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EDITED BY

Felipe Ascencio,
Centro de Investigación Biológica del
Noroeste (CIBNOR), Mexico

REVIEWED BY

Juan Manuel Pacheco-Vega,
Autonomous University of Nayarit, Mexico
Alvaro Anibal Israel,
University of Haifa, Israel

*CORRESPONDENCE

Eliana Ruiz Martínez

✉ elrm@hvl.no

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Brown algae (Phaeophyceae) stressors and illnesses: a review for a sustainable aquaculture under climate change

Eliana Ruiz Martínez^{1*}, Declan C. Schroeder², Gunnar Thuestad¹
and Ingunn A. Hoell¹

¹Department of Safety, Chemistry and Biomedical Laboratory Sciences, Western Norway University of Applied Sciences, Haugesund, Norway, ²Department of Veterinary Population Medicine, College of Veterinary Medicine, University of Minnesota, St. Paul, MN, United States

Brown algae (Phaeophyceae) dominate intertidal and shallow subtidal areas globally, where larger species form extensive underwater forests. These structurally complex and highly productive habitats enhance local biodiversity and support food webs in coastal areas through secondary production, thereby shaping local oceanography and ecology. Macroalgal aquaculture is an important and growing sector, where approximately 40% of all cultivated algae belong to Phaeophyceae. However, both cultured and natural brown algae have been under increasing pressure due to climate-driven factors, such as ocean warming, eutrophication, and herbivore outbreaks. We conducted a comprehensive literature review on abiotic (temperature, light intensity, and UV radiation, nutrients, water motion, salinity, and substrata and sediment) and biotic (bacteria, viruses, fungi, eukaryotic endophytes and endoparasites, epiphytes, and grazers) stressors and illnesses in marine brown macroalgae, as well as brown algae defense mechanisms, and discuss how these parameters may affect the production of a sustainable crop for the aquaculture industry under future climate change scenarios.

KEYWORDS

macroalgae, stressors, illnesses, seaweed, aquaculture, industry, Phaeophyceae, climate change

1 Brown algae

Eukaryotes developed about 2.7 billion years ago, but multicellular organisms did not evolve from unicellular eukaryotes until at least 1.7 billion years ago (Cooper, 2000). Multicellularity has evolved numerous times within eukaryotes, and brown algae are among the few groups that have reached complex multicellularity, along with animals, fungi, plants, and amoebozoans (Baldauf, 2003; Bringloe et al., 2020). However, brown algae are distantly related to other eukaryotic groups, and their peculiar metabolic,

physiological, cellular, and ecological traits, have turned them into the main components of the marine ecosystem, as well as important ecosystem services for humans (Charrier et al., 2008).

Brown algae (Phaeophyceae) are, therefore, multicellular eukaryotic macroalgae (or seaweeds), which comprise 19 orders with a total number of 2,110 species (Guiry and Guiry, 2018). The older orders started diverging during the Mesozoic Era (≈ 250 Ma), but most of them, including the most ecologically and economically important ones nowadays, diverged during the so-called “Brown Algal Crown Radiation” (Cretaceous, 145–66 Ma) (Bringloe et al., 2020). The distribution of brown algae is determined by climate and geology over time (Bringloe et al., 2020). They can be found in coastal areas all over our oceans and can be divided into temperate (cold and warm), polar, and tropical groups (Bringloe et al., 2020). Brown algae dominate intertidal and shallow subtidal areas globally, where larger species form extensive marine forests that shape local oceanography and ecology (Bringloe et al., 2020). Kelp forests are probably one of the most well-known and studied canopy-forming brown algae; however, they include only members of the order Laminariales. Fucales, Tilopteridales, and Desmarestiales can also form these underwater forests (Bringloe et al., 2020); therefore, due to the similar functions they perform and for practical reasons, the term kelp forest will be used in here when referring to all the previously mentioned orders of brown algae.

Underwater forests can alter local oceanography and ecology by dampening wave surges, which influence water flow, coastal erosion, sedimentation, benthic productivity (primary and secondary), and recruitment (Duggins et al., 1990). They can also influence interspecific competition among algae because their canopy shades the seafloor, allowing low-light intensity species to grow (Santelices and Ojeda, 1984; Dayton, 1985). Kelp forest architecture provides

physical habitat, nursery grounds, and food for organisms above the benthic boundary layer, such as marine mammals, fish, crabs, sea urchins, mollusks, other algae, and epibiota (Mann, 1973; Steneck et al., 2002). Coastal vegetated habitats, such as kelp forests among others (e.g., mangrove forests and seagrass meadows), are known to be one of the most productive ecosystems on Earth (Duarte et al., 2013). Atlantic underwater forests of *Laminaria hyperborea* have been estimated to be between $110 \text{ g C m}^{-2} \text{ year}^{-1}$ and $1,780 \text{ g C m}^{-2} \text{ year}^{-1}$, whereas phytoplanktonic production ranges between $100 \text{ g C m}^{-2} \text{ year}^{-1}$ and $300 \text{ g C m}^{-2} \text{ year}^{-1}$ in temperate coastal regions (Mann, 2000; Smale et al., 2013). Approximately 80% of kelp annual production enters the food web in the form of macroalgal detritus, thereby fueling secondary production and making their carbon available to detritivores and the microbial community, thereby supporting complex food webs in coastal zones (Duggins et al., 1989; Steneck et al., 2002; Wernberg et al., 2019). Macroalgal-derived carbon can travel long distances and sink deep enough to contribute to carbon storage. Even the kelp forest itself can represent an important organic carbon reservoir in the ocean, as refractory carbon compounds are contained within the macroalgal tissues (Wada et al., 2008; Krause-Jensen and Duarte, 2014). For example, kelp forests of *Laminaria hyperborea* in the North-East Atlantic have been estimated to release particulate carbon at a rate of $\approx 5.71 \text{ Tg C/year}$ (Pessarrodona et al., 2018), and to have carbon sequestration potential of 0.46 million tons of carbon per year (Gundersen et al., 2021).

Such productive habitats not only provide us with a wide range of indirect ecosystem services of great ecological value, but also provide us with direct and intrinsic benefits with social and economic value (Figure 1) (Wernberg et al., 2019).

The socioeconomic importance of kelp dates back to some of the oldest times in human history (Erlandson et al., 2007). The

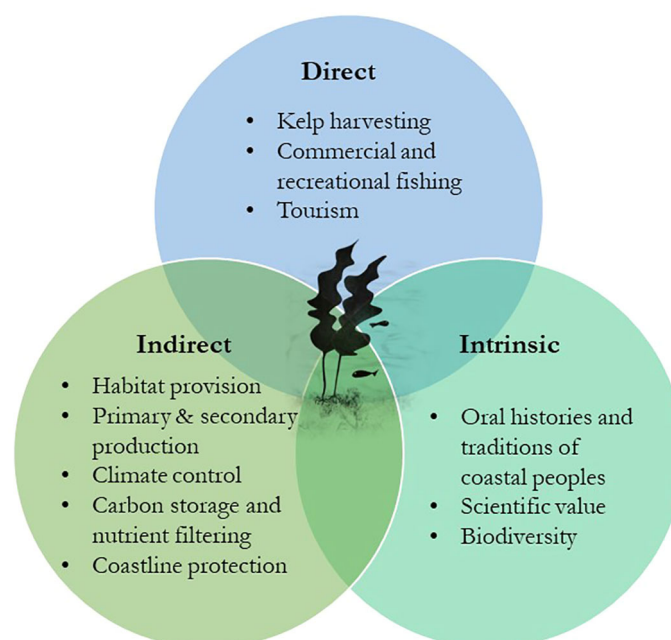


FIGURE 1

Direct, indirect, and intrinsic ecosystem services of kelp forests. Adapted from the study by Wernberg et al. (2019).

consumption of seaweed as food goes back to the Viking age in Norway (Mouritsen et al., 2013), and it remains a traditional food for some coastal communities in Scandinavia today, as well as in Japan, and for the Inuit and Sami peoples (Wernberg et al., 2019). Early humans were aware that seaweed biomass is a rich source of nutrition, even for animals, and their consumption may have helped first colonizers of the American continent to travel along the Pacific rim following the “Kelp Highway” (Erlandson et al., 2007). Moreover, it is thought that the consumption of marine food rich in omega-3 fatty acids and other essential nutrients may have helped the human brain develop in early *Homo* ancestors (Cornish et al., 2017). Kelps have also remained part of the culture and histories of these coastal peoples, being transmitted through oral tradition, as one of the most important deities in the Maori myth: Hine-nui- (i)-te-po. Hine-nui- (i)-te-po, or the “Great lady of the night,” is considered the queen of the underworld and it has been described to have greenstone eyes, kelp-like hair, teeth like obsidian and a mouth like a barracouta (Perris, 2018).

