detect emerging trends, and evaluate research performance over time. SCIMAT performs co-word analysis by clustering keyword co-occurrences, helping to reveal the conceptual structure of a research area. It also tracks the evolution of research themes across different time periods, showing how topics develop or disappear. Additionally, the software provides performance analysis by offering statistical insights into the productivity and impact of authors, institutions, and countries. Its graphical visualization capabilities generate easy-to-interpret maps, graphs, and networks to represent bibliometric relationships. SCIMAT supports the analysis of data from major bibliographic databases such as Web of Science (WoS) and Scopus.

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METHODOLOGY FOR SCIENCE MAPPING WITH SCIMAT 1.1.06 (as used in this study)

All the analyses carried out to complete this report have followed the same methodology.

1.- Bibliographic search in Scopus (www.scopus.com) limited to a maximum of approximately 300 records, but relevant in terms of subject matter and chronology (from the 80´s to the present).

2.- Grouping in group set/words group by distances mode in Scimat v1.1.06.

3.- Selection of groups with elimination if they induced tautology or were not representative.

4.- Exporting groups and group statistics

5.- Analysis following the following protocol and parameter values (selection based on Cobos thesis).

1. Define Time Periods:_Split the dataset into relevant time periods for your analysis (e.g., 2010–2014, 2015–2019, etc.).

Configure the Analysis

- Select defined time periods.

- Choose 'Words' as the unit of analysis.

- Set the minimum repetition threshold (e.g., 2).

- Select 'Co-occurrence matrix'.

- Define edge thresholds (e.g., minimum value: 2).

- Choose normalization method: recommend the Equivalence Index.

Clustering Algorithm

Select the clustering method. Recommended: Simple Centers Algorithm.

Define minimum and maximum number of clusters (e.g., 2 to 10).

Map Generation

Generate maps using Core Mapper and Secondary Mapper.

Add quality metrics, such as total citations per cluster.

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If using the h-index, make sure to extract it from Scopus.

Longitudinal Maps

To analyze topic evolution, use Evolution Equivalence Index and Longitudinal Equivalence Index.

Save and Document

Save the analysis to your desktop for later transfer.

Export maps via File > Save HTML. This allows recovery of visualizations later.

6.- Generation of reference tables.

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Bradley, P.M., Cheney, D.P.	Some effects of plant growth regulators on tissue cultures of the marine red alga *Agardhiella subulata* (Gigartinales, Rhodophyta)	1990	Hydrobiologia	Vol. 204-205, pp. 353-360
Gross, W.	Preparation of protoplasts from the carrageenophyte *Gigartina corymbifera* (KÃ¼tz.) J. Ag. (Rhodophyta)	1990	Journal of Microbiological Methods	Vol. 12, pp. 217-223
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Robaina, R.R., Garcia-Jimenez, P., Luque, A.	The Growth Pattern and Structure of Callus from the Red Alga *Laurencia* sp. (Rhodophyta, Ceramiales) Compared to Shoot Regeneration	1992	Botanica Marina	Vol. 35, pp. 267-272
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Amano, H., Noda, H.	Effects of Plant Growth Regulators, Organic Acids, and Sugars on Growth and	1994	Fisheries Science	Vol. 60, pp. 449-454

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Titlyanov, E.A., Titlyanova, T.V., Kadel, P., LÃ¼ning, K.	New methods of obtaining plantlets and tetraspores from fragments and cell aggregates of meristematic and submeristematic tissue of the red alga *Palmaria palmata*	2006	Journal of Experimental Marine Biology and Ecology	Vol. 339, pp. 55-64
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Yong, W.T.L., Chin, J.Y.Y., Thien, V.Y., Yasir, S.	Evaluation of growth rate and semi-refined carrageenan properties of tissue-cultured *Kappaphycus alvarezii* (Rhodophyta, Gigartinales)	2014	Phycological Research	Vol. 62, pp. 316-321
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Yokoya, N.S., Ã□vila, M., Piel, M.I., Villanueva, F., Alcapan, A.	Effects of plant growth regulators on growth and morphogenesis in tissue culture of *Chondracanthus chamissoi* (Gigartinales, Rhodophyta)	2014	Journal of Applied Phycology	Vol. 26, pp. 819-823
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Jong, L.W., Thien, V.Y., Yong, Y.S., Rodrigues, K.F., Yong, W.T.L.	Micropropagation and protein profile analysis by SDS-PAGE of *Gracilaria changii* (Rhodophyta, Solieriaceae)	2015	Aquaculture Reports	Vol. 1, pp. 10-14
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Luhan, M.R.J., Mateo, J.P.	Clonal production of *Kappaphycus alvarezii* (Doty) Doty in vitro	2017	Journal of Applied Phycology	Vol. 29, pp. 2339-2344
Muhamad, S.N.S., Ling, A.P.-K., Wong, C.-L.	Effect of plant growth regulators on direct regeneration and callus induction from *Sargassum polycystum* C. Agardh	2018	Journal of Applied Phycology	Vol. 30, pp. 3299-3310
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Lumbessy, S.Y.	Sem-sterile culture of *Gracilaria salicornia* seaweed (parental) on various media	2019	AIP Conference Proceedings	Vol. 2199
Febriyanti, F., Aslan, L.O.M., Iba, W., Patadjai, A.B., Nurdin, A.R.	Effect of various planting distances on growth and carrageenan yield of *Kappaphycus alvarez*ii (doty) using	2019	IOP Conference Series: Earth and	Vol. 278

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	seedlings produced from mass selection combined with tissue-cultured method		Environmental Science	
Aslan, L.O.M., Iba, W., Patadjai, A.B., Rahim, M., Febriyanti, F., Hafid, H., Armin, A.	Effect of Different Initial Weight on Growth and Carrageenan Yield of *Kappaphycus alvarezii* (Gigartinales, Rhodophyta) farmed using Seedlings Produced from Mass Selection Combined with Tissue-Cultured Method	2019	IOP Conference Series: Earth and Environmental Science	Vol. 382
Kasim, M., Abadi, S.Y.	Growth and carrageenan content of local and tissue culture seed of *Kappaphycus alvarezii* cultivated in floating cage	2019	AACL Bioflux	Vol. 12, pp. 167-178
Cahyani, H., Kurnia, D.P., Aslan, L.O.M.	Cultivation of seaweed *Kappaphycus alvarezii* (Doty) doty ex silva using tissue-cultured seedlings in encircling tank culture system	2020	IOP Conference Series: Earth and Environmental Science	Vol. 473
Aslan, L.O.M., Cahyani, H., Hardianti, H., Kurnia, D.P., Febriani, A., Prity, N.A., Anastasia, H., Iba, W., Sulistiani, E.	Field cultivation of *Kappaphycus alvarezii* (DOTY) doty ex silva using tissue-cultured seedlings at bungin permai costal waters, south konawe, Southeast (SE) Sulawesi:	2020	IOP Conference Series: Earth and Environmental Science	Vol. 473

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Kraai, J.A., Rorrer, G.L.	Immobilized cultivation of the red macroalga *Ochtodes secundiramea* via fluid injection of clonal shoot tissues onto porous mesh panels	2021	Algal Research	Vol. 55
Pinteus, S., Alves, C., Horta, A., Silva, J., Pedrosa, R.	*Fucus spiralis* tissue culture for sustainable phlorotannins production	2022	Aquatic Botany	Vol. 179
Ahmed, N., Mohamed, H.F., Xu, C., Lin, X., Huang, L.	A novel surface sterilization method using Artemisia dracunculus extract for tissue culturing of endangered species *Sargassum fusiforme*	2022	Plant Cell, Tissue and Organ Culture	Vol. 149, pp. 135-145

