



Macroalgal Diseases: Exploring Biology, Pathogenesis, and Management Strategies

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Abstract: The global seaweed market is expected to reach USD 17.8 billion by 2032, fuelled by growing demand for sustainable and healthy food solutions and expanding applications in agriculture and aquaculture. However, this rapid growth poses significant challenges, particularly in managing diseases that often establish themselves in intensive macroalgal culture facilities. Red rot disease, *Olpidiopsis*, and green spot disease often affect marine macroalgae species of high commercial interest, as seen in *Pyropia/Porphyra* as has already happened for "ice-ice" malaise on *Kappaphycus*, causing huge economic losses. These diseases are caused by infectious agents that find their place in extreme environmental conditions, such as those characterized by sudden changes in temperature and pollution. Despite technological advances aimed at monitoring the well-being of cultivated seaweed, discrepancies between regions' technological capabilities and species vulnerability exacerbate management difficulties. This review provides an overview of diseases prevalent among marine algae, their impact on aquaculture, and the effectiveness of currently adopted treatments. This study highlights the need to improve disease management strategies and highlights the importance of understanding host–pathogen interactions in order to mitigate future epidemics.

Keywords: seaweed diseases; aquaculture management; sustainable farming; marine biology; disease management; macroalgal cultivation; environmental impact

1. Introduction

The global seaweed market is expected to reach USD 17.8 billion by 2032, driven by growing demand for healthy and sustainable foods, expanding applications in the food and beverage industry and growing interest in agriculture and sustainable aquaculture [1,2]. The search for sustainable foods will determine the increase in the intensive cultivation of macroalgae, and consequently, the problems linked to the management of the plants and, above all, the pathologies that settle there will also increase. In fact, in intensive macroalgae cultivation, the costs required for the prevention and treatment of diseases are estimated to take up 30% to 50% of a company's budget [3], and up to half of the biomass produced can be lost [4]. Currently, advanced quality control technologies are often used for cultivation [5], but there is often a discrepancy in the technological progress of nations and the cultivated species that is not closely related to the market price of algae or derived products [6].

Cultured macroalgae are frequently affected by numerous parasites that cause diseases that alter the morphology of the thallus, but despite this, this topic is largely underdocumented. Parasites are increasingly considered key players in natural ecosystems, but they are also one of the most serious economic and environmental threats to macroalgae aquaculture.

There are two types of diseases in algae: infectious and non-infectious diseases. The former type involves a transmissible infectious agent (bacteria, fungi, viruses, etc.), while the latter type is induced by physiological factors such as extreme temperatures, salinity, light intensity, or pollution [7]. Non-infectious diseases are caused by unfavourable



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Copyright: © 2024 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). environmental conditions; anthropogenic activities such as heavy metal pollution can also cause diseases in marine algae. The symptoms caused by non-infectious diseases are numerous: high temperature and light intensity, for example, can lead to whitening and hardening of the thallus. But above all, algae stressed and weakened by unfavourable environmental conditions are more susceptible to infectious diseases. Very often, there is a synergy between the infectious agent and environmental conditions [8]; in algae, in fact, the pathogen–disease concept is not always appropriate, and pathologies often worsen on farms, where they become real technopathies. Added to this are grazing and nutrient deficiencies, which too often are accompanied by other disorders.

The marine environment is rich in life, and the microbial part has long been underestimated [9], even if some of this is pathogenic and very diversified, sometimes playing a fundamental role in natural ecosystems [10]. Research aimed at pathogens is driven by the impact they have on human health; therefore, the interest in algal diseases and their economic impact is becoming an important driver for research, especially in Europe, where interest in macroalgae is growing exponentially [11].

The biological, physical, and chemical properties of the surface of macroalgae certainly play a role in structuring the associated microbial community and its metabolic activity, subsequently influencing its state of health and the attack of pathogens. Several factors that influence the surface environment of macroalgae include algal metabolites, the resident microbial community and their secondary metabolites, and the physicochemical conditions that the surface of the thallus is subjected to, which can include carbon dioxide and oxygen, which can influence the surface pH and the overall microbial community [12]. Many of these parameters are subject to daily and seasonal modulations; cultivated algae may have altered parameters and therefore altered holobionts, and this could be one of the factors triggering diseases in cultivation. Of note, bacteria that enter into a stable association with a macroalgal host must therefore possess adaptive traits that reflect these niche conditions [12].