In addition to direct consumption, kelp forests play a crucial role in coastal fisheries, which benefit local communities not just by providing food but also through tourism, as in the Great Southern Reef in Australia (Wernberg et al., 2019). Growing awareness of the potentially high market value of brown algae has led to an expansion of kelp harvesting and cultivation (Holdt and Kraan, 2011; Kim and Bhatnagar, 2011; Schiener et al., 2014). Today, Brown algae are used in the production of fertilizers and feed for the agriculture and aquaculture industries (Hwang et al., 2013; Correa et al., 2016; Kim et al., 2017), as a current and future food source for an increasing human population (Duarte et al., 2009), for the production of pharmaceuticals (Smit, 2004; Lordan et al., 2011; Batista et al., 2019; Purcell-Meyerink et al., 2021), and for sustainable biofuel production (John et al., 2011; Wargacki et al., 2012; Jung et al., 2013; Song et al., 2015). On this matter, increased environmental awareness and sustainability are pushing towards the use of natural sources for the production of bioactive products (Reboleira et al., 2021). Brown algae polymers such as laminarin, alginate, and fucoidan are excellent structural polysaccharides for fermentation, as well as sugars such as mannuronic and guluronic acids, fucose, and glucose (Reboleira et al., 2021). During fermentation, these carbon molecules are converted into smaller molecules with lower molecular weights (molecular oxidation/reduction), such as acetic, lactic, and other organic acids, through the action of microorganisms, such as *Lactobacillus*, *Leuconostoc*, *Lactococcus*, *Streptococcus*, and *Pediococcus* (fermentative gram-positive bacteria) (Monteiro et al., 2021). Ethanol and methane are obtained through seaweed fermentation and represent a sustainable alternative source for the biofuel industry (Reboleira et al., 2021). Fermentation is a highly energy-efficient process compared to other biomass processing technologies that are capable of converting perishable and low-value natural resources into stable and valuable bio-products (Reboleira et al., 2021), as well as making seaweed more palatable, edible, and non-toxic (Bruhn et al., 2019). Therefore, fermentation is a key tool in the discovery, extraction, and processing of novel compounds with industrial applications (Philippesen et al., 2014), and is expected to become more relevant in the future, not just for the

biofuel industry, but also for the food, feed, and pharmaceutical industries (Uchida and Miyoshi, 2013).

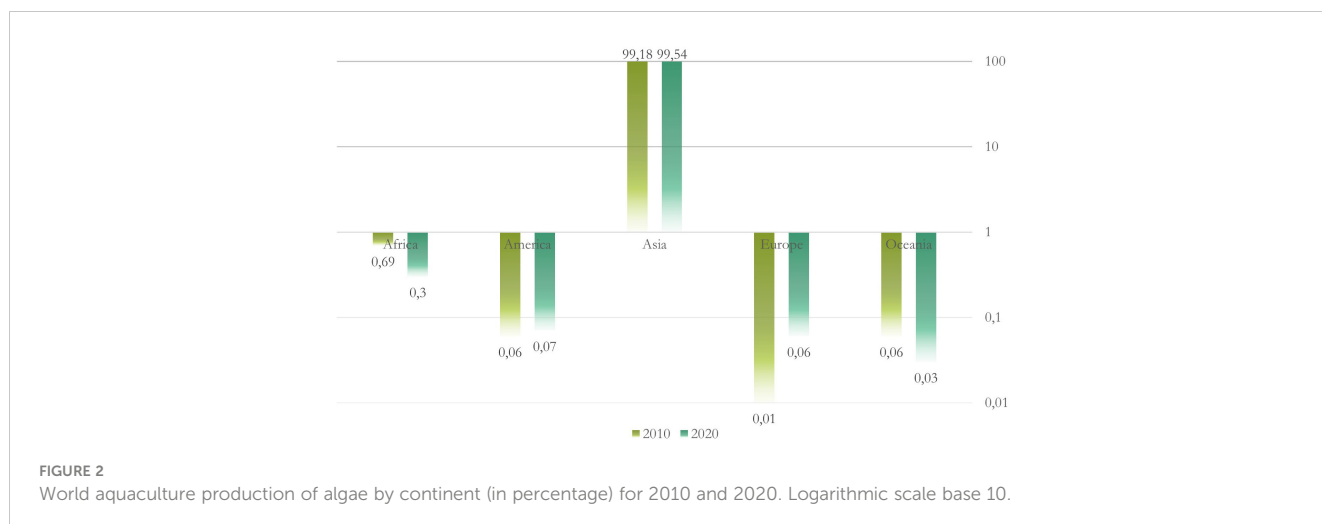
2 Algal aquaculture

Although wild macroalgal harvesting is still used, the pressure imposed on natural marine ecosystems has led to macroalgal farming, which can occur on land, sea, desert, and even in integrated aquaculture systems (Zhang L. et al., 2022). For example, in 2020, inland aquaculture produced 64,490 tons of fresh weight of algae, whereas coastal and marine aquaculture produced 35,013,089 tons of live weight globally (FAO, 2022). These values represent 0.1% and 51.4% of the total inland, coastal and marine aquaculture, respectively, on a global scale (FAO, 2022). Brown algae exhibit a complex and broad range of cycles, ranging from isomorphic, haploid–diploid (with two morphologically identical generations) to diploid (with only one multicellular generation). Therefore, their cultivation will depend on their life cycle. In kelp species, harvested spores from wild fertile plants can be grown into gametophytes in the laboratory. Sporeling from these microscopic stages (zoospores or gametophytes) are directly seeded onto appropriate substrata such as ropes or nets, which are posteriorly deployed at sea, where the sporophytes will develop further under natural conditions until harvest (Stévant et al., 2017).

To date, the major macroalgal species produced worldwide are Japanese kelp *Saccharina japonica*, *Euclima* spp., *Gracilaria* spp., wakame *Undaria pinnatifida*, nori *Porphyra* spp., Elkhorn sea moss *Kappaphycus alvarezii*, *Sargassum fusiforme*, and *Euclima denticulatum* (FAO, 2022). Among these top macroalgal species, *S. japonica*, *U. pinnatifida*, and *S. fusiforme* are brown algae from the order Laminariales (*Saccharina* and *Undaria* species) and Fucales (*Sargassum* species) representing 35.5%, 8%, and 0.8% of the world's algal production in 2020, respectively (FAO, 2022).

These kelp species are extensively farmed in East-North Asia (e.g., China, Japan, and Korea) (Figure 2) for human and animal consumption, as well as for their biochemical content (Adams et al., 2008; Song et al., 2015; Kim et al., 2017). *Saccharina* species are mainly commercially cultivated for alginate, iodine, and mannitol, whereas *Undaria* species are used for their medicinal nutrients, such as omega-3 fatty acids, essential minerals, and fucoxanthin, and as a food crop (Song et al., 2015). *Sargassum* species have traditionally been consumed in Asia because of their high nutritional content and are used in traditional Chinese medicine (Song et al., 2015).

The African continent is the world's second largest producer of algae (Figure 2); however, its production is mainly based on red algae aquaculture, which mainly occurs in Zanzibar (Tanzania), Madagascar, and South Africa (FAO, 2022; Msuya et al., 2022). *Ecklonia maxima* and *Laminaria pallida* are two endemic kelp species that dominate the coastal area of South Africa (Troell et al., 2006), and *Macrocystis pyrifera* is also found in a few small beds in the southwest. The first two brown algae have been collected as beach-casts since the early 1950s to be exported for alginate extraction, and more recently to be used as feed for the abalone



industry (Troell et al., 2006; January et al., 2019); however, there has been no commercial aquaculture of kelps in the region to date, except for a pilot aquafarm that is currently being tested (Msuya et al., 2022). There have been many studies on the commercial potential of some brown algae species in Africa, such as *Sargassum oligocystum* in Kenya for animal and human consumption, and *Cystoseira myrica*, *Padina pavonica*, *Sargassum fluitans*, *S. ilifolium*, *Sargassum* sp., *Turbinaria triquetra*, and *T. turbinata* for their natural products in Djibouti (Msuya et al., 2022). In Mauritius and Rodrigues, *Sargassum aquifolium* and *Padina gymnospora* have also been studied for the development of seaweed-based food items, livestock feed supplements, cosmetics, and bio-fertilizers, and *Sargassum* spp. have been converted into alginates in Ghana and Nigeria, including the invasive *Sargassum muticum* in Morocco (Msuya et al., 2022).