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Obando, J.M.C., dos Santos, T.C., Martins, R.C.C., Teixeira, V.L., Barbarino, E., Cavalcanti, D.N.	Current and promising applications of seaweed culture in laboratory conditions	2022	Aquaculture	Vol. 560
Tirtawijaya, G., Negara, B.F.S.P., Lee, J.-H., Cho, M.-G., Kim, H.K., Choi, Y.-S., Lee, S.-H., Choi, J.-S.	The Influence of Abiotic Factors on the Induction of Seaweed Callus	2022	Journal of Marine Science and Engineering	Vol. 10
Veeragurunathan, V., Mantri, V.A., Gwen Grace, P., Gurumoorthy, U.	Seaweed biotechnology implications to aquaculture	2022	Frontiers in Aquaculture Biotechnology	pp. 219-237
Jiksing, C., Ongkudon, M.M., Thien, V.Y., Rodrigues, K.F., Yong, W.T.L.	Recent advances in seaweed seedling production: a review of eucheumatoids and other valuable seaweeds	2022	Algae	Vol. 37, pp. 105-121
Tuiyo, R., Pasisingi, N.	Growth optimization of *Kappaphycus alvarezii* with Basmingro-nutrient technology through mass tissue culture	2023	AACL Bioflux	Vol. 16, pp. 1691-1699
Meiyana, M., Dhoe, S.B., Minjoyo, H., Rivaie, A.R.	Growth of *Eucheuma cottonii* seaweed from tissue culture with different time acclimatization in Hurun Bay	2023	E3S Web of Conferences	Vol. 442

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Borlongan, I.A., Gaya, H.C., Dimaano, A.L., Hennequart, F., Critchley, A., Hurtado, A.	Applications of liquid extracts from the brown algae *Ascophyllum nodosum* (Fucales) and *Laminaria digitata* (Laminariales) to enhance the growth of eucheumatoids in tissue culture	2024	Aquaculture International	Vol. 32, pp. 8649-8665
Hlaing, W.M.M., Jarukamjorn, K.	Plantlet Regeneration from Callus Cultures of *Kappaphycus alvarezii* for Cultivation in Coastal Waters at Myeik Archipelago, Myanmar	2024	Pakistan Journal of Biological Sciences	Vol. 27, pp. 479-486
Lee, J.-H., Bashir, K.M.I., Tirtawijaya, G., Negara, B.F.S.P., Choi, J.-S.	Establishment of Effective Callus Induction in the Economically Important Brown Seaweed Ecklonia cava	2024	Applied Sciences (Switzerland)	Vol. 14
Guo, L., Pang, G., Luo, L., Gao, C., Chen, B., Ma, Z.	Asexual proliferative seedling technology for *Sargassum fusiforme* constructed using tissue culture method	2024	Frontiers in Marine Science	Vol. 11
Chandimali, N., Park, E.H., Bak, S.-G., Lim, H.-J., Won, Y.-S., Lee, S.-J.	Seaweed callus culture: A comprehensive review of current circumstances and future perspectives	2024	Algal Research	Vol. 77

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Toroy, L.A., Borlongan, I.A., Roco, O.	Efficacy of Seaweed Liquid Extract from *Ulva* spp. in Improving Growth and Chlorophyll-a Content of Eucheuma denticulatum in Tissue Culture	2024	Philippine Journal of Fisheries	Vol. 31, pp. 126-136
Zuo, X., Sheng, X., Wu, M., Kuang, Y., Bao, D., Guo, L., Chen, B.	Evaluation of tissue-regenerated *Sargassum fusiforme* (Harvey) Setchell: Perspective of physiological and nutritional quality	2025	Aquaculture	Vol. 600

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Spore induction and culture with plant growth regulators

Author(s)	Title	Year	Journal	Pages
Pacheco-Ruiz, I., García-Esquivel, Z., Aguilar-Rosas, L.E.	Spore discharge in the carragenophyte *Gigartina canaliculata* Harvey (Rhodophyta, Gigartinales)	1989	Journal of Experimental Marine Biology and Ecology	Vol. 126, pp. 293-299
Rao, G.M.N., Rangaiah, G.S.	Control of spore shedding from some marine algae of the visakhapatnam coast, india	1991	British Phycological Journal	Vol. 26, pp. 353-360
Glenn, E.P., Moore, D., Fitzsimmons, K., Azevedo, C.	Spore culture of the edible red seaweed, *Gracilaria parvispora* (Rhodophyta)	1996	Aquaculture	Vol. 142, pp. 59-74
Alveal, K., Romo, H., Werlinger, C., Oliveira, E.C.	Mass cultivation of the agar-producing alga *Gracilaria chilensis* (Rhodophyta) from spores	1997	Aquaculture	Vol. 148, pp. 77-83
Glenn, E.P., Moore, D., Brown, J.J., Tanner, R., Fitzsimmons, K., Akutigawa, M., Napolean, S.	A sustainable culture system for *Gracilaria parvispora* (Rhodophyta) using sporelings, reef growout and floating cages in Hawaii	1998	Aquaculture	Vol. 165, pp. 221-232
Rabanal, S.F., Azanza, R.V.	Outplanting of laboratory-generated carposporelings of *Gracilariopsis bailinae* off northern Philippines	1999	Hydrobiologia	Vol. 398-399, pp. 463-468

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Guzmán-Urióstegui, A., Robledo, D.	Factors affecting sporulation of *Gracilaria cornea* (Gracilariales, Rhodophyta) carposporophytes from Yucatan, Mexico	1999	Hydrobiologia	Vol. 398-399, pp. 285-290
Azanza, R.V., Aliaza, T.T.	In vitro carpospore release and germination in *Kappaphycus alvarezii* (Doty) Doty from Tawi-Tawi, Philippines	1999	Botanica Marina	Vol. 42, pp. 281-284
Garcia-Jimenez, P., Marian, F.D., Rodrigo, M., Robaina, R.R.	Sporulation and sterilization method for axenic culture of *Gelidium canariensis*	1999	Journal of Biotechnology	Vol. 70, pp. 227-229
Jayasankar, R., Varghese, S.	Cultivation of marine red alga *Gracilaria edulis* (Gigartinales, Rhodophyta) from spores	2002	Indian Journal of Marine Sciences	Vol. 31, pp. 75-77
Callow, M.E., Jennings, A.R., Brennan, A.B., Seegert, C.E., Gibson, A., Wilson, L., Feinberg, A., Baney, R., Callow, J.A.	Microtopographic cues for settlement of zoospores of the green fouling alga *Enteromorpha*	2002	Biofouling	Vol. 18, pp. 237-245
Mizuta, H., Yasui, H., Saga, N.	A simple method to mass produce monospores in the thallus of *Porphyra yezoensis Ueda*	2003	Journal of Applied Phycology	Vol. 15, pp. 345-349
Macchiavello A, J.E., Bulboa C, C.R., Edding V, M.	Vegetative propagation and spore-based recruitment in the carrageenophyte *Chondracanthus chamissoi* (Gigartinales, Rhodophyta) in northern Chile	2003	Phycological Research	Vol. 51, pp. 45-50