Macroalgae are under constant colonization pressure from billions of microorganisms present in the surrounding seawater, some of which are potential pathogens [10]. To defend themselves from harmful colonizers, macroalgae require general or specific strategies to control microbial growth. Macroalgae lack a cellular adaptive immune response but have defensive capabilities that fall into two broad categories: constitutive ones, those which are always expressed and do not depend on the qualitative and quantitative presence of the microbial community, and regulated ones, which are activated from "tissue" damage and cause oxidative bursts or hypersensitive responses [13]. Macroalgae diseases have been linked to bacteria, viruses, fungi, and other eukaryotes. However, the specific role of bacterial or fungal pathogens in these diseases remains largely unclear. This lack of understanding is partly due to the difficulty in distinguishing true pathogens, especially from saprophytes or other secondary colonizers that benefit from damaging macroalgae. All these diseases are exacerbated by global warming and intensive high-density biomass farming (e.g., Ulva spp. in Europe and Eucheuma spp. in Africa, especially in Tanzania), and the expansion of aquaculture increases the impact of these diseases, potentially leading to economic losses in several areas.

This review aims to illustrate an updated overview of the most known pathologies and pathogens related to macroalgae cultivation to improve crop management strategies.

2. Pyropia/Porphyra Species

Genera *Pyropia/Porphyra* (Bangiales) is among the most valuable aquaculture algae in the world and has been cultivated in Japan, China, and Korea for thousands of years and, recently, also in many other countries of the world. In Japan, it is most often used as nori (known in China as "zicai" and in Korea as "gim"), an ingredient of sushi. In Wales and England, it is used in a traditional dish, laver. In the last decade, many studies have been conducted on its nutritional value and pharmaceutical properties; for these reasons, these cultivations represent one of the most advanced algal industries, with a market value of over EUR 2 billion per year (EUR 2.5 billion in 2017). Nori farms, in terms of appearance and commercial approach, look more like crop agriculture areas rather than aquaculture areas, and nori was one of the first real macroalgae studied in "Phyconomist", after Eu*cheuma*/*Kappaphycus* [14]. This economic interest shifted the attention to production, and various pathologies have therefore been discovered. About more than ten/fifteen different diseases attack nori farms, including bacteria, viruses, and fungal-like organisms [3,14,15]. Very often, some pathologies can be seen to be "overlapping"; up to a few decades ago, various causes were attributed to the same pathology. With the advent of molecular analysis, these evaluation errors have been reduced, and such analysis techniques have been used to clarify the three major diseases listed above. Frequently, the pathologies are caused by Pythium sp., Olpidiopsis sp. (Oomycetes), and the virus "PyroV1" (green rot disease). Among bacterial agents, there are Flavobacterium spp. In Korea, where Pyropia/Porphyra cultivation has recently rapidly expanded, new disease outbreaks are reported every year, and they have reduced the crop output by around 20% in certain areas, causing a general decrease in product quality and considerably lowering the market value of harvested Pyropia blades [3,8].