In Western countries (Figure 2), kelp cultivation has become one of the fastest growing industries, and species such as *Saccharina latissima* and *Alaria esculenta* have been cultured in the North Atlantic Ocean in the United States (Kim et al., 2017), Canada (Kim et al., 2017), Iceland (Kim et al., 2017), Norway (Broch et al., 2013; Skjermo et al., 2014), Sweden (Kim et al., 2017), Denmark (Marinho et al., 2015), Germany (Buck and Buchholz, 2004), Scotland (Kim et al., 2017), Ireland (Kim et al., 2017), Spain (Peteiro et al., 2016), and Portugal (Kim et al., 2017). In addition, in the eastern Pacific Ocean, *M. pyrifera* has also grown, especially in Chile (Buschmann et al., 2008; Camus and Buschmann, 2017; Kim et al., 2017) and Alaska (Kim et al., 2017; Stekoll et al., 2021).

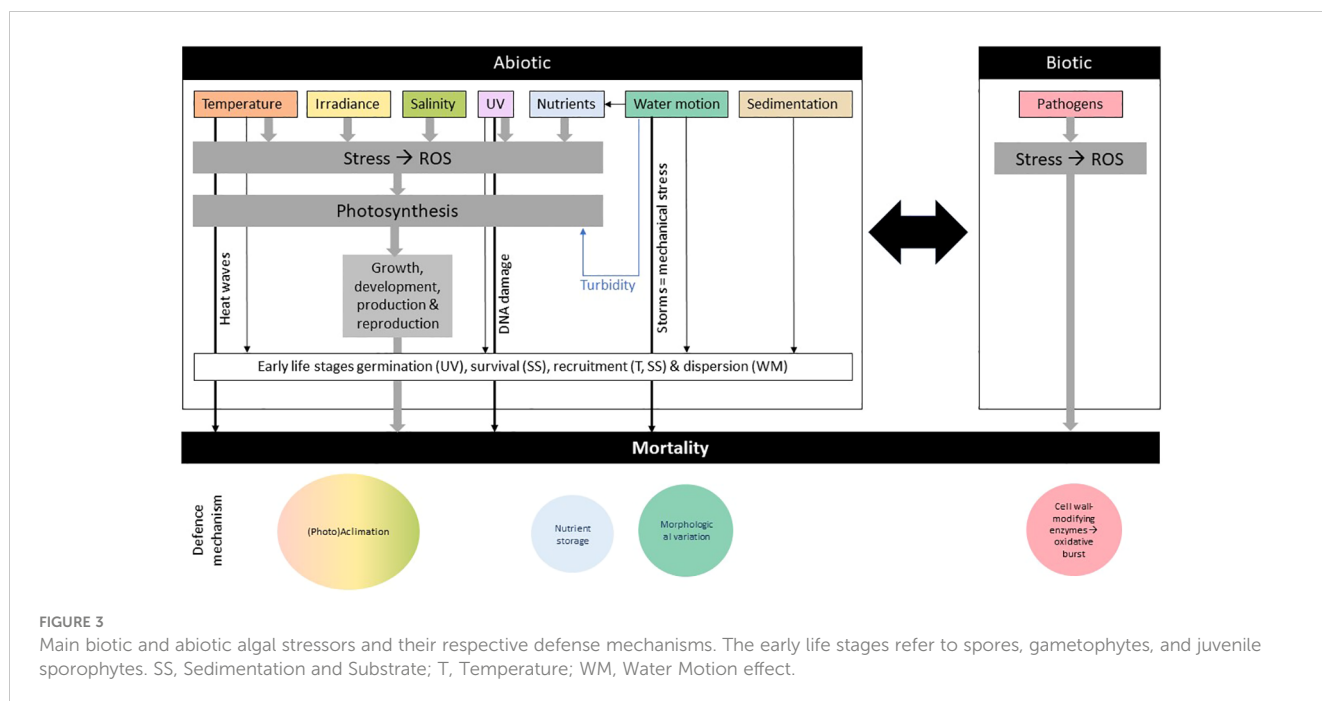
Australian algae aquaculture is still under development (Figure 2); however, high species diversity and high endemism are moving forward from the perspective of introducing Australian macroalgae into food and animal feed markets (Phillips, 2001; Biancacci et al., 2022). For example, *Sargassum rugosum* and *Durvillaea* species are found only in the southern hemisphere, such as the Australian and New Zealand coastlines (Hurd et al., 2004; January et al., 2019). In New Zealand, ecological harvesting impacts and alginate content of different brown algae (e.g., *Ecklonia radiata*, *Papenfussiella lutea*, *Myriogloia intestinalis*, *Cystophora*, *Undaria*, and *Durvillaea* species, *Xiphophora chondrophylla*,

Hormosira banksii, *Lessonia variegata*, *M. pyrifera*, *Carpophyllum maschalocarpum*, *Scytosiphon lomentaria*, *Marginariella boryana*, and *Splachnidium rugosum*) have also been studied recently (Hurd et al., 2004).

3 Brown algae stressors

Brown algae are influenced by a range of abiotic (e.g., changes in light attenuation, sedimentation, nutrients, salinity, and temperature) and biotic (e.g., epiphytes and grazers) factors (Dayton, 1985) (Figure 3). Most of these factors are not easy to measure because they are interconnected, but in general, adverse environmental conditions generate oxidative stress in marine algae; meaning the excessive production and accumulation of reactive oxygen species (ROS) such as hydrogen peroxide (H_2O_2), singlet oxygen (1O_2), superoxide radical (O_2^-) and hydroxyl radical (OH.) (Dring, 2005; Lesser, 2006). Abiotic stressors tend to result in a gradual and continued build-up of ROS because photosynthesis is inhibited and excess energy results in the formation of singlet oxygen, whereas the response to other stressors, like infection or mechanical stress, can be more rapid and intense, but short-lived production of ROS, or “oxidative burst” (attributed to activation of NADPH oxidases in the plasma membrane). If the algal capacity to remove these reduced oxygen intermediates is insufficient (normally achieved through a high cellular content of antioxidant compounds or a high activity of antioxidant enzymes), cellular lipids, proteins, and DNA can be damaged (Dring, 2005; Lesser, 2006).

During the last century, kelp forests have been in decline worldwide most likely due to different processes, such as heatwaves, storms, or herbivore outbreaks (Steneck et al., 2002), which have become increasingly intense over the last two decades as a result of anthropogenic pressure (Steneck et al., 2002; Eggert et al., 2010; Krumhansl et al., 2016; Wernberg et al., 2019). However, climate change has different effects in different areas of the world, and species may be affected differently, depending on their location. For example, in recent years, the Mexican Caribbean coast has received massive atypical influxes of pelagic *Sargassum* spp (Chávez



et al., 2020). These blooms have been attributed to an increase in the nutrient load in the Atlantic Basin via river discharges due to deforestation and other land-use changes upstream, as well as increased sea temperatures, among others (Chávez et al., 2020). While *Sargassum*'s growth does not suffer adverse effects in this case, the negative impacts associated with these influxes include mortality of nearshore benthic flora and fauna, beach erosion, and pollution, which directly affect ecosystem services such as tourism and involve high management costs (Chávez et al., 2020).

Intensive algal aquaculture itself can be another source of disease outbreaks (Gachon et al., 2010), which can not only be harmful for the aquaculture industry but also for the natural marine ecosystem (Valero et al., 2017). For example, *Pyropia* farms in Korea experienced an approximately US \$1.6 million loss (~24.5% of total sales) during 2012–2013, and about US \$1.1 million (~10.7% of total sales), due to disease (Kim et al., 2014). In the Philippines, the disease caused a 15% loss in the production of another red algae, *K. alvarezii*, between 2011 and 2013, corresponding to a loss of over US\$ 310 million (Cook et al.,

2016). Within brown algae, up to 42% of sporophyte length was lost daily during 2017–2018 in cultivated *S. japonica* in China due to disease (Wang et al., 2021).

3.1 Abiotic stressors

There are a few known physiological diseases in brown algae (Table 1) caused by one or more of the environmental factors described below, including environmental pollution (Wang et al., 2014).

3.1.1 Temperature

Globally, sea surface temperatures have increased at a rate of $>0.1^{\circ}\text{C}$ per decade since the mid-20th century (Pörtner et al., 2022). Increased temperatures can directly and indirectly affect brown algae, especially those found at lower latitudes, where temperature plays a strong role in shaping their geographical distribution (Steneck et al., 2002; Wernberg et al., 2019). Species shifts have already been observed (Smale and Moore, 2017), and future

TABLE 1 Physiological diseases in brown algae.