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Jun Pang, S., Lüning, K.	Breaking seasonal limitation: Year-round sporogenesis in the brown alga *Laminaria saccharina* by blocking the transport of putative sporulation inhibitors	2004	Aquaculture	Vol. 240, pp. 531-541
Le Gall, L., Pien, S., Rusig, A.-M.	Cultivation of *Palmaria palmata* (Palmariales, Rhodophyta) from isolated spores in semi-controlled conditions	2004	Aquaculture	Vol. 229, pp. 181-191
Halling, C., Aroca, G., Cifuentes, M., Buschmann, A.H., Troell, M.	Comparison of spore inoculated and vegetative propagated cultivation methods of *Gracilaria chilensis* in an integrated seaweed and fish cage culture	2005	Aquaculture International	Vol. 13, pp. 409-422
Pang, S.J., Lüning, K.	Tank cultivation of the red alga *Palmaria palmata*: Year-round induction of tetrasporangia, tetraspore release in darkness and mass cultivation of vegetative thalli	2006	Aquaculture	Vol. 252, pp. 20-30
Westermeier, R., Patiño, D., Piel, M.I., Maier, I., Mueller, D.G.	A new approach to kelp mariculture in Chile: Production of free-floating sporophyte seedlings from gametophyte cultures of *Lessonia trabeculata and Macrocystis pyrifera*	2006	Aquaculture Research	Vol. 37, pp. 164-171
Titlyanov, E.A., Titlyanova, T.V., Kadel, P., Lüning, K.	New methods of obtaining plantlets and tetraspores from fragments and cell aggregates of meristematic	2006	Journal of Experimental	Vol. 339, pp. 55-64

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	and submeristematic tissue of the red alga *Palmaria palmata*		Marine Biology and Ecology	
Blouin, N., Xiugeng, F., Peng, J., Yarish, C., Brawley, S.H.	Seeding nets with neutral spores of the red alga *Porphyra umbilicalis* (L.) Kützing for use in integrated multi-trophic aquaculture (IMTA)	2007	Aquaculture	Vol. 270, pp. 77-91
Strain, L.W.S., Isdepsky, A., Borowitzka, M.A., Daume, S.	Three algal propagation methods assessed to create a Rhodophyta diet for juvenile greenlip abalone (*Haliotis laevigata*) in the later nursery phase	2007	Journal of Shellfish Research	Vol. 26, pp. 737-744
Bulboa, C., De Paula, E.J., Chow, F.	Germination and survival of tetraspores of *Kappaphycus alvarezii var. alvarezii* (Solieriaceae, Rhodophyta) introduced in subtropical waters of Brazil	2008	Phycological Research	Vol. 56, pp. 39-45
Agrawal, S.C.	Factors affecting spore germination in algae - review	2009	Folia Microbiologica	Vol. 54, pp. 273-302
Qing, J., Wang, Y., Liu, S., Tang, X.-X.	Effects of artificial seawater with different N/P ratio on early development of *Laminaria japonica* embryo spore	2009	Chinese Journal of Applied Ecology	Vol. 20, pp. 1947-1951
Mantri, V.A., Thakur, M.C., Kumar, M., Reddy, C.R.K., Jha, B.	The carpospore culture of industrially important red alga *Gracilaria dura* (Gracilariales, Rhodophyta)	2009	Aquaculture	Vol. 297, pp. 85-90

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del Carmen Hernández-González, M., Aroca, G., Furci, G., Buschmann, A.H., Filún, L., Espinoza, R.	Population dynamics and culture studies of the edible red alga *Callophyllis variegata* (Kallymeniaceae)	2010	Phycological Research	Vol. 58, pp. 108-115
Macchiavello, J., Araya, E., Bulboa, C.	Production of *Macrocystis pyrifera* (Laminariales; Phaeophyceae) in northern Chile on spore-based culture	2010	Journal of Applied Phycology	Vol. 22, pp. 691-697
Xie, X., Wang, G., Pan, G., Gao, S., Xu, P., Zhu, J.	Variations in morphology and PSII photosynthetic capabilities during the early development of tetraspores of *Gracilaria vermiculophylla* (Ohmi) Papenfuss (Gracilariales, Rhodophyta)	2010	BMC Developmental Biology	Vol. 10
Mizuta, H., Yasui, H.	Significance of radical oxygen production in sorus development and zoospore germination in *Saccharina japonica* (Phaeophyceae)	2010	Botanica Marina	Vol. 53, pp. 409-416
Luhan, M.R.J., Sollesta, H.	Growing the reproductive cells (carpospores) of the seaweed, *Kappaphycus striatum*, in the laboratory until outplanting in the field and maturation to tetrasporophyte	2010	Journal of Applied Phycology	Vol. 22, pp. 579-585

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Bulboa, C., Macchiavello, J., Véliz, K., Oliveira, E.C.	Germination rate and sporeling development of *Chondracanthus chamissoi* (Rhodophyta, Gigartinales) varies along a latitudinal gradient on the coast of Chile	2010	Aquatic Botany	Vol. 92, pp. 137-141
Pacheco-Ruíz, I., Cabello-Pasini, A., Zertuche-González, J.A., Murray, S., Espinoza-Avalos, J., Dreyfus-Leon, M.J.	Carpospore and tetraspore release and survival in *Chondracanthus squarrulosus* (Rhodophyta: Gigartinaceae) from the Gulf of California	2011	Botanica Marina	Vol. 54, pp. 127-134
Plá, P.C., Alveal, K.	Development of *Macrocystis pyrifera* from spores and gametes on artificial substrate. Algal production in a surface culture	2012	Latin American Journal of Aquatic Research	Vol. 40, pp. 292-299
Imchen, T.	Effect of temperature, salinity and biofilm on the zoospores settlement of *Enteromorpha flexuosa* (Wulfen) J.Agardh	2012	Indian Journal of Marine Sciences	Vol. 41, pp. 355-358
Yan, T., Cao, W.H., Liu, S.S., Yang, J., Xie, E.Y., He, M.X., Zhang, S.	Ethylacetate extracts from the gorgonian coral *Subergorgia reticulata* reduce larval settlement of *Balanus* (=Amphibalanus) *reticulatus* and *Pinctada martensii* and spore germination of *Ulva linza, U. lactuca and Gracilaria tenuistipitata*	2012	Journal of the Marine Biological Association of the United Kingdom	Vol. 92, pp. 1349-1355

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de Miranda, G.E.C., Yokoya, N.S., Fujii, M.T.	Effects of temperature, salinity and irradiance on carposporeling development of *Hidropuntia caudata* (Gracilariales, Rhodophyta)	2012	Revista Brasileira de Farmacognosia	Vol. 22, pp. 818-824
Murúa, P., Westermeier, R., Patiño, D.J., Müller, D.G.	Culture studies on early development of *Lessonia trabeculata* (Phaeophyceae, Laminariales): Seasonality and acclimation to light and temperature	2013	Phycological Research	Vol. 61, pp. 145-153
Shan, T.F., Pang, S.J., Gao, S.Q.	Novel means for variety breeding and sporeling production in the brown seaweed *Undaria pinnatifida* (Phaeophyceae): Crossing female gametophytes from parthenosporophytes with male gametophyte clones	2013	Phycological Research	Vol. 61, pp. 154-161
Yu, C.-H., Lim, P.-E., Phang, S.-M.	Effects of irradiance and salinity on the growth of carpospore-derived tetrasporophytes of *Gracilaria edulis* and *Gracilaria tenuistipitata var liui* (Rhodophyta)	2013	Journal of Applied Phycology	Vol. 25, pp. 787-794
Bulboa, C., Véliz, K., Sáez, F., Sepúlveda, C., Vega, L., Macchiavello, J.	A new method for cultivation of the carragenophyte and edible red seaweed *Chondracanthus chamissoi* based on secondary attachment disc: Development in outdoor tanks	2013	Aquaculture	Vol. 410-411, pp. 86-94