2.1. Red Rot Disease (RRD)

Red rot disease (RRD) is primarily caused by the necrotrophic oomycete Pythium porphyrae [3,8,16] and is the most widely studied disease of the gametophytic generation of *Porphyra* spp. Like the systematics of Bangiales [17], the systematics of fungi are also constantly evolving [18]. Red rot disease was first reported in Pyropia tenera in Japan by Arasaki [19], and its pathogenesis was characterized in *Puropia* spp. [20]. The first symptoms that can be recognized are characterized by small red patches or bleached parts (a few micrometres in diameter); between 2 and 3 days after symptom onset, their natural reddish-brown colour becomes violet-red, before they turn green and, in the end, colourless, and the blades degenerate completely (Figures 1–3). Mycelium of Pythium colonize the host-cell intracellularly, killing them and progressively forming the distinct patches described before. The infection spreads quickly to other areas on the blade, mainly via cell-to-cell spreading, and dead host tissue deteriorates, forming numerous small holes; the holes could "merge" into bigger holes, ultimately disintegrating the entire blade. To date, Pythium porphyrae and Pythium chondricola have been reported as the main causative agents of RRD [21,22], although some studies suggest that a fungus of the genus Alternaria is another causative agent of this disease [23]. In Japan, around 20% of biomass is lost due to RRD [24]. Pathogen zoospores' adherence to the thalli is promoted by conditions characterized by a high temperature, low salinity, and the absence of free-change tide [25], and pathogen zoospores infect the thallus. A very modern approach was suggested in a recent study about exploiting the biocontrol of two strains of Pseudoalteromonas piscicida to fight against red rot disease in *Pyropia yezoensis*. Both strains inhibited the growth of the pathogen Pythium porphyrae without harming the algae. P6, combined with air drying, showed significant disease inhibition, suggesting that it is an effective method for controlling red rot in *Pyropia* [26].

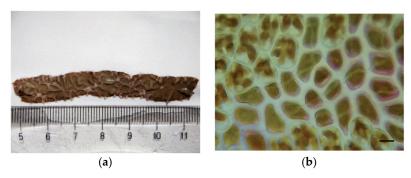


Figure 1. Clinical symptoms of *Pyropia yezoensis* red rot disease: (**a**) Macroscopic symptoms evident in infected thallus; (**b**) histopathology of the lesion area, presenting abnormal cells being penetrated by fungal mycelia, with an accumulation of released phycoerythrobilin-like material. Scale bar represents 10 μm [21].

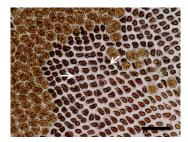


Figure 2. Mycelia of *Pythium chondricola* formed over the lesioned area in *Pyropia yezoensis* (arrows). Scale bars represents 50 μm [27].

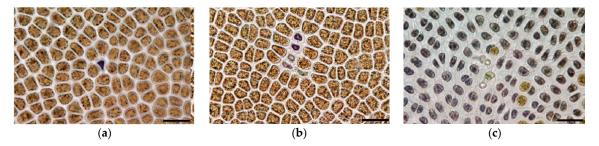


Figure 3. Infected cells of *Pyropia plicata* after 1 day (**a**), 3 days (**b**), and 9 days (**c**). Dark cells are newly infected cells, while light cells are older infected cells. After 9 days, almost all cells were dead. *Pythium porphyrae* hyphae were visible between cells. Scale bar represents 50 μm [22].

2.2. Olpidiopsis Disease (OD), Chytrid Disease (CD), Olpidiopsis-Blight (O-B)

Infections caused by organisms of the *Olpidiopsis* genus are more aggressive than RRD [28]. Olpidiopsis Disease (OD) (often call Chytrid Disease or Olpidiopsis-Blight) OD is caused by the attack of obligate endoparasitic oomycetes and has been reported in China, Korea, and Japan [29]. In the last decade, it has also been reported in Europe, and the classification of the genus has been revised [28,30]. Symptoms initially manifest as distinct blanched areas on the blades, which progress to greenish lesions as the disease spreads. The infection route is like that of *Pythium*, but the spread seems more disordered on the surface of the thallus. The infection process begins when encysted *Olpidiopsis* zoospores attach to the surface of *Pyropia/Porphyra* and produce thin germ tubes that penetrate the host's cell walls. Subsequently, the parasite forms multinucleated spherical thalli, which, after 2–3 days, develop into zoosporangia, which release the zoospores. The rotting of the "tissue" in the infected areas promotes the death of the entire blade (Figure 4). Many strategies have been adopted to control this pathology, but their effectiveness is not always certain [31]. A recent study explored non-acidic alternatives to control these pathogens. Among the calcium salts tested, calcium propionate emerged as the most effective. When

Pyropia blades were briefly immersed in calcium propionate solutions, both the infection rate and the spread of oomycetes were significantly reduced [32].