Disease name	Host	Causative agents	Symptoms/effects	References
Blister disease	<i>S. japonica</i>	Incoming of large quantities of fresh water following heavy rainfall.	Blisters on different parts of the fronds and decay spots resulting from the disruption of those blisters.	Wang et al. (2014)
White rot disease	<i>S. japonica</i>	Strong light, high water temperature and insufficient nitrogen.	Pigment loss in kelp fronds (from brown to yellowish, and finally to white), followed by decay of the frond, and drop from the ropes	Wang et al. (2014)
White spot disease	<i>S. japonica</i>	Mud siltation caused by intensive cultivation and low movement of seawater.	Different size white spots scattered in the middle of the blade, near the stipe. Blisters up to 10cm diameter are occasionally found and most affected sporophytes can rot and become black and porous, even if the disease rarely causes the decay of the whole sporophyte.	Wang et al. (2021).

projections have consistently shown significant reductions and northward migrations of canopy-forming species (e.g., *L. digitata* and *L. hyperborea*) in the southern limits (Breeman, 1990; Eggert et al., 2010; Raybaud et al., 2013; Assis et al., 2016). Although kelp forests are considered to be highly resilient (Krumhansl et al., 2016; Lind and Konar, 2017), and some populations and species may tolerate or adapt better to higher thermal ranges (because of the presence of alleles or genotypes beneficial under future climatic conditions within genetically diverse species) (Smale and Moore, 2017; Vranken et al., 2021), their capacity to respond to physical and biological disturbances might be negatively affected by the reduced ecological performance of kelp recruits (Wernberg et al., 2010). Moreover, marine heatwaves can lead to direct mortality (Wernberg et al., 2019) because they expose species and ecosystems to environmental conditions beyond their tolerance and acclimation limits (Pörtner et al., 2022), replacing kelp forests with other warm-tolerant or even invasive species (Arafah-Dalmou et al., 2019). Since the 1980s, marine heat waves have become more frequent, intense, and last longer; therefore, global warming will most likely be accompanied by diversity loss and kelp forest removal (Wernberg et al., 2019; Pörtner et al., 2022).

3.1.2 Light intensity and UV radiation

The amount and quality of irradiance are important factors for many physical and biological processes during all life stages of algae (Dayton, 1985), affecting algal growth through its impact on photosynthesis (Stockenreiter et al., 2013). The growth rate of algae is maximal at saturation intensity and decreases with both rising and falling light intensities (Kaur et al., 2022). Light affects the distribution of marine algae because irradiance in marine ecosystems is highly variable in both space (water depth and latitude) and time (day and season) (Han and Kain (Jones), 1996). Photoadaptation (a change in genotype that occurs over many generations in response to a change in light intensity), however, can help algae survive through these changes in light intensity (Kaur et al., 2022). Changes in pigment types and quantities, growth rate, dark respiration rate, and essential fatty acid supply could be some of the processes that occur during photoadaptation (Fábregas et al., 2004).

It has been shown that the algal establishment stage (gametophytes or young sporophytes) affects the performance of the adult. Light demands can also vary according to the algal life stage; for example, it has been determined that the minimum photon irradiance allowing growth in different kelp species is between $1 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $2 \mu\text{mol m}^{-2} \text{s}^{-1}$, whereas the growth saturated at $20 \mu\text{mol m}^{-2} \text{s}^{-1}$ – $30 \mu\text{mol m}^{-2} \text{s}^{-1}$ of continuous photon irradiance (Han and Kain (Jones), 1996).

Exposure to ultraviolet (UV) light (wavelengths 215 nm–400 nm) has harmful effects on algae, especially UV-B wavebands, affecting their growth and development, and causing oxidative stress (Pessoa, 2012). UV-B radiation directly damages DNA molecules, whereas UV-A radiation induces indirect damage by generating reactive oxygen and hydroxyl radicals (Kaur et al., 2022). It has been shown that early life stages of many macroalgae (meiospore, gametophyte, and juvenile sporophyte) are sensitive

to UV (Roleda et al., 2010). For example, an hour of exposure to UV can reduce the germination of meiospores as well as the photosynthetic efficiency of gametophytes and juvenile sporophytes in both *L. digitata* and *S. latissima* (Dring et al., 1996).

3.1.3 Nutrients

All algae require macro- (e.g., N, P, and C) and micronutrients (e.g., Fe, Zn, Cu, Mn, and Mo), as well as vitamins (vitamin B12, thiamine, and biotin) to support their growth (Harrison and Hurd, 2001). Among these, nitrate and phosphate are extremely important, and the optimum growth ratio for macroalgae is 30N:1P, with a range from 10:1 to 80:1 (Atkinson and Smith, 1983). Since inorganic nutrient concentrations in surface waters differ according to geographic region and vary throughout the year, they can become limiting (Harrison and Hurd, 2001). Therefore, some kelps, such as *Laminaria* and *Macrocystis*, can store nutrients to maintain their growth even during nutrient depletion periods, particularly during summer (Dayton, 1985; Young et al., 2009).

3.1.4 Water motion

According to Gaylord et al. (2012), fluid-dynamic transport and mixing processes affect birth, death, immigration, and emigration rates in kelp forests, and can modulate broader community interactions. Thus, water motion can influence spore transport and settlement, algal population connectivity, and the impact of sedimentation and scour, as well as affect light by moving canopies (Dayton, 1985; Gaylord et al., 2012). Breaking waves and high velocities during storms can also lead to mortality, resulting in the destruction of kelp forests (Seymour et al., 1989), and wave exposure can influence the prevalence of viral infections within Ectocarpales (McKeown et al., 2018). Brown macroalgae can, however, adapt to water motion through morphological variation, such as *E. radiata*, which has been shown to exhibit wide, thin thalli in sheltered habitats and narrow, thick thalli with thick stipes in exposed habitats (Fowler-Walker et al., 2006).

Most importantly, water motion also influences the macroalgae's nutrient uptake. High flow rates enhance uptake rates by accelerating nutrient transport through the diffusion boundary layer adjacent to the plant surface, which is faster in turbulent rather than laminar boundary layers (Gerard, 1982). Stagnant or slow-moving waters not only reduce the nutrient uptake rate but also limit the carbon dioxide supply, leading to reduced growth rates (Gerard and Mann, 1979; Kerrison et al., 2015). Therefore, current velocity is positively correlated to photosynthetic and nutrient uptake rates, until these metabolic processes become saturated (velocities of approximately 0.1 m s^{-1}) (Wheeler, 1980; Hurd, 2000; Kerrison et al., 2015).

3.1.5 Salinity

Salinity influences osmotic pressure within algal cells, and both hyper- and hypo-salinity conditions can affect various physiological processes in marine algae (Kerrison et al., 2015; Kaur et al., 2022). Most brown algae, such as *Laminaria*, can balance salinity stress by increasing mannitol concentrations (Reed et al., 1985); however, under extreme salinity stress, turgor pressure, ion distribution, and

organic solutes in the cell can be disrupted, resulting in cell oxidative damage (Tropin et al., 2003; Kaur et al., 2022).

Most macroalgae thrive at salinities between 33 psu and 35 psu, although some algal species are more tolerant than others (Kerrison et al., 2015). For example, when different brown algae collected in Kongsfjorden (Spitsbergen) were exposed to salinities ranging from 5 psu to 60 psu, *Fucus distichus* was not affected, whereas *A. esculenta*, *S. latissimi*, and *Laminaria solidungula* experienced loss of pigments (bleaching) or even high mortality under hyposaline conditions (Karsten, 2007). In the same study, *L. digitata* and *Saccharina dermatodea* survived all salinities, but showed reduced photosynthetic activities in the lowest and highest salt treatments (Karsten, 2007). It has been shown that salinity acclimation mechanisms involve the upregulation and downregulation of genes related to photosynthesis and energy production, cytoskeleton and membrane transport, and stress responses (Rugiu et al., 2020).

3.1.6 Substrata and sedimentation

Most brown algae grow on rocky substrates, especially mature kelp populations; however, some can also grow on sandy bottoms. All of these substrates can be unstable, promoting sediment deposition, burial/smothering, and water turbidity, negatively affecting kelp plants (Dayton, 1985; Araujo et al., 2012). Sediment deposition can interfere with the attachment of microscopic stages of seaweeds, as demonstrated for various kelps, such as *M. pyrifera*, notably reducing the probability of survival (Devinny and Volsé, 1978). Moreover, burial/smothering may also reduce recruitment rates by significantly lowering the survival and germination rates of successfully attached spores as well as by reducing growth and impairing the regeneration ability of adults (Devinny and Volsé, 1978; Chapman et al., 2002).

Turbidity can affect photosynthesis in brown algae, and some species such as *E. radiata* can present higher photosynthetic pigment levels and photosynthetic efficiency at turbid sites, compared to high-light sites, demonstrating a clear capacity to photoacclimate to a degrading light environment (Blain and Shears, 2019).