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Hughes, M.H., Michetti, K.M., Leonardi, P.I.	Settlement of *Gracilaria gracilis* carpospores (gracilariales, rhodophyta) on natural substrates from the southwestern Atlantic coast (chubut, argentina)	2014	Botanica Marina	Vol. 57, pp. 131-137
Marambio, J., Mansilla, A., Ávila, M., Rosenfeld, S., Ojeda, J.	The effects of different light intensities on the culture of *Gigartina skottsbergii* (Rhodophyta, Gigartinales) tetrasporophytes and gametophytes in the Magellan region, Chile	2014	Journal of Applied Phycology	Vol. 26, pp. 1963-1969
Chen, S., Chen, L., Zhu, C., Guo, Y., Guo, Y.	Spore Culture of Red Seaweed, *Gloiopeltis furcata*	2014	Journal of the World Aquaculture Society	Vol. 45, pp. 487-492
Xu, D., Wang, D., Li, B., Fan, X., Zhang, X.W., Ye, N.H., Wang, Y., Mou, S., Zhuang, Z.	Effects of CO2 and seawater acidification on the early stages of *Saccharina japo*nica development	2015	Environmental Science and Technology	Vol. 49, pp. 3548-3556
Wang, H., Lin, A., Gu, W., Huan, L., Gao, S., Wang, G.	The sporulation of the green alga *Ulva prolifera* is controlled by changes in photosynthetic electron transport chain	2016	Scientific Reports	Vol. 6

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Zhou, W., Sui, Z., Wang, J., Hu, Y., Kang, K.H., Kim, H.B., Niaz, Z.	Mass cultivation of economically important red alga *Gracilariopsis lemaneiformis* (Gracilariaceae, Rhodophyta) from tetraspores and carpospores	2016	Aquaculture	Vol. 460, pp. 25-31
Garcia-Jimenez, P., Robaina, R.R.	Volatiles in the aquatic marine ecosystem: Ethylene and related plant hormones and sporulation in red seaweeds	2017	Systems Biology of Marine Ecosystems	pp. 99-116
McNeill, S.E., Falshaw, R.	Aquaculture of *Sarcothalia atropurpurea* tetraspores in New Zealand for carrageenan production	2017	New Zealand Journal of Marine and Freshwater Research	Vol. 51, pp. 528-542
Harwinda, F.K., Satyantini, W.H., Masithah, E.W.	The effects of salinity and temperature shock on *Kappaphycus alvarezii* seaweed spores release	2018	IOP Conference Series: Earth and Environmental Science	Vol. 137
Jung, S.M., Lee, J.H., Lee, H.J., Jeon, J.Y., Park, T.H., Yoon, J.H., Shin, H.W.	The growth of alginate-encapsulated macroalgal spores	2018	Aquaculture	Vol. 491, pp. 333-337

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González, C.P., Edding, M., Torres, R., Manríquez, P.H.	Increased temperature but not pCO2 levels affect early developmental and reproductive traits of the economically important habitat-forming *kelp Lessonia trabeculata*	2018	Marine Pollution Bulletin	Vol. 135, pp. 694-703
Alfonso, B., Hernández, J.C., Sansón, M.	Tetraspore germination of two vulnerable marine algae, *Gelidium canariense* and *G. arbusculum* (Rhodophyta, Gelidiales)	2018	Botanica Marina	Vol. 61, pp. 111-114
Arbaiza, S., Gil-Kodaka, P., Arakaki, N., Alveal, K.	First stages of cultivation from *chondracanthus chamissoi* carpospores from three locations on the peruvian coast	2019	Revista de Biologia Marina y Oceanografia	Vol. 54, pp. 204-213
Bahri, S., Hartanto, N., Laining, A., Tassakka, A.C.M.A.R.	Releasing, attaching and growing of seaweed (*Gracilaria* sp.) spores in several culture media	2019	AACL Bioflux	Vol. 12, pp. 2137-2146
Hughes, M.H., Michetti, K.M., Leonardi, P.I.	Spore release and germling development on different substrates in the carrageenophyte *Sarcothalia crispata* from the southwestern Atlantic coast	2019	Journal of Applied Phycology	Vol. 31, pp. 1285-1295
Balar, N.B., Mantri, V.A.	Insights into life cycle patterns, spore formation, induction of reproduction, biochemical and molecular aspects of sporulation in green algal genus *Ulva*: implications for commercial cultivation	2020	Journal of Applied Phycology	Vol. 32, pp. 473-484

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Pereira, D.T., Ouriques, L.C., Bouzon, Z.L., Simioni, C.	Effects of high nitrate concentrations on the germination of carpospores of the red seaweed *Pyropia acanthophora var. brasiliensis* (Rhodophyta, Bangiales)	2020	Hydrobiologia	Vol. 847, pp. 217-228
Pérez Massad, I., Ávila, M., Contreras-Porcia, L., Bulboa Contador, C.	Spores re-suspending technology, a new system improving spore seeding for culture of commercial red seaweeds	2020	Aquaculture	Vol. 526
Knoop, J., Griffin, J.N., Barrento, S.	Cultivation of early life history stages of *Porphyra dioica* from the British Isles	2020	Journal of Applied Phycology	Vol. 32, pp. 459-471
Su, L., Shan, T.F., Li, J., Pang, S.J., Leng, X.F., Zhang, Y., Gao, H.T.	Aquaculture of the hybrid cultivars of *Saccharina japonica:* Removing the obstacle of sori production by photoperiodic control	2020	Aquaculture	Vol. 519
Choi, H.G.	A study on carpospore release induction method of *Agarophyton vermiculophyllum*	2020	Ocean and Polar Research	Vol. 42, pp. 225-231
Balar, N., Jaiswar, S., Mantri, V.A.	Effects of extrinsic abiotic factors on induction of gametogenesis and efficacy of a device for the segregation of non-fused gametes and zygotes in the green alga *Ulva lactuca*	2021	Applied Phycology	Vol. 2, pp. 1-9

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Freitas, M.V., Mouga, T., Correia, A.P., Afonso, C., Baptista, T.	New insights on the sporulation, germination, and nutritional profile of *Gracilaria gracilis* (Rhodophyta) grown under controlled conditions	2021	Journal of Marine Science and Engineering	Vol. 9
Kim, J.-H., Zhao, Z.X., Kim, Y.S.	Variation in germling growth in the green tide–forming alga *Ulva intestinalis* (Chlorophyta) in response to gradients in salinity, temperature, light, and nutrients	2021	Journal of Applied Phycology	Vol. 33, pp. 3951-3962
Uji, T., Mizuta, H.	The role of plant hormones on the reproductive success of red and brown algae	2022	Frontiers in Plant Science	Vol. 13
Luhan, M.R.J., Mateo, J.P., Sollesta-Pitogo, H.	Growth and Carrageenan Quality of Sporophyte and Gametophyte of the Commercially Important Red Seaweed *Kappaphycus alvarezii*	2022	Philippine Journal of Science	Vol. 151, pp. 129-134
Uji, T., Mizuta, H.	The role of plant hormones on the reproductive success of red and brown algae	2022	Frontiers in Plant Science	Vol. 13
Umanzor, S., Han, S., Song, H.-I., Park, J.-S., Critchley, A.T., Yarish, C., Kim, J.K.	Ascertaining the interactions of brown seaweed-derived biostimulants and seawater temperature on spore release, germination, conchocelis, and newly formed blades of the commercially important red alga *Neopyropia yezoensis*?	2022	Algal Research	Vol. 64