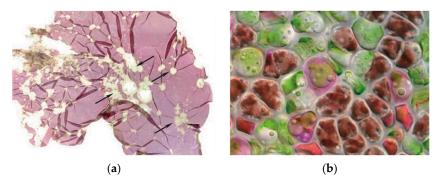


Figure 4. Macroscopic and microscopic symptoms of olpidiopsis disease observed on *Pyropia* blades: (a) Arrows show decaying greenish areas (b); each green cell contains one *Olpidiopsis* thallus. Scale bar represents 50 μm [3].

2.3. Green Spot Disease

Green spot disease of the genera *Pyropia/Porphyra* was reported more than twenty years ago in Korea. However, to date, there have been no detailed studies describing its specific symptoms and infective agents. Green spot disease in *Pyropia* is identified by the presence of small, distinct lesions on the blade, characterized by broad green borders. These lesions can appear anywhere on the blade and are often accompanied by severe bacterial contamination. As the lesions grow and coalesce, slimy rot occurs as the host tissue breaks down (Figure 5). Subsequently, many types of Gram-negative bacteria attach to the surface of the thallus, such as *Flavo-bacterium* sp., *Pseudoalteromonas* sp., and *Vibrio* sp.; this has historically led to the incorrect attribution of this disease to bacterial agents [3]. Current understanding suggests that bacterial invasion should be considered secondary to the viral infection, as these bacteria act as opportunistic pathogens. *PyroV1* is considered responsible for green spot disease [33].

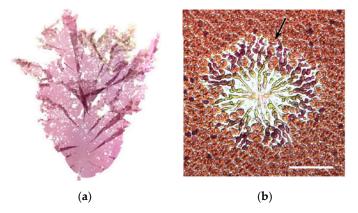


Figure 5. Typical symptoms of green spot disease infection in *Pyropia* sp.: (**a**) Infected blade with numerous lesions that look like bullet holes; (**b**) upon progression of infection, a chain of pinkish cells develops, encircling the green lesion. Scale bar represents 50 μm [3].

2.4. Cyanobacteria Felt

Green spot disease and cyanobacterial infestations often occur at the same time on *Pyropia*, causing their symptoms to overlap. The cell wall structure of *Pyropia* cells loosens and degenerates in the presence of abundant bacteria and cyanobacteria on the surface, forming a long distinct "bristle" visible on the thallus [15]. Both single cells and large colonies of mucilage-secreting coccoid cyanobacteria are observable with TEM.

2.5. Diatom Felt

"Diatom felt" on *Pyropia*/*Porphyra* appears as a distinct brown fringe across the entire surface of the blade. When touched with the fingers, detached diatoms can be seen, so this disease can be easily recognized by non-professionals. *Pyropia* growth can be seriously affected by epiphytic diatoms, as they shade light, compete for nutrients, and cause bleaching of macroalgae thalli [3]. Infected *Pyropia* has a distinct, unpleasant, earthy odour. This disease does not cause serious production losses but directly affects the price of raw materials, creating concern among farmers.

2.6. Genetic Toolkits against Common Diseases in Porphyra/Pyropia Species

In recent years, we have introduced the diseases with the highest incidence into *Porphyra* farms, and efforts have been made to develop toolkits, including molecular ones, for faster identification to prevent disease progression (Table 1) [33]. The rapid expansion of seaweed aquaculture has resulted in sudden ecological consequences, including epidemics, the introduction of non-indigenous pathogens, and a reduction in the genetic diversity of native seaweed stocks. Thus, to overcome these challenges, it is crucial to understand the molecular basis of host–pathogen interactions and possible resistance. *Porphyra/Pyropia* have a large pool of defence genes, and the expression of these genes is differentially regulated during infection in response to pathogen types [34].

Table 1. Table summarizing *Porphyra/Pyropia* diseases, with the pathology names, pathogens, symptoms, current treatments, treatment effectiveness, and severity as the average between mortality, incidence, and treatment effectiveness. Grey colour: no sufficient data.