3.2 Biotic stressors

Macroalgae are colonized by diverse micro- and macroorganisms, that live and grow on (epiphytes) or inside (endophytes), such as bacteria, fungi, viruses, oomycetes, or filamentous algae of all three macroalgal lineages (Dayton, 1985; Bartsch et al., 2008; Gachon et al., 2010; Vallet et al., 2018). While some of these interactions can be neutral or beneficial for the host, others can be detrimental; these are the ones we are going to focus on here.

Brown algae have different defense mechanisms against pathogenic organisms. The first barrier of defense is composed of innate receptors that perceive microbe-associated molecular patterns (MAMPs) (Weinberger, 2007). MAMPs are non-pathogen specific but can, for example, perceive bacterial lipopolysaccharides and lipoteichoic acids (Weinberger, 2007). In

addition, macroalgae also possess pathogen-induced molecular patterns (PIMPs) that perceive breakdown products of their own cell walls that are released when they are being attacked by pathogens, such as alginate, in the case of kelps (Weinberger, 2007).

The response after recognition of PIMPs or MAMPs is normally an oxidative burst, but an upregulated expression of defense-related proteins has also been observed in brown algae (Weinberger, 2007). Signaling cascades of oxylipins and oxidized polyunsaturated fatty acids are activated after the perception of external molecular signals, activating the transcription of these compounds (Weinberger, 2007), such as polyphenol oxidase in *S. japonica* (Lili et al., 2004) and aromatic compounds in *L. digitata* (Küpper et al., 2002). These secondary metabolites function as primary defenses against herbivores, competitors (allelopathy), pathogens, and fouling organisms (epiphytes) (Jennings and Steinberg, 1997). The most common secondary metabolites in brown algae are phlorotannins, dehydropolymers of phloroglucinol (1,3,5-trihydroxybenzene) with antifouling and anti-herbivory activities, which also serve as UV protectants and antioxidants (Jennings and Steinberg, 1997; Gómez and Huovinen, 2020).

Macroalgae also count with hypersensitive responses such as programmed cell death (apoptosis), in which infected and adjacent cells are sacrificed to control the spread of the disease by the activation of key enzymes such as nucleases and caspases (Weinberger, 2007). Lastly, many macroalgae, including kelp, have haloperoxidases in their cell walls that produce hypohalous acids and halocarbons, such as bromoform, which increases algal protection by interfering with bacterial quorum sensing and biofilm formation (Weinberger, 2007).

3.2.1 Bacteria

Macroalgae are normally colonized by diverse microorganisms such as bacteria. The phyla Proteobacteria, Bacteroidetes, and Firmicutes are among the most abundant bacterial communities found in brown algae (de Mesquita et al., 2019). Bacteria specifically associate with particular macroalgal species and even with certain parts of the algal body, finding a protected microniche from which they can also uptake nutrients released by the alga, such as organic carbon (Goecke et al., 2010). In turn, bacteria can contribute to algal growth and development and even prevent secondary biofouling or pathogen invasion (Goecke et al., 2010; de Mesquita et al., 2019). However, not all algal-bacteria interactions are beneficial, and some bacterial communities can compromise algal tissue and photosynthetic capability, induce diseases, and compromise the algae's health (Goecke et al., 2010; de Mesquita et al., 2019). With such a long tradition of seaweed cultivation, Asian countries have extensive experience with many of these bacterial diseases (Wang et al., 2014; Ward et al., 2019), such as the Green Rot Disease, one of the major infections affecting the Chinese aquaculture industry of *S. japonica*, leading to a complete failure of hatchery operations when it breaks out (Li et al., 2020) (Table 2). However, some of these bacteria are believed to be secondary colonizers (de Mesquita et al., 2019). Therefore, while some bacteria can be found on brown algae as commensals, stressful conditions or macroalgal infections may turn them into saprophytes or

decomposers (de Mesquita et al., 2019). For example, white rot disease (Table 1) is considered to be a physiological disease, but opportunistic alginic acid-decomposing bacteria might also take advantage of the situation (Wang et al., 2014).

Macroalgae influence bacterial metabolism and quorum sensing, and produce antibiotic compounds that inhibit settlement, growth, and biofilm formation by bacteria (Goecke et al., 2010).

3.2.2 Viruses

The first observations of brown algae infected with viruses were *Ectocarpus* plants collected around Europe, which presented abnormal sporangia (Sauvageau, 1896). Electron microscopy allowed us to observe infected organs full of densely packed hexagonal virus-like particles in different brown algae species, confirming viral disease (Müller et al., 1990, Müller et al., 1998). The virus type species is *Ectocarpus siliculosus* virus (ESV-1), which belongs to the genus Phaeovirus, and in turn belongs to the

Phycodnaviridae family within the giant virus phylum Nucleocytoviricota (Koonin et al., 2020). Phycodnaviruses comprise large icosahedral viruses with dsDNA genomes ranging from 160 kb to 560 kb (Wilson and Allen, 2011), infecting numerous taxa of algae (Dunigan et al., 2006). However, only a few seaweed viruses have been fully characterized. Phaeoviruses are the only giant viruses known to infect multicellular algae (Müller and Parodi, 1993; Müller et al., 1996a, Müller et al., 1996b). Seven species were grouped within four different families within Ectocarpales, and eight species belonged to three different families of the order Laminariales, commonly known as kelp (McKeown et al., 2017, McKeown et al., 2018) (Table 3).

Viral particles infecting multicellular brown algae enter their wall-less life cycle stages, motile spores, or gamete forms (Müller and Parodi, 1993; Maier et al., 1998, Maier et al., 2002). Upon entry, the genome of the virus can integrate within the host genome without killing it and persist as a provirus (Meints et al., 2008). After the host

TABLE 2 Bacterial diseases and disease agents in brown algae.

Disease name	Host	Causative agents	Symptoms/effects	References
Green spot disease	<i>U. pinnatifida</i>	Unspecified bacteria.	Small holes with green margins that grow until the frond decays.	Kang (1982a)
Green rot disease/falling-off disease	<i>S. japonica</i>	Insufficient light and opportunistic bacteria from the genera <i>Granulosicoccus</i> , <i>Litorimonas</i> , <i>Tenacibaculum</i> , and <i>Blastopirellula</i> .	Loss of brown pigmentation at the tip of the seedling and gradual rotting of the whole frond.	Tseng (1962); Liu et al. (2002); Wang et al. (2014); Li et al. (2021).
Green decay disease	<i>U. pinnatifida</i>	<i>Vibrio logei</i>	Blade tips burn into unhealthy green color, following by decay, slowly spreading to the basal parts.	Jiang et al. (1997)
Malformation disease (MD)	<i>S. japonica</i>	Sulfate-reducing bacteria (<i>Micrococcus</i>).	Abnormal cell division, characterized by expanded cell size and/or irregular division in early stage of young sporophytes	Wu et al. (1983)
		Light exposure and the maturity level of parent kelp are significantly associated with MD severity, as well as determinate epiphytic bacterial communities like <i>Nesterenkonina</i> , <i>Glycocalis</i> , <i>Halomonas</i> , <i>Pseudoalteromonas</i> , <i>Pseudomonas</i> , <i>Loktanella</i> , and <i>Cobetia</i>		Yan et al. (2023)
Twisted frond disease	<i>S. japonica</i>	Mycoplasma-like organism	Abnormally twisted fronds with swollen stipes and shortened holdfasts.	Wang et al. (1983)
Red-spot disease	<i>S. japonica</i>	Gram negative bacteria like <i>Pseudoalteromonas</i> and <i>Alteromonas</i> species	Swelling of gametophyte cells, followed by filamentous fading and decaying of the thallus.	Ezura et al. (1988).
Hole-rotten disease	<i>S. japonica</i>	<i>Pseudoalteromonas</i> , <i>Vibrio</i> , and <i>Halomonas</i> . Change in seawater microflora linked to environmental factors like salinity and temperature	Decomposition of host cell walls, leading to rotting and holes in the blades.	Wang et al. (2008). Lei et al. (2022).
Shot-hole disease	<i>U. pinnatifida</i>	Various strains of <i>Aeromonas</i> , <i>Flavobacterium</i> , <i>Moraxella</i> , <i>Pseudoalteromonas</i> , and <i>Vibrio</i> .	Brown spots appearing on the thallus blade near the midrib which subsequently fuse together and spread onto the pinnate part of the blade.	Tsukidate (1991).