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Jaiswar, S., Mungalapara, U., Kazi, M.A., Balar, N.	Evidence from preliminary experiments revealed drifted *Ulva* biomass has seedling and aquaculture potential	2022	Aquaculture International	Vol. 30, pp. 2833-2846
Liu, Y., Liang, Z., Zhang, P., Yuan, Y., Wu, Y., Zhang, D., Duan, M., Liu, F.	Sorus developmental biology of hybrid cultivar in *Saccharina japonica*: Environmental and endogenous regulation	2023	Aquaculture	Vol. 565
Del Rosario-Santana, D., Robaina, R., Garcia-Jimenez, P.	Jasmonates disrupt carrageenan synthesis during carposporogenesis in the red seaweed *Grateloupia imbricata*	2023	Frontiers in Marine Science	Vol. 10
Han, H., Zhao, S., Song, X., Wang, H.	The Overwintering Capability of *Ulva prolifera* Spores and Gametes in the Yellow Sea, China	2023	Journal of Ocean University of China	Vol. 22, pp. 509-516
Arbaiza, S., Avila-Peltroche, J., Castañeda-Franco, M., Mires-Reyes, A., Advíncula, O., Baltazar, P.	Vegetative Propagation of the Commercial Red Seaweed *Chondracanthus chamissoi* in Peru by Secondary Attachment Disc during Indoor Cultivation	2023	Plants	Vol. 12
Mihaila, A.A., Lawton, R.J., Glasson, C.R.K., Magnusson, M.	Early hatchery protocols for tetrasporogenesis of the antimethanogenic seaweed *Asparagopsis armata*	2023	Journal of Applied Phycology	Vol. 35, pp. 2323-2335

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Zhou, X.-Y., Sun, D.-G., Sun, X., Xu, N.-J.	The physiological effects and transcriptome analysis of exogenous acc on carpospore release *in Gracilariopsis lemaneiformis*	2024	Oceanologia et Limnologia Sinica	Vol. 55, pp. 1245-1257
Sundarraj, D.K., Majumder, A., Suhail, H.R., Eswar, I., Shek Mohamed, I.S.	Spore-Based Seaweed Propagation for Germplasm Selection and Cultivation	2024	Biotechnological Interventions to Aid Commercial Seaweed Farming	pp. 257-293
Thirumurugan, N.K., Dhinakarasamy, I., Chakraborty, S., Sivakumar, M., Clements, C., Chandrasekar, A., Vinayagam, J., Kumar, C., Rajendran, T.	Synergistic effects of plastic debris and elevated nitrate concentrations on the proliferation of *Ulva lactuca* micro-propagules	2024	Journal of Hazardous Materials	Vol. 480
Theobald, E.J., Rule, M.B., Jackson, T.L., Rula, N.A., Diaz-Pulido, G., Jackson, E.L.	Abiotic triggers for maximising germling numbers in *Asparagopsis taxiformis* (Rhodophyta, Bonnemaisoniales) via tetrasporogenesis	2024	Journal of Applied Phycology	Vol. 36, pp. 3561-3579
Lin, S.-M., Chen, S.-J., Huang, P.-Y., Liu, L.-C., Chiou, Y.-S.	Sporelings and growth of the marine red alga*, Gelidium elegans* (Gelidiaceae), from Northern Taiwan	2024	Journal of Applied Phycology	Vol. 36, pp. 3581-3590

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Lawton, R.J., Magnusson, M.	Effects of seeding twine type and seeding density on hatchery performance and initial at-sea cultivation performance of the kelp *Ecklonia radiata*	2024	Algal Research	Vol. 84
Farrugia Drakard, V., Hollarsmith, J.A., Stekoll, M.S.	Hyposaline conditions impact the early life-stages of commercially important high-latitude kelp species	2025	Journal of Phycology	
Mihaila, A.A., Glasson, C.R.K., Lawton, R.J., Huerlimann, R., Magnusson, M.	Transcriptomic changes during induction of tetrasporogenesis in the red seaweed *Asparagopsis armata*	2025	Algal Research	Vol. 87
Crossett, D., Biancacci, C., Clark, D.E., South, P.M.	Experimental assessment of growing substrates for the early life stages of five large brown seaweeds	2025	New Zealand Journal of Marine and Freshwater Research	Vol. 59, pp. 615-636
Kim, B.Y., Ko, J.-C., Shan, T., Choi, H.G.	Reproductive capacity of *Meristotheca papulosa* (Solieriaceae, Rhodophyta) and effects of temperature on carpospore release and sporeling growth	2025	Phycological Research	Vol. 73, pp. 70-78
Tian, P., Li, Y., Xue, N., Wang, W., Chen, S., Liu, Y., Sun, J., Liang, G., Zhao, J., Shi, L., Zhao, N., Li, X., Li, X., Zhang, L.	Polyploid breeding of *Saccharina japonica*: *Harnessing aposporous* reproduction	2025	Aquaculture	Vol. 604

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Holanda, T.D.B.L., Bessa, É.F., Lima, F.E.D.S., Lopes, F.L.D.S., Martins, J.R.P., Benevides, N.M.B., Araújo, M.L.H.	Growth and iota-carrageenan from the red seaweed *Solieria filiformis* (Rhodophyta, Solieriaceae) cultivated in the Ceara State coast, Brazil	2025	Aquaculture International	Vol. 33

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Genetic characterization of species. The first step to breeding

Author(s)	Title	Year	Journal	Pages
Qin, S., Jiang, P., Tseng, C.-K.	Molecular biotechnology of marine algae in China	2004	Hydrobiologia	Vol. 512, pp. 21-26
Guillemin, M.-L., Destombe, C., Faugeron, S., Correa, J.A., Valero, M.	Development of microsatellites DNA markers in the cultivated seaweed, *Gracilaria chilensis* (Gracilariales, Rhodophyta)	2005	Molecular Ecology Notes	Vol. 5, pp. 155-157
Wang, X., Wang, D., Li, D., Duan, D.	Genetic analysis of the gametophytes of *Undaria pinnatifida* (Phaeophyceae) with ISSR method	2006	Aquaculture	Vol. 258, pp. 250-256
Hu, Z., He, Y., Xia, P., Duan, D.	Molecular identification of Chinese cultivated *Porphyra* (Bangiaceae, Rhodophyta) based on the rDNA internal transcribed spacer-1 sequence and random amplified polymorphic DNA markers	2007	Marine Biology Research	Vol. 3, pp. 20-28

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Guillemin, M.-L., Faugeron, S., Destombe, C., Viard, F., Correa, J.A., Valero, M.	Genetic variation in wild and cultivated populations of the haploid- diploid red alga *Gracilaria chilensis*: How farming practices favor asexual reproduction and heterozygosity	2008	Evolution	Vol. 62, pp. 1500-1519
Bi, Y., Hu, Y., Zhou, Z.	Genetic variation of *Laminaria japonica* (Phaeophyta) populations in China as revealed by RAPD markers	2011	Acta Oceanologica Sinica	Vol. 30, pp. 103-112
Yu, S., Deng, Y., Yao, J., Li, S., Xin, X., Duan, D.	Population genetics of wild *Hizikia fusiformis* (Sargassaceae, Phaeophyta) along China's coast	2012	Journal of Applied Phycology	Vol. 24, pp. 1287-1294
Li, S., Qiao, K., Shan, T., Pang, S., Hou, H.	Genetic diversity and relationships of the brown alga *Undaria pinnatifida* cultivated along the Dalian Coast as revealed by amplified fragment length polymorphism markers	2013	Journal of Applied Phycology	Vol. 25, pp. 1255-1263
Halling, C., Wikström, S.A., Lilliesköld-Sjöö, G., Mörk, E., Lundsør, E., Zuccarello, G.C.	Introduction of Asian strains and low genetic variation in farmed seaweeds: Indications for new management practices	2013	Journal of Applied Phycology	Vol. 25, pp. 89-95