Disease Name	Causative Organism/ Taxonomy	Symptoms	Current Treatment	Effectiveness of Treatment	Severity	References
Red rot disease	Pythium porphyrae, Pythium chondri- cola/Oomycete Alternaria sp./Ascomycota	Red patches on the blade; blade's colour changes from natural brownish-red to violet-red; formation of numerous holes, followed by disintegration of the blade	Exposure of culture nets to air; acid wash	Partially effective	High	[3,8,16–27]
<i>Olpidiopsis</i> disease	Olpidiopsis porphyrae, Olpidiopsis pyropiae, Olpidiopsis sp./Oomycete	Bleached portion on the blades; appearance of greenish lesions; formation of numerous holes, followed by disintegration of the entire blade	Exposure of culture nets to air; decrease in density of culture nets; acid wash; calcium propionate	No	High	[3,28–32]
Green-spot disease	Primary: PyroV1/Virus Secondary: Flavobacterium sp., Pseudoalteromonas sp., Vibrio sp./Gram-negative bacteria	Lesions with wide green borders; slimy rots and holes in the blade	Exposure of culture nets to air; acid wash	No	High	[3,33]

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Disease Name	Causative Organism/ Taxonomy	Symptoms	Current Treatment	Effectiveness of Treatment	Severity	References
"Cyanobacteria felt"	Filamentous and coccoid blue-green algae/Cyanobacteria	Dirty blade surface; lesions and holes in the blade	Drying of culture nets; acid wash	Partially effective	Medium	[15]
"Diatom felt"	Fregellaria sp., Licmopohora flabellata, Melosira sp., Navicula sp./Bacillariophyceae	Dirty blade surface; blade bleaching; rust-coloured powder	Drying of culture nets; acid wash	Partially effective	Medium	[3]
White blight disease	?	Random bleached areas on the blade; cell lysis	No treatment	No	Low	[15]
White rot disease	<i>Vibrio</i> sp./Gram-negative bacteria	Random circular bleached areas of thallus	No treatment	No	Low	[15]
"Suminori" disease	Gaetbulibacter saemankumensis, Arthrobacter tumbae, Flavobacterium spp., Vibrio spp./Gram-negative bacteria	Black lustreless colour of blade; plasmoptysis of blade cells	Exposure of culture nets to air; acid wash	Partially effective	Medium	[35]
"Anaaki" disease (often associated with green spot)	Flavobacterium sp., Pseudoalteromonas sp., Vibrio sp./Gram-negative bacteria	Random holes on the blade; fast degradation of the blade	Exposure of culture nets to air; acid wash	Partially effective	Medium	[3]
Unnamed disease	"Pseudomonas-like" bacteria/Gram- negative bacteria	Similarity to white rot disease	No treatment	No	Low	[15]
White spot disease	Phoma sp./Coelomycete	Bleaching of oyster shell with shell-boring <i>conchocelis</i>	Discarding infected oyster shells	Yes	Low	[36]
Yellow spot disease	<i>Vibrio mediterranei 117-T6/</i> Gram- negative bacteria	Yellow spots gradually spread around and form lesions of different sizes	/	/	n/a	[37]

Table 1. Cont.

3. Kappaphycus sp. and Eucheuma sp.

3.1. "Ice-Ice" Malaise

Kappaphycus alvarezii cultivations in the Philippines have always highlighted a phenomenon known as "Ice-ice" [4]. The whitening effect (Figure 6) is mainly caused by a defence response mechanism of the algae, triggered by the presence of halogenated volatile organic compounds which cause an oxidative burst. Stressors release H_2O_2 (hydrogen peroxide), which bleaches thalli after prolonged exposure [4,6]. Members of the *Cytophaga-Flavobacterium-Bacteroides* group and various genera of marine fungi, such as *Aspergillus* sp. and *Phoma* sp., were isolated from affected thalli. However, their main role is to exert a secondary effect, which occurs after the macroalgae have been weakened by physiological stresses. This secondary infection manifests itself in complete necrosis of the thalli, caused by both bacteria and fungi present in the affected algae. These microbial agents decompose the fibrillar component of the cell wall and use the amorphous part as the primary carbon source [4].