(Continued)

TABLE 2 Continued

Disease name	Host	Causative agents	Symptoms/effects	References
Spot decay disease	<i>U. pinnatifida</i>	<i>Halomonas venusta</i>	Discolored spots on the thallus, followed by decaying of the kelp tissue.	Ma et al. (1998)
Yellow hole disease	<i>U. pinnatifida</i>	Unspecified bacterium.	Abrasions and holes on the thallus.	Ishikawa and Saga (1989).
Spot-rotting disease	<i>U. pinnatifida</i>	Unspecified bacteria.		Kito et al. (1976)
Decay disease	<i>U. pinnatifida</i>	<i>Pseudoalteromonas arctica</i> and <i>Psychrobacter aquimaris</i> .	Ulceration.	Li et al. (2021).
Bleaching disease	<i>Laminaria religiosa</i>	Seawater salinity drop and air and seawater temperature increase. The change in these abiotic parameters are thought to make kelp more susceptible to bacterial infection, and <i>Alteromonas</i> sp. is suggested as the possible disease causing organism.	Thallus bleaching.	Vairappan et al. (2001)
	<i>S. japonica</i>	<i>Vibrio</i> , <i>Pseudoalteromonas</i> , and <i>Colwellia</i>		Zhang et al. (2022), Ling et al. (2022).
	<i>E. radiata</i> *	Specific bacterial pathogens have not yet been extensively characterized.		Marzinelli et al. (2015); Beattie et al. (2018)
Falling-off disease	<i>S. japonica</i>	Alginic decomposing bacteria (<i>Pseudomonas</i>)	Sporelings falling off from the seeding ropes, especially during summer.	Chen et al. (1979)

*same, or similar disease.

TABLE 3 Features of Phaeovirus subgroups (McKeown, Brown, n.d.; McKeown et al., 2018).

Virus name	Genome size (kb)	Host Order, Family	Replication occurs in	No. of genotypes	References
Subgroup A: Evolutionary strategy is single infections, persistent + K-selected					
<i>Ectocarpus siliculosus virus 1</i> (EsV-1)	336	EC, ec	spo + gam	1	Delarouque et al. (2001)
<i>Ectocarpus fasciculatus virus 1</i> (EfasV-1)	320	EC, ec	spo + gam	1	Kapp et al. (1997)
<i>Pylaiella littoralis virus 1</i> (PlitV-1)	280	EC, ac	spo	1	Maier et al. (1998)
<i>Hincksia hincksiae virus 1</i> (HincV-1)	240	EC, ac	spo	1	Kapp et al. (1997)
<i>Myriotrichia clavaeformis virus 1</i> (MclaV-1)	320	EC, ch	spo	1	Kapp et al. (1997)
<i>Ecklonia maxima virus</i> (EmaxV)	–	LA, le	–	–	McKeown et al. (2018)
<i>Ecklonia radiata virus</i> (EradV)	–	LA, le	–	–	McKeown et al. (2018)
<i>Undaria pinnatifida virus</i> (UpV)	–	LA, al	–	–	McKeown et al. (2018)
Subgroup B: evolutionary strategy is multiple infections, acute + r-selected					
<i>Feldmannia simplex virus 1</i> (FlexV-1)	220	EC, ac	spo	8	Kapp et al. (1997)
<i>Feldmannia irregularis virus 1</i> (FirrV-1)	158–178	EC, ac	spo	3	Delarouque et al. (2003)
<i>Feldmannia species virus 158</i> (FsV-158)	170	EC, ac	spo	2	Schroeder et al. (2009)

(Continued)

TABLE 3 Continued

Virus name	Genome size (kb)	Host Order, Family	Replication occurs in	No. of genotypes	References
Subgroup C: evolutionary strategy is multiple infections, acute + r-selected					
<i>Laminaria digitata virus</i> (LdV)	–	LA, la	gam + veg	–	Mckeown et al. (2018)
<i>Laminaria hyperborea virus</i> (LhypV)	–	LA, la	gam + veg	–	Mckeown et al. (2018)
<i>Saccharina latissima virus</i> (SlatV)	–	LA, la	gam + veg	–	Mckeown et al. (2018)
<i>Macrocystis pyrifera virus</i> (MpyrV)	–	LA, la	–	–	Mckeown et al. (2018)
Subgroup D: evolutionary strategy is multiple infections, acute + r-selected					
<i>Saccharina japonica virus</i> (SjV)	–	LA, la	–	3	Gallot-Lavallée and Blanc (2017)

Hypothetical for Laminariales phaeoviruses due to missing data indicated by –. EC, Ectocarpales; LA, Laminariales; ac, Acinetosporaceae; al, Alariaceae; ch, Chordariaceae; ec, Ectocarpaceae; la, Laminariaceae; le, Lessoniaceae; gam, gametangia; spo, sporangia; veg, vegetative cells.

zoid has settled into a suitable substrate, a copy of the virus is transmitted through mitosis to all the cells of the developing alga (Müller et al., 1990; Maier et al., 2002; Schroeder, 2011). Adult sporophytes or gametophytes carrying the provirus can appear without any visible signals of survival or growth impairment (Müller and Stache, 1992), and with the ability to produce viable spores or gametes that contain the proviral genome (Cock et al., 2010). However, deformed reproductive organs can appear after viral induction, which severely reduces algal reproduction (Grimsley et al., 2012; Schroeder and C., 2015). The persistent life strategy represents a stable evolutionary co-existence of virus and host that is unique within nucleocytoviruses (Schroeder and C., 2015), where r-strategies (phaeoviral subgroups B, C, and D) are more commonly found than K-like ones (phaeoviral subgroup A) (Müller et al., 1998; Schroeder and C., 2015). Despite being widely distributed and highly prevalent (Sengco et al., 1996; Müller et al., 2000; Schroeder, 2011; McKeown et al., 2018; Ruiz Martínez et al., 2023; Schroeder et al., 2023), Phaeoviruses, as well as other potential viruses infecting brown algae, remain to be discovered (Ruiz Martínez et al., 2023).

3.2.3 Fungi and fungus-like organisms

Macroalgae harbor a large diversity of filamentous fungi that colonize their inner tissues without causing any apparent damage or disease (Vallet et al., 2018). Obligate fungal endosymbionts such as *Stigmidium ascophylli* were first described in the brown algae *Ascophyllum nodosum* and *Pelvetia canaliculata* in the 1900s (Cotton, 1907), and they have been suggested to protect their algal host from desiccation, while obtaining nutrients in exchange (Garbary, 2005). However, many fungal endophytes are opportunistic pathogens that can produce toxic metabolites that are detrimental to their hosts (Vallet et al., 2018) (Table 4). Like other parasites, they can affect the host's growth, fecundity, and mortality, regulating host population dynamics and influencing the community structure (Marcogliese, 2004). In this section, parasitic marine fungi and oomycetes are reviewed together since the last ones are normally referred to as “fungus-like” organisms and it is considered that they have similar ecological roles as true zoosporic fungi, even if they do not belong to the kingdom Fungi (Hassett et al., 2019). However, Oomycota are globally distributed zoosporic

heterokonts that phylogenetically branch within the Stramenopila–Alveolata–Rhizaria superkingdom (Burki and Keeling, 2014).

Brown algae defend themselves against fungi through oxidative bursts and chemical defenses (Amsler and Fairhead, 2005), such as *E. siliculosus*, which induces oxidative stress and halogen metabolism in response to *Eurychasma dicksonii* infection (Strittmatter et al., 2016), and *Lobophora variegata*, which produces the cyclic lactone lobophorolide, which presents high antifungal activity (Kubanek et al., 2003).

3.2.4 Algae endophytes and other eukaryotic endoparasites

Many algae from all three macroalgal lineages, especially filamentous brown algae of the order Ectocarpales, are known to live as kelp epi-endophytes, such as *Laminariocolax* or *Laminarionema*, producing galls and severe thallus deformations, leading to biomass loss and decay (Bringloe et al., 2021) (Table 5). Since certain species are found both inside and outside their algal hosts, a clear distinction between epi- and endophytes is not always possible (Peters et al., 2003). For example, some algal endophytes may grow entirely within their host, but form reproductive structures on the host's surface (Peters and Schaffelke, 1996). Both endophytic and epiphytic algae (reviewed in Okida, 1960) are listed in Table 5. Endophyte zoospores are produced in plurilocular sporangia and can attach to and penetrate the healthy host surface without needing an open wound in the host for successful invasion of the host (Eggert et al., 2010). Disruption of host tissues and the fact that some endophytes can also obtain nutrients from them affect host survival and reproductive potential (Correa and McLachlan, 1992; Faugeron et al., 2000).

3.2.5 Epiphytes

Epiphytes attach directly or live in tubes that are attached to the algae's thallus or fronds. Among these fouling organisms are hydroids, bryozoans, bivalve mollusks, tubicolous amphipods, tubicolous polychaetes, and colonial tunicates (Dixon et al., 1981) (Table 6). Algae carrying epiphytes can experience mechanical problems on the thallus and blade deformities due to their extra weight, as well as surface friction and drag, chemical changes at the

TABLE 4 Fungal and fungus-like diseases and disease agents in brown algae.