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Robuchon, M., Couceiro, L., Peters, A.F., Destombe, C., Valero, M.	Examining the bank of microscopic stages in kelps using culturing and barcoding	2014	European Journal of Phycology	Vol. 49, pp. 128-133
Lim, P.E., Tan, J., Phang, S.M., Nikmatullah, A., Hong, D.D., Sunarpi, H., Hurtado, A.Q.	Genetic diversity of K*appaphycus Doty and Eucheuma J. Agardh* (Solieriaceae, Rhodophyta) in Southeast Asia	2014	Journal of Applied Phycology	Vol. 26, pp. 1253-1272
Ren, J.R., Yang, R., He, Y.Y., Sun, Q.H.	Genetic variation of *Sargassum horneri* populations detected by inter-simple sequence repeats	2015	Genetics and Molecular Research	Vol. 14, pp. 619-625
Zhang, J., Wang, X., Yao, J., Li, Q., Liu, F., Yotsukura, N., Krupnova, T.N., Duan, D.	Effect of domestication on the genetic diversity and structure of Saccharina japonica populations in China	2017	Scientific Reports	Vol. 7
Li, X., Pang, S.J., Shan, T.F.	Genetic diversity and population structure among cultivars of *Saccharina japonica* currently farmed in northern China	2017	Phycological Research	Vol. 65, pp. 111-117

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Guzinski, J., Ballenghien, M., Daguin-Thiébaut, C., Lévêque, L., Viard, F.	Population genomics of the introduced and cultivated Pacific kelp *Undaria pinnatifida*: Marinas—not farms—drive regional connectivity and establishment in natural rocky reefs	2018	Evolutionary Applications	Vol. 11, pp. 1582-1597
Yao, J., Shuai, L., Li, S., Xu, C., Wang, X.	Genetic analysis of selected *Sargassum fusiforme* (Harvey) Setchell (Sargassaceae, Phaeophyta) strains with RAPD and ISSR markers	2019	Journal of Oceanology and Limnology	Vol. 37, pp. 783-789
Wang, X., Yao, J., Zhang, J., Duan, D.	Status of genetic studies and breeding of *Saccharina japonica* in China	2020	Journal of Oceanology and Limnology	Vol. 38, pp. 1064-1079
Thien, V.Y., Yong, W.T.L., Anton, A., Chin, G.J.W.L.	A multiplex PCR method for rapid identification of commercially important seaweeds *Kappaphycus alvarezii, Kappaphycus striatus and Eucheuma denticulatum (*Rhodophyta, Solieriaceae)	2020	Regional Studies in Marine Science	Vol. 40
Cascella, K., Potin, P., Guiry, M., Fort, A., Usadel, B., Sulpice, R., & McHale, M.	Foliose *Ulva* Species Show Considerable Inter-Specific Genetic Diversity, Low Intra-Specific Genetic Variation, and the Rare Occurrence of Inter-Specific Hybrids in the Wild	2020	Journal of Phycology	57, 219 - 233

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Wi, J., Choi, D., Hwang, M., Kim, M., Cho, W., Kim, G., Jeong, W., Park, E., Lee, J., & Choi, S. (2021).. . https://doi.org/10.1007/s10811-021-02536-7	Development of genomic simple sequence repeat (SSR) markers of *Pyropia yezoensis* (Bangiales, Rhodophyta) and evaluation of genetic diversity of Korean cultivars	2021	Journal of Applied Phycology,	33, 3277 - 3285
Ghriofa, C., Fort, A., Inaba, M., Mols-Mortensen, A., Bringloe, T., & Sulpice, R.	Branding and tracing seaweed: Development of a high-resolution genetic kit to identify the geographic provenance of *Alaria esculenta*.	2022	Algal Research.	
Xu, H., Jia, R., Liang, Z., Lu, X., Wang, W.	SSR and 18S rDNA based molecular profiling of *Neopyropia yezoensis* (Rhodophyta) in China: insight into genetic impact of laver aquaculture on wild resource	2023	Frontiers in Marine Science	Vol. 10
Satriani, G.I., Soelistyowati, D.T., Alimuddin, A., Arfah, H., Effendi, I.	Molecular Assessment of *Kappaphycus alvarezii* Cultivated in Tarakan based on cox2-3 Spacer	2023	Squalen Bulletin of Marine and Fisheries Postharvest and Biotechnology	Vol. 18, pp. 52-64
Bråtelund, S., Ruttink, T., Goecke, F., Broch, O.J., Klemetsdal, G., Ødegård, J., Ergon, Å.	Characterization of fine geographic scale population genetics in sugar kelp (*Saccharina latissima*) using genome-wide markers	2024	BMC Genomics	Vol. 25

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Li, X., Wang, Y., Xiao, L., Huang, E., Liu, X., Shan, T., Pang, S.	Saccharina sporophytes settling on kelp cultivation rafts come from wild intertidal populations and not from the farmed cultivars	2024	Botanica Marina	Vol. 67, pp. 231-238
Gnayem, N., Unis, R., Gnaim, R., Chemodanov, A., Israel, Á., Gnaim, J., Golberg, A.	Seasonal and culture period variations in the lipid and fatty acid content of *Ulva lactuca* cultivated in Mikhmoret onshore (Israel)	2024	Botanica Marina	Vol. 67, pp. 101-114
Usandizaga, S., Guillemin, M.L., Buschmann, A.H.	Genetic and Environmental Challenges Facing *Gracilaria* and *Gracilariopsis* Aquaculture Industry	2024	Biotechnological Interventions to Aid Commercial Seaweed Farming	pp. 51-79
Wang, J., Xu, K., Tang, L., Wang, Z., Yu, X., Wang, S., Mo, Z., Mao, Y.	Insights into the genetic structure and domestication patterns in cultivated populations of *Neopyropia yezoensis*	2024	Aquaculture	Vol. 592
Xie, C., Ji, D., Guo, Y., Xu, Y., Chang, J., Liao, Y., Wang, W., & Chen, C.	Identification of orange color-related gene, PhcpcC, in *Pyropia haitanensis*.	2024	Frontiers in Marine Science	