Figure 6. "Ice-ice" infected Kappaphycus alvarezii [38].

3.2. Goose Bumps Disease

The disease 'Goose bumps', unlike "ice-ice", is properly classified as a pathology. The initial obvious symptom is some "black pimples" appearing on the surface of the thallus of *Kappaphycus/Eucheuma* (Rhodophyta) and on the sites of sedimentation of the spores of the filamentous red alga *Neosiphonia* spp. (Figure 7). Germinating spores penetrate the cortical and medullary layers of host algae and develop into an endophytic filamentous algae (EFA) infestation [4]. Infestations by *Kappaphycus* spp. cultivation sites were first recorded in 1994 in the Philippines. The disease was initially erroneously ascribed to a red algae *Polysiphonia* sp. epiphytic outbreak (due to incorrect identification), only later being confirmed as *Neosiphonia apiculata*. Other *Neosiphonia* species have since been implicated; this genus is a genus with common epiphytic (but necessarily endophytic) species of brown algae *Sargassum* spp. [30] and may have been transferred by drift *Sargassum* being involved in the cultivation of *Kappaphycus* by epiphyte transfer [39–41], where it was very successful in carrying out attachment and subsequent reproduction through copious spore production under favourable conditions [42].

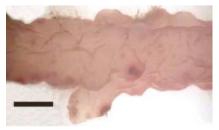


Figure 7. Host thallus of *Kappaphycus* sp. with "goose-bump"-like symptoms at the end of the epiphyte infection phase. Scale bar represents 300 µm [42].

4. Gracilaria sp.

Like *Kappaphycus* cultivation companies, *Gracilaria* production also suffers from the attack of epiphytes on the thalli, which hinders productivity and reduces the market value of the crop. Overall, most of these epiphytes also belong to the order of red algae Ceramiales, including *Ceramium* spp. and *Polysiphonia* spp. [43]. The diseases affecting *Gracilaria* spp. are not clearly defined, and no attention has been paid to specific symptoms. However, the correlation between pathogens and mortality rate of *Gracilaria gracilis* in production facilities have led to the establishment of positive correlations between disease symptoms ("white tip" and "rotten thallus" syndromes, Figure 8) [44,45] and the presence of epiphytic agarolithic [46]. Among these, marine bacteria species of genus *Pseudoalteromonas* are particularly widespread and are the cause of "whitening stripe disease" in *Gracilaria cordicata*. Recently, many studies have provided a list of confirmed and presumed pathogenic bacteria of macroalgae, some of which attack *Gracilaria* thalli (Table 2). The disease hinders or stunts growth, shortens shelf life, and causes morphological deformities, making it difficult to market affected plants. Infected thalli show unusual lesions or small bump-like structures (galls) on the surface, and the thallus appears to have "witch's broom"-like branches at the end.



Figure 8. Tip whitening of Gracilaria lemaneiformis [45].

Table 2. Summary of *Gracilaria* spp. diseases, with the pathology names, pathogens, symptoms, current treatments, treatment effectiveness, and severity as the average between mortality, incidence, and treatment effectiveness. Grey colour: no sufficient data.

Disease Name	Causative Organism /Taxonomy	Symptoms	Current Treatment	Effectiveness of Treatment	Severity	References
Epiphytes	<i>Ceramium minuta,</i> <i>Polysiphonia forfex,</i> <i>Hypnea</i> spp., and more species/ Rhodophyta	Generally, epiphytes are attached superficially to the surface of the host; however, genera such as <i>Polysiphonia</i> spp. and <i>Ceramium</i> spp. can penetrate the host tissue, affecting its growth and, hence, its productivity	Control of nutrients; move and shift growing structures	Partially effective	Medium	[44]
Rotten thallus syndrome or "Thalluswhiten- ing"	Vibrioparahaemolyticus, Vibrio spp., Thalassospira spp./Gram- negative bacteria (agarolytic)	Slow growth, whitening of axesand branches, increased thallusfragility	Transfer to areas with slightly greater water current	Partially effective	Medium	[45,46]
Bleaching Stripe Disease or "Cell-wall degradation"	Pseudoalteromonas spp./Gram- negative bacteria (agarolytic)	Cell wall degradation	/	/	n/a	[46]
White-tip disease	Bacterial strain OR-11?	Fast development of white necrotic tissues, followed by thallus fragmentation	/	/	n/a	[44]
Brown points disease	Bacterial strain OR-11?	"Tumour-like" growth, leading to proliferations of nearly1 mm diameter	/	/	n/a	[47]
Gracilaria Gall syndrome	Bacterial?	Small bump-like structures	/	/	Medium	[44]
Grazing	Fishes and invertebrates	Loss of biomass	Floating culture; control grazing	Yes	Medium	-