Causative agents	Taxonomy	Host	Symptoms/effects	References
<i>Anisolpidium rosenvingei</i>	Chromista, Oomycota	<i>P. littoralis</i>	Infection of the host's sporangia and/or vegetative cells, disrupting the reproductive processes of the host.	Küpper and Müller (1999)
<i>A. ectocarpii</i> <i>A. minutum</i> <i>A. sphacellarum</i> <i>A. joklianum</i> <i>A. olpidium</i>		<i>Ectocarpus</i> spp., <i>Hincksia</i> spp. <i>Chorda filum</i> <i>Sphacelaria</i> spp., <i>Chaetopteris plumosa</i> and <i>Cladostephus spongiosus</i> <i>Hincksia granulosa</i> ; <i>P. littoralis</i>		Reviewed in Marano et al. (2012)
<i>Chytridium polysiphoniae</i>	Fungi, Chytridiomycota	<i>P. littoralis</i> 23 species of brown algae (see reference)	Heavy parasite attack of the host's sporangia. Infected host cells became depleted and eventually died.	Petersen (1905); Müller et al. (1999)
<i>Eurychasma dicksonii</i>	Chromista, Oomycota	<i>P. littoralis</i> 45 species of brown algae (see reference)	Heavy parasite attack on the microscopic stages of host species. Infected host cells became depleted and eventually died.	Dangard (1934); Müller et al. (1999)
<i>Haloguignardia oceanica</i>	Fungi, Ascomycota	<i>Sargassum</i> spp.	Galls with ascocarps and spermogonia.	Kohlmeyer (1971), Kohlmeyer (1972)
<i>Lindra thalassiae</i>	Fungi, Ascomycota	<i>Sargassum</i> spp.	"Raisin disease," causing a shedding of infested vesicles	Kohlmeyer (1971)
<i>Olpidiopsis</i>	Chromista, Oomycota	<i>U. pinnatifida</i>	"Chytrid blight disease," infecting sporophyte cells and killing them slowly.	Akiyama (1977a)
<i>Ophiobolus laminariae</i>	Fungi, Ascomycota	<i>S. digitata</i>	Blackened patches of stipes	Sutherland (1915b)
<i>Petersenia lobata</i>	Chromista, Oomycota	<i>Pylaiella</i> spp.	Infected cells appear distinctly brownish.	Li et al. (2010)
<i>Phycomelaina laminariae</i>	Fungi, Ascomycota	<i>S. digitata</i> <i>Alaria esculenta</i> , <i>Saccharina latissima</i> <i>Saccharina longicruris</i> <i>Laminaria digitata</i>	"Stipe blotch disease" causing necrosis.	Sutherland (1915a); Schatz (1983)
<i>Sirolopidium andreei</i>	Chromista, Oomycota	<i>Ectocarpus</i> spp.	Infected cells appear distinctly brownish.	Li et al. (2010)
<i>Sphaceloma cecidii</i>	Fungi, Ascomycota	<i>Sargassum</i> spp.	Galls with ascocarps and spermogonia.	Kohlmeyer (1972)

TABLE 5 Eukaryotic epi-endophytic diseases and disease agents in brown algae.

Causative agents	Taxonomy	Host	Symptoms/effects	References
<i>Bolbocoleon piliferum</i>	Green algae Chlorophyta, Ulvales	<i>Alaria marginata</i> , <i>Chorda filum</i> , <i>Cymathere triplicata</i> and <i>Pleurophycus gardneri</i> .	Dense network of filaments in the superficial and deeper tissues	South (1968), O'Kelly (1983)
<i>Colaconema desmarestiae</i>	Red algae <i>Florideophyceae</i> , Colaconematales	<i>Desmarestia aculeata</i>		Selivanova and Zhigadlova (2013)
<i>Ectocarpus</i> spp.	Brown algae <i>Phaeophyceae</i> , Ectocarpales	<i>L. digitata</i>	Epiphyte. Light and nutrient competition.	Okida (1960), Russell (1983).
<i>Halenchus dumnonicus</i>	Animalia, Nematoda	<i>Ascophyllum</i> spp. & <i>Fucus</i> spp.	Galls	Coles (1958)

(Continued)

TABLE 5 Continued

Causative agents	Taxonomy	Host	Symptoms/effects	References
<i>Herpodiscus durvillaeae</i>	Brown algae <i>Phaeophyceae</i> , Sphacelariales	<i>Durvillaea antarctica</i>	Velvet-like red-brown patches on the surface of the host thallus that lead to blade perforations and, more rarely, complete loss of the blade.	South (1974)
<i>Laminariocolax aecidioides</i>	Brown algae <i>Phaeophyceae</i> , Ectocarpales	<i>U. pinnatifida</i> , <i>S. latissima</i> , <i>Costaria costata</i> , <i>E. maxima</i> , <i>Fucus vesiculosus</i> , <i>Himantothallus grandifolius</i> , <i>L. digitata</i> , <i>L. hyperborea</i> , <i>Lessonia berteriana</i> , <i>Lessonia nigrescens</i> , <i>Macrocystis pyrifera</i> , <i>Saccharina nigripes</i> , <i>Saccharina sessilis</i> , and <i>Saccorhiza polyschides</i>	From dark spots on the blade and stipe to heavy deformations and completely crippled thalli.	Akiyama (1977b), Peters and Schaffelke (1996), Bernard et al. (2019)
<i>Laminariocolax atlanticus</i>	Brown algae <i>Phaeophyceae</i> , Ectocarpales	<i>L. digitata</i> , <i>L. hyperborea</i> , and <i>S. latissima</i> .		Bernard et al. (2019)
<i>Laminarionema elsbetiae</i>	Brown algae <i>Phaeophyceae</i> , Ectocarpales	<i>S. japonica</i>	Dark spots on the lamina.	Kawai and Tokuyama (1995)
		<i>S. latissima</i> <i>L. digitata</i>		Ellertsdóttir and Peters (1997)
<i>Laminariocolax tomentosoides</i>	Brown algae <i>Phaeophyceae</i> , Ectocarpales	<i>Ectocarpus tomentosoides</i>	Continuous felt of filaments on the host surface, that can emerge to the surface to form a localized aecidium-like pustule.	Farlow (1889)
		<i>U. pinnatifida</i> , <i>S. latissima</i> , <i>L. digitata</i> , <i>L. hyperborea</i> , <i>Alaria esculenta</i> , <i>Himantothallus elongata</i> , <i>Saccorhiza polyschides</i> .		Russell (1964); Bernard et al. (2019)
<i>Maullinia braseltonii</i>	Rhizaria, Phycomyxea, Phagomyxida	<i>Durvillaea</i> spp.	Galls	Murúa et al. (2017)
<i>Maullinia ectocarpii</i>	Rhizaria, Phycomyxea, Phagomyxida	Many species belonging to <i>Ectocarpales</i> , <i>Laminariales</i> , <i>Scytothamnales</i> , and <i>Desmarestiales</i> (see reference)	Galls	Maier et al. (2000)
<i>Microcladia coulteri</i>	Red algae Chlorophyta, Ulvaes	<i>Egrecia menziesii</i>	Surface tissue penetration	Gonzalez and Goff (1989)
<i>Microspongium alariae</i>	Green algae <i>Phaeophyceae</i> , Ectocarpales	<i>Alaria esculenta</i> , <i>Fucus</i> spp., and <i>S. latissima</i> .	Dark spots or areas or with deformations, such as warts, galls or twisted thalli.	Peters et al. (2003); Murúa et al. (2018)
<i>Phagomyxa algarum</i>	Rhizaria, Phycomyxea, Phagomyxida	<i>Pylaiella fulvescens</i>	Color changes on the host (from brown to green) and galls. Host cells quickly disintegrate.	Karling (1944)
<i>Pyropia moriensis</i>	Red algae Rhodophyta, Bangiales	<i>Chorda filum</i>	Epiphyte. Light and nutrient competition.	Ohmi (1954), Notoya and Miyashita (1999)
<i>Pyropia nereocystis</i>	Red algae Rhodophyta, Bangiales	<i>Nereocystis luetkeana</i>	Epiphyte. Light and nutrient competition.	Krishnamurthy (1972)
<i>Sporocladopsis novae-zelandiae</i>	Green algae Chlorophyta, Chaetophorales	<i>Lessonia nigrescens</i>	Dark spots or areas or with deformations, such as warts, galls or twisted thalli.	Correa and Martínez Mosqueira (2017)
<i>Ulva</i> spp.	Green algae Chlorophyta, Ulvaes	<i>Sargassum fusiforme</i>	Epiphyte. Light and nutrient competition.	Pang et al. (2007)
<i>Ulvella geniculata</i>	Green algae Chlorophyta, Ulvaes	<i>Egrecia menziesii</i> , <i>Cymathere triplicata</i> , <i>Laminaria sinclairii</i> , <i>Saccharina dentigera</i> , and <i>Dictyonereum californicum</i> .	Diffuse green patches up to 5 mm diameter in the terminal areas of the vegetative lamina of the host,	O'Kelly (1983)