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Schmid, M., Bartle, R., Mortensen, A., Maggs, C., Endal, A., Sulpice, R., Inaba, M., Fort, A., McHale, M., Edwards, M., Rosignoli, S., & Baud, A.	Draft genome of *Palmaria palmata* and intraspecific genetic variations in the North-East Atlantic.	2024	bioRxiv.	
Ma, Y., Zhang, J., Qiao, H., Du, Y., Yotsukura, N., Klimova, A.V., Klochkova, N.G., Krupnova, T.N., Galanin, D.A., Duan, D.	Distinct genetic groups with restricted gene flow in wild crop relatives *Saccharina cichorioides* from the northwestern Pacific	2025	Aquaculture	Vol. 609
Ahmed, N., El-Tabakh, M.A.M., Mohamed, H.F., Xu, C., Huang, L.	Micropropagation and ISSR Molecular Analysis of the Endangered Species *Sargassum fusiforme*: A Biotechnological Approach	2025	Journal of Ocean University of China	Vol. 24, pp. 783-791
Li, X., Chang, L., Han, F., Li, X., Xiao, L., Huang, E., Yang, Y., Su, L., Pang, S.	Challenges of genetic homogeneity in aquaculture of the kelp *Saccharina japonica*: Insights from China in ten year's retrospect	2025	Aquaculture Reports	Vol. 43
Cock, J., Mauger, S., Destombe, C., Valero, M., Potin, P., Coudret, J., Ruggeri, P., & Jaugeon, L.	Wild and farmed *Saccharina latissima* in Europe: genetic insights for sustainable cultivation, traceability and environmental challenges	2025	bioRxiv	

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Cryopreservation for germplasm conservation

Author(s)	Title	Year	Journal	Pages
Arbault, S., Renard, P., Pérez, R., Kass, R.	Cryopreservation trials on the gametophytes of the food alga *Undaria pinnatifida* (Laminariale)	1990	Aquatic Living Resources	Vol. 3, pp. 207-215
Renard, P., Arbault, S., Kaas, R., Perez, R.	A method for the cryopreservation of the gametophytes of the food alga *Undaria pinnatifida* (Laminariales)	1992	Comptes Rendus de l'Academie des Sciences - Series III	Vol. 315, pp. 445-451
Kuwano, K., Aruga, Y., Saga, N.	Cryopreservation of the conchocelis of the marine alga *Porphyra yezoensis* Ueda (Rhodophyta) in liquid nitrogen	1993	Plant Science	Vol. 94, pp. 215-225
Vigneron, T., Arbault, S., Kaas, R.	Cryopreservation of gametophytes of *Laminaria digitata* (L) lamouroux by encapsulation dehydration	1997	Cryo-Letters	Vol. 18, pp. 93-98
Kono, S., Kuwano, K., Saga, N.	Cryopreservation of *Eisenia bicyclis* (Laminariales, Phaeophyta) in liquid nitrogen	1998	Journal of Marine Biotechnology	Vol. 6, pp. 220-223
Liu, H., Yu, W., Dai, J., Gong, Q., Yang, K., Lu, X.	Cryopreservation of protoplasts of the alga *Porphyra yezoensis* by vitrification	2004	Plant Science	Vol. 166, pp. 97-102

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Kuwano, K., Kono, S., Jo, Y.-H., Shin, J.-A., Saga, N.	Cryopreservation of the gametophytic cells of Laminariales (Phaeophyta) in liquid nitrogen	2004	Journal of Phycology	Vol. 40, pp. 606-610
Quan, S.Z., Yi, Z.C., Shan, C.Q., Shi, J.L., Xue, X.T.	Cryopreservation of gametophytes of *Laminaria japonica* (Phaeophyta) with two-step cooling: Interactions between variables related to post-thaw survival	2007	Cryo-Letters	Vol. 28, pp. 215-222
Zhang, Q.S., Cong, Y.Z., Qu, S.C., Luo, S.J., Tang, X.X.	Cryopreservation of gametophytes of *Laminaria japonica* (phaeophyta) with two-step cooling: interactions between variables related to post-thaw survival.	2007	Cryo letters	Vol. 28, pp. 217-224
Bhattarai, H.D., Paudel, B., Hong, Y.-K., Shin, H.W.	A simple method to preserve algal spores of *Ulva* spp. in cold storage with ampicillin	2007	Hydrobiologia	Vol. 592, pp. 399-404
Zhang, Q.S., Cong, Y.Z., Qu, S.C., Luo, S.J., Li, X.J., Tang, X.X.	A simple and highly efficient method for the cryopreservation of *Laminaria japonica* (Phaeophyceae) germplasm	2007	European Journal of Phycology	Vol. 42, pp. 209-213
Lalrinsanga, P.L., Deshmukhe, G., Chakraborty, S.K., Dwivedi, A., Barman, N., Kumar, N.	Preliminary studies on cryopreservation of vegetative thalli of some economically important seaweeds of india	2009	Journal of Applied Aquaculture	Vol. 21, pp. 250-262

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Wang, B., Zhang, E., Gu, Y., Ning, S., Wang, Q., Zhou, J.	Cryopreservation of brown algae gametophytes of *Undaria pinnatifida* by encapsulation-vitrification	2011	Aquaculture	Vol. 317, pp. 89-93
Nakazawa, A., Nishii, I.	Amidic and acetonic cryoprotectants improve cryopreservation of volvocine green algae	2012	Cryo-Letters	Vol. 33, pp. 202-213
Choi, Y.H., Nam, T.J.	Toxicity of cryoprotectants to gametophytic thalli of red algae *Porphyra yezoensis*	2012	Fisheries and Aquatic Sciences	Vol. 15, pp. 77-81
Heesch, S., John, G.D., Yamagishi, T., Kawai, H., Müller, D.G., Küpper, F.C.	Cryopreservation of the model alga *Ectocarpus* (phaeophyceae)	2012	Cryo-Letters	Vol. 33, pp. 327-336
Heesch, S., John, G.D., Yamagishi, T., Kawai, H., Müller, D.G., Küpper, F.C.	Cryopreservation of the model alga *Ectocarpus* (phaeophyceae)	2012	Cryo-Letters	Vol. 33, pp. 327-336
Green, L.A., Neefus, C.D.	The effects of short- and long-term freezing on *Porphyra umbilicalis* Kützing (Bangiales, Rhodophyta) blade viability	2014	Journal of Experimental Marine Biology and Ecology	Vol. 461, pp. 499-503

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Piel, M.I., Avila, M., Alcapán, A.	Cryopreservation of early stages of *Macrocystis pyrifera* gametophytes (Laminariales, Ochrophyta) under controlled laboratory conditions	2015	Revista de Biologia Marina y Oceanografia	Vol. 50, pp. 157-162
Zhuang, Y., Gong, X., Zhang, W., Gao, W.	Cryopreservation of filaments of *Scytosiphon lomentaria* by vitrification	2015	Journal of Applied Phycology	Vol. 27, pp. 1337-1342
Zhuang, Y., Gong, X., Zhang, W., Gao, W.	Cryopreservation of filaments of *Scytosiphon lomentaria* by vitrification	2015	Journal of Applied Phycology	Vol. 27, pp. 1337-1342
Gao, G., Clare, A.S., Rose, C., Caldwell, G.S.	Non-cryogenic preservation of thalli, germlings, and gametes of the green seaweed *Ulva rigida*	2017	Aquaculture	Vol. 473, pp. 246-250
Jung, S.M., Lee, J.H., Lee, H.J., Jeon, J.Y., Park, T.H., Yoon, J.H., Shin, H.W.	The growth of alginate-encapsulated macroalgal spores	2018	Aquaculture	Vol. 491, pp. 333-337
Fernandes, M.S., Calsing, L.C.G., Nascimento, R.C., Santana, H., Morais, P.B., de Capdeville, G., Brasil, B.S.A.F.	Customized cryopreservation protocols for chlorophytes based on cell morphology	2019	Algal Research	Vol. 38