5. Laminaria sp., Saccharina sp., and Undaria sp.

Brown algae are include several edible species, some of which also represent an important source of alginates. Species belonging to the genera *Saccharina, Laminaria,* and *Undaria* are commonly used for human nutrition and therefore subject to massive cultivation. The growth conditions to which they are subjected frequently expose them to alterations attributable to different causes. "Technopathologies" closely related to cultivation conditions are often found [48]. An example is the blister disease caused by a decrease in salinity (Figure 9). As regards real diseases, i.e., those caused by a pathogen, research on them, as is also the case for other groups of algae, has still made few steps. Among the presumed pathogens are some endophytic filamentous algae that, in addition to fungi, bacteria, and viruses, can have a negative impact on algal growth. For example, the most frequent endophytes are the genera Ochrophyta, *Laminariocolax*, and *Laminarionema*, which could be more widespread than believed among cultivated populations. Preliminary investigations have led to the conclusion that these endophytes invade the algal thallus early, causing significant disruptions to morphogenesis [49].



Figure 9. The clinical symptoms of a technopathology, namely blister disease, caused by a sudden decrease in salinity due to the mixing of rainwater with seawater: (a) *Laminaria hyperborea*; (b) *Laminaria digitata*. Scale bar represents 1 cm (photo courtesy of Derek Mayes).

6. Ulva sp.

The genus *Ulva* includes green macroalgae widely used for human consumption. They are harvested worldwide from both natural populations and mass cultivation systems. Research on natural populations has revealed that species belonging to the genus *Myrionema* (Phaeophyceae, Ochrophyta) can be common epiphytes on *Ulva* thalli [50,51]. Their presence causes the onset of brown spots on the blade that can extend over the entire surface (Figure 10a). The presence of epiphytes leads to a reduction in the growth rates of green algae, probably also due to competition for nutrients. This leads to a significant reduction in the market value of the blade, both due to the appearance of the thalli and their size, consequently causing concern for commercial producers. Another pathogen found on *Ulva* spp. thalli is the mycelium of *Pythium* sp. This pathogenic parasite, being also present on *Porphyra/Pyropia* thalli and on terrestrial plants, is certainly a little more well studied, even if the mechanism of action remains uncertain (Figure 10b) [52].

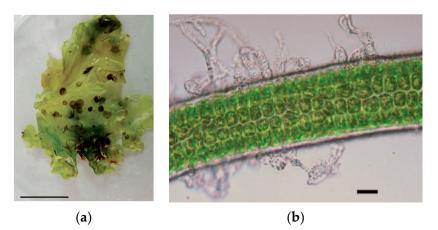


Figure 10. Brown spot disease caused by Phaeophyceae species and fungal infestation on *Ulva* species: (**a**) Epiphytic brown algal genus *Myrionema*, cause of brown spot disease; (**b**) *Pythium* on the surface of *Ulva intestinalis* after inoculation. Scale bar in (**a**) represents 3 cm, and in (**b**), it represents 20 μm [50,52].