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Visch, W., Rad-Menéndez, C., Nylund, G.M., Pavia, H., Ryan, M.J., Day, J.	Underpinning the development of seaweed biotechnology: Cryopreservation of brown algae (*Saccharina latissima*) gametophytes	2019	Biopreservation and Biobanking	Vol. 17, pp. 378-386
Pence, V.C., Ballesteros, D., Walters, C., Reed, B.M., Philpott, M., Dixon, K.W., Pritchard, H.W., Culley, T.M., Vanhove, A.-C.	Cryobiotechnologies: Tools for expanding long-term ex situ conservation to all plant species	2020	Biological Conservation	Vol. 250
Yang, H., Huo, Y., Yee, J.C., Yarish, C.	Germplasm cryopreservation of macroalgae for aquaculture breeding and natural resource conservation: A review	2021	Aquaculture	Vol. 544
Yang, H., Huo, Y., Yee, J.C., Yarish, C.	Germplasm cryopreservation of macroalgae for aquaculture breeding and natural resource conservation: A review	2021	Aquaculture	Vol. 544
Ma, M.-J., Wei, C.-L., Zhu, J.-K., Liu, Q.-Q., Luo, Q.-J., Chen, H.-M., Yang, R.	The role of abscisic acid and cold adaptation in improving the cryopreservation efficiency of *Pyropia haitanensis conchocelis*	2022	Acta Hydrobiologica Sinica	Vol. 46, pp. 184-193
Mayekar, T.S., Sreekanth, G.B., Lal, M.	Cryopreservation Technique for Seaweed Germplasm Storage-Potential Applications in Aquaculture and Conservation	2024	Biotechnological Interventions to Aid Commercial Seaweed Farming	pp. 443-468

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Seaweed microbiome and aquaculture

Author(s)	Title	Year	Journal	Pages
Wichard, T.	Exploring bacteria-induced growth and morphogenesis in the green macroalga order Ulvales (Chlorophyta)	2015	Frontiers in Plant Science	Vol. 6, pp. 1-19
Martin, M., Barbeyron, T., Martin, R., Portetelle, D., Michel, G., Vandenbol, M.	The cultivable surface microbiota of the brown alga *Ascophyllum nodosum* is enriched in macroalgal-polysaccharide-degrading bacteria	2015	Frontiers in Microbiology	Vol. 6
Zozaya-Valdés, E., Roth-Schulze, A.J., Thomas, T.	Effects of temperature stress and aquarium conditions on the red macroalga *Delisea pulchra* and its associated microbial community	2016	Frontiers in Microbiology	Vol. 7
Busetti, A., Maggs, C.A., Gilmore, B.F.	Marine macroalgae and their associated microbiomes as a source of antimicrobial chemical diversity	2017	European Journal of Phycology	Vol. 52, pp. 452-465
Lian, J., Wijffels, R.H., Smidt, H., Sipkema, D.	The effect of the algal microbiome on industrial production of microalgae	2018	Microbial Biotechnology	Vol. 11, pp. 806-818

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van der Loos, L.M., Eriksson, B.K., Falcão Salles, J.	The Macroalgal Holobiont in a Changing Sea	2019	Trends in Microbiology	Vol. 27, pp. 635-650
Fisher, C.L., Ward, C.S., Lane, P.D., Kimbrel, J.A., Sale, K.L., Stuart, R.K., Mayali, X., Lane, T.W.	Bacterial communities protect the alga *Microchloropsis salina* from grazing by the rotifer *Brachionus plicatilis*	2019	Algal Research	Vol. 40
Califano, G., Kwantes, M., Abreu, M.H., Costa, R., Wichard, T.	Cultivating the Macroalgal Holobiont: Effects of Integrated Multi-Trophic Aquaculture on the Microbiome of *Ulva rigida* (Chlorophyta)	2020	Frontiers in Marine Science	Vol. 7
Polikovsky, M., Califano, G., Dunger, N., Wichard, T., Golberg, A.	Engineering bacteria-seaweed symbioses for modulating the photosynthate content of *Ulva* (Chlorophyta): Significant for the feedstock of bioethanol production	2020	Algal Research	Vol. 49
Badis, Y., Klochkova, T.A., Brakel, J., Arce, P., Ostrowski, M., Tringe, S.G., Kim, G.H., Gachon, C.M.M.	Hidden diversity in the oomycete genus *Olpidiopsis* is a potential hazard to red algal cultivation and conservation worldwide	2020	European Journal of Phycology	Vol. 55, pp. 162-171

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Ghaderiardakani, F., Quartino, M.L., Wichard, T.	Microbiome-Dependent Adaptation of Seaweeds Under Environmental Stresses: A Perspective	2020	Frontiers in Marine Science	Vol. 7
Abdul Malik, S.A., Bedoux, G., Garcia Maldonado, J.Q., Freile-Pelegrín, Y., Robledo, D., Bourgougnon, N.	Defence on surface: macroalgae and their surface-associated microbiome	2020	Advances in Botanical Research	Vol. 95, pp. 327-368
Alsufyani, T., Califano, G., Deicke, M., Grueneberg, J., Weiss, A., Engelen, A.H., Kwantes, M., Mohr, J.F., Ulrich, J.F., Wichard, T.	Macroalgal-bacterial interactions: Identification and role of thallusin in morphogenesis of the seaweed *Ulva* (Chlorophyta)	2020	Journal of Experimental Botany	Vol. 71, pp. 3340-3349
Menaa, F., Wijesinghe, P.A.U.I., Thiripuranathar, G., Uzair, B., Iqbal, H., Khan, B.A., Menaa, B.	Ecological and Industrial Implications of Dynamic Seaweed-Associated Microbiota Interactions	2020	Marine Drugs	Vol. 18
Ahmed, A., Khurshid, A., Tang, X., Wang, J., Khan, T.U., Mao, Y.	Structural and functional impacts of microbiota on *Pyropia yezoensis* and surrounding seawater in cultivation farms along coastal areas of the yellow sea	2021	Microorganisms	Vol. 9

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Variem, S.S., Kizhakkedath, V.K.	Phycosphere associated bacteria; a prospective source of bioactive compounds	2021	Biologia	Vol. 76, pp. 1095-1098
Kopprio, G.A., Luyen, N.D., Cuong, L.H., Duc, T.M., Fricke, A., Kunzmann, A., Huong, L.M., Gärdes, A.	Insights into the bacterial community composition of farmed *Caulerpa lentillifera*: A comparison between contrasting health states	2021	MicrobiologyOpen	Vol. 10
van der Loos, L.M., D'hondt, S., Willems, A., De Clerck, O.	Characterizing algal microbiomes using long-read nanopore sequencing	2021	Algal Research	Vol. 59
Capistrant-Fossa, K.A., Morrison, H.G., Engelen, A.H., Quigley, C.T.C., Morozov, A., Serrão, E.A., Brodie, J., Gachon, C.M.M., Badis, Y., Johnson, L.E., Hoarau, G., Abreu, M.H., Tester, P.A., Stearns, L.A., Brawley, S.H.	The microbiome of the habitat-forming brown alga *Fucus vesiculosus* (Phaeophyceae) has similar cross-Atlantic structure that reflects past and present drivers	2021	Journal of Phycology	Vol. 57, pp. 1681-1698
Wang, J., Tang, X., Mo, Z., Mao, Y.	Metagenome-Assembled Genomes From *Pyropia haitanensis* Microbiome Provide Insights Into the Potential Metabolic Functions to the Seaweed	2022	Frontiers in Microbiology	Vol. 13

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Seedling materials to increase seeding efficiency and sustainability

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Toolkits for Seaweed Hatchery Operations

Background, Current Practices, and Innovations

I3-4 SEAWEED

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