7. A Case Study on Kappaphycus: What We Can Learn from Past Mistakes?

Regarding the diseases and their influence on cultivation, we need to take into consideration the worldwide production of *Kappaphycus*. This type of cultivation is spread worldwide, especially in many developing countries, wherein some regional cultivation and harvesting areas represent a substantial part of the economy (Table 3). In these developing countries, after a grace period of a few years, diseases typically worsen due to intensification of cultivation, sometimes leading to the collapse of the local industry (like the shrimp industry 20 years ago in South America). All of this happens for several reasons:

- The main one is the neglect of cultivation rules (which are much more careful for the cultivation of terrestrial plants, agronomy, etc.), which occurs very often because you do not have the knowledge of certain pathologies or do not know the symptoms [53].
- Another reason is the low genetic variation and loss of strain vigour, which has further ramifications in that the biomass becomes susceptible to pathogens, diseases, and epior endophyte infestations [6].
- A third reason is lack of development in commercial utilization of local seaweed biodiversity leading to seemingly unnecessary introductions of non-indigenous Eucheumatoids and their unfettered expansion into new farming areas. Some of these introductions have caused serious environmental issues, such as an increased prevalence of invasive organisms. Also, a lot of the time, it is difficult to establish correlations with pathogens [54].
- The final reason is the failure to innovate new techniques for Eucheumatoid farming, and the indigenous utilization of raw materials merely fuels the expansion of commercial operations through the unregulated transfer of seedlings to new farming areas to meet increasing global demands [14].

Country/Region/State	Start Massive Cultivation	First Report of Disease	Collapse	Recovered
Philippines	1969	1975 ("ice-ice")	2002	2005/2008
Indonesia	1975	2000	-	-
Malaysia	1978	-	2012	2019/2022
Tanzania	1990	1995	2006	Arguably never
South America	2000	2010	-	-

Table 3. Countries where a crisis in the cultivation of Kappaphycus occurred and where it is expected.

The new industries, for example, those in Europe, must take care of all of these things just to not commit the same errors. Environmental and cultivation policies must

be carefully monitored, implementing insights from the study of alien species (not only those cultivated), attempting to promote a common policy, as has been seen in fields like agronomy. As such, the new term "Phyconomy" [14,54–56] is hereby coined to describe a general concept that embraces large-scale, sustainable seaweed farming for economic benefit in coastal waters. Phyconomic lessons learned from the successful/unsuccessful mass cultivation of red seaweeds are guidelines which can be applied to technology transfer and capacity building for other forms of commercial marine macroalgal production.

8. Conclusions

The study of diseases affecting seaweeds reveals important insights and poses challenges that operators in the sector must address. Cultivated species are an integral part of an industry that can have a high economic value, and maintaining high-quality system productivity is the goal for the future in this field. The limited research conducted so far has highlighted that some pathogens can significantly impact production by affecting particularly susceptible or high-commercial-value algal species (e.g., Pyropia affected by red rot disease). Effective monitoring and timely interventions could be essential to mitigating the impact on the entire production chain. Sustainable cultivation protocols and genetic resistance programmes could be essential strategies for combatting these problems. It is necessary to avoid the introduction of non-native species whose expansion could become uncontrollable, as this would cause serious problems, ranging from the alteration of the ecological balance to the emergence of new pathogens. To develop better management practices, it is important to understand host-pathogen interactions and the environmental factors triggering epidemics. Addressing the need for an integrated approach in disease management, combining traditional methods with modern biotechnological advances, is certainly the way forward. Environmental and cultivation policies must be carefully monitored, implementing insights from the study of alien species (not only cultivated ones), trying to promote a common policy like for agronomy. For this reason, we can use the newly coined term "Phyconomy" to describe a general concept that encompasses sustainable large-scale seaweed agriculture for economic benefit in coastal waters. Regular monitoring, early detection, and the development of resistant strains are key components of a robust defence strategy against algal diseases. Research focusing on the molecular mechanisms of disease resistance and pathogen virulence will provide the information needed to implement effective algal disease management strategies. Finally, it will be necessary to promote the implementation of environmentally sustainable cultivation practices, such as polyculture systems and the use of biocontrol agents, to reduce dependence on chemical treatments and produce healthier algal populations.

Strengthening collaboration between researchers, industry stakeholders, and policy makers will facilitate the dissemination of knowledge and the adoption of best practices in marine biotechnology. By improving our understanding and the response to these challenges, we can ensure the long-term viability and productivity of the increasingly essential marine resources.

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