(Continued)

TABLE 5 Continued

Causative agents	Taxonomy	Host	Symptoms/effects	References
			giving a faint, grass-green cast on the host's surface.	
<i>Ulveella viridis</i>	Green algae Chlorophyta, Ulvales	<i>L. digitata</i> and <i>S. latissima</i>		(Nielsen (1979))
<i>Streblonema</i> sp.	Brown algae <i>Phaeophyceae</i> , Ectocarpales	<i>Nereocystis luetkeana</i> , <i>Saccharina sessilis</i> , <i>Alaria tenuifolia</i> , and <i>Laminaria setchellii</i> .	Tumors	Apt (1988)
		<i>L. hyperborea</i>		Lein et al. (1991)
<i>Vertebrata lanosa</i>	Red algae Rhodophyta, Ceramiales	<i>Ascophyllum nodosum</i>	Epiphyte	Lobban and Baxter (1983)

host–epiphyte interface, and competition for light and nutrients (Dixon et al., 1981; Correa and McLachlan, 1992). Moreover, collateral effects can also occur, such as increased susceptibility to secondary pathogens, accidental grazing by carnivores or herbivores eating epiphytes, or increased blade loss during storms (Dixon et al., 1981; Correa and McLachlan, 1992; James et al., 2020).

Consequently, algal growth and production can be impaired, affecting the seaweed industry for farmed brown algal species.

Field observations from different parts of the world, such as the North-East Atlantic or the western Baltic Sea, have documented massive rates of infection prevalence by endophytic brown algae (Eggert et al., 2010).

TABLE 6 Eukaryotic epibionts in brown algae.

Causative agents	Taxonomy	Host	Symptoms/effects	References
<i>Alcyonidium hirsutum</i>	Briozoa	<i>F. serratus</i>	Shading, defoliation, and degeneration of the underlying thallus	Hagerman (1966), Saderne and Wahl (2013)
<i>Campanularia</i> sp.	Cnidaria Hydrozoa	<i>M. pyrifera</i>		Bernstein and Jung (1979)
<i>Didemnum</i> sp.	Chordata Ascidiacea			Dixon et al. (1981)
<i>Electra pilosa</i>	Briozoa	<i>F. serratus</i>	Shading, defoliation, and degeneration of the underlying thallus	Hagerman (1966), Saderne and Wahl (2013)
<i>Hippothoa hylina</i>	Briozoa	<i>M. pyrifera</i>	Blade loss.	Bernstein and Jung (1979), Dixon et al. (1981)
<i>Lepas pacifica</i>	Arthropoda Crustacea	<i>M. pyrifera</i>		Dixon et al. (1981)
<i>Leptopecten latiauratus</i>	Mollusca	Kelp species	Sinking of kelp plants	Dixon et al. (1981)
<i>Lichenopora buskiana</i>	Briozoa	<i>M. pyrifera</i>		Bernstein and Jung (1979)
<i>Membranipora membranacea</i>	Briozoa	<i>M. pyrifera</i>	Light shading Dysbiosis	Dixon et al. (1981); James et al. (2020)
		<i>F. serratus</i>		Hagerman (1966)
<i>Obelia</i> sp.	Cnidaria Hydrozoa	<i>M. pyrifera</i>		Bernstein and Jung (1979)
<i>Sertularia</i> sp.	Cnidaria Hydrozoa	<i>M. pyrifera</i>		Neushul and Haxo (1963)
<i>Spirorbis</i> sp.	Annelia Polychaeta	<i>F. serratus</i> <i>M. pyrifera</i>	Shading, overweight and brittleness	Hagerman (1966); Dixon et al. (1981)
<i>Tubularia crocea</i>	Cnidaria Hydrozoa	<i>M. pyrifera</i>		Dixon et al. (1981)
<i>Turritellinella tricarinata</i>	Mollusca Gastropoda	<i>Cladostephus spongiosum</i>		Quigley and Fenwick (2017)

Macroalgae can combine chemical responses synergistically with physical responses, such as epithelial sloughing, and possibly gelatinous and microtopographically designed surfaces, to defend themselves from epiphytes (da Gama et al., 2014). Epithelial sloughing or periodic shedding of surface tissue has been reported in some brown algae, such as *A. nodosum*, *Halidrys siliquosa*, *E. menziesii*, *Myagropsis myagroides*, and *Sargassum* spp (da Gama et al., 2014).

3.2.6 Grazers

A wide variety of herbivores, including sea urchins, gastropods, crustaceans, and fishes, consume live kelp sporophytes, gametophytes, and their spores (Dayton, 1985; Duffy and Hay, 1990) (Table 7). Therefore, grazing can alter recruitment, demography, and seaweed abundance (Leonard, 1994). Grazers can remove large amounts of seaweed biomass, especially sea urchins, provoking trophic cascades that can affect the entire marine ecosystem (Pinnegar et al., 2000; Iken, 2012). For

example, kelp forests and their associated invertebrates and fishes can disappear into an urchin-barren state, where few seaweeds, except for encrusting corallines, prevail (Steneck et al., 2002). Even if smaller invertebrates do not exert such pressure on macroalgae, they can lead to increased mortality by tunneling into the holdfast, causing the sporophyte to become dislodged (Lobban, 1978).

Algal defense strategies against herbivores have been divided into non-coexistence and coexistence strategies, with the latter encompassing structural and chemical defenses (Lubchenco and Gaines, 1981; Duffy and Hay, 1990; Iken, 2012) (Figure 4).

In non-coexistence strategies, the encounter of seaweeds with herbivores is minimized, and this is accomplished by escaping in time, space, and size and by associational defense (Iken, 2012). Escaping in time and space is a self-explanatory strategy that occurs when seaweeds escape grazing by completing important life history phases (e.g., initial growth or reproduction) in places or moments where herbivores are not present or active (Iken, 2012). Escape in size occurs when seaweeds outgrow the sporeling stage, becoming

TABLE 7 Brown algae grazers.

Causative agents	Taxonomy	Host	Symptoms/effects	References
<i>Amenophia orientalis</i> , <i>Parathalestris infesta</i> , <i>Scutellidum</i> sp., & <i>Thalestris</i> sp.	Crustacea Copepoda	<i>U. pinnatifida</i>	"Pinhole disease," characterized by the appearance of small holes in the thalli.	Tsukidate (1991).
<i>Ampithoe marcuizii</i>	Crustacea Malacostraca Amphipoda	<i>S. filipendula</i>	Grazing damage	Duffy (1990)
<i>Amphitholina cuniculus</i>	Crustacea Malacostraca Amphipoda	<i>A. esculenta</i>	Boring of stipes and production of hollow.	Myers (1974)
<i>Ceinina japonica</i>	Crustacea Malacostraca Amphipoda	<i>U. pinnatifida</i>	"Tunnel disease," causing the longitudinal separation of the algae's frond through the midrib after tunneling it.	Kang (1982b)
<i>Cymodoce japonica</i>	Crustacea Malacostraca Isopoda	<i>U. pinnatifida</i>	Juvenile sporophyte grazing	Endo et al. (2021)
<i>Jassa falcata</i>	Mollusca Chitonida		Grazing damage	Dixon et al. (1981)
<i>Katharina tunicata</i>	Crustacea Malacostraca Amphipoda	<i>Hedophyllum sessile</i>	Grazing damage	Markel and DeWreede (1998)
<i>Limnoria</i> sp.	Crustacea Malacostraca Isopoda	<i>M. pyrifera</i>	Grazing damage and plant mortality.	M. and Boraso (1979)
<i>Medialuna californiensis</i> , <i>Girella nigricans</i> & <i>Oxyjulis californica</i>	Chordata Actinopterygii Perciformes	<i>M. pyrifera</i>	Grazing damage	North (1971); Bernstein and Jung (1979)
<i>Megathura crenulata</i>	Mollusca Gastropoda	<i>Cystoseira osmundacea</i>	Grazing damage	Mazariegos-Villarreal et al. (2013)
<i>Patiria miniata</i>	Echinodermata Asteroidea	<i>M. pyrifera</i>	Decreased recruitment due to gametophyte and microscopic sporophyte consumption.	Leonard (1994)
<i>Platynereis dumerili</i>	Annelida Polychaeta	<i>Dictyota dichotoma</i>	Grazing damage	Duffy (1990)

(Continued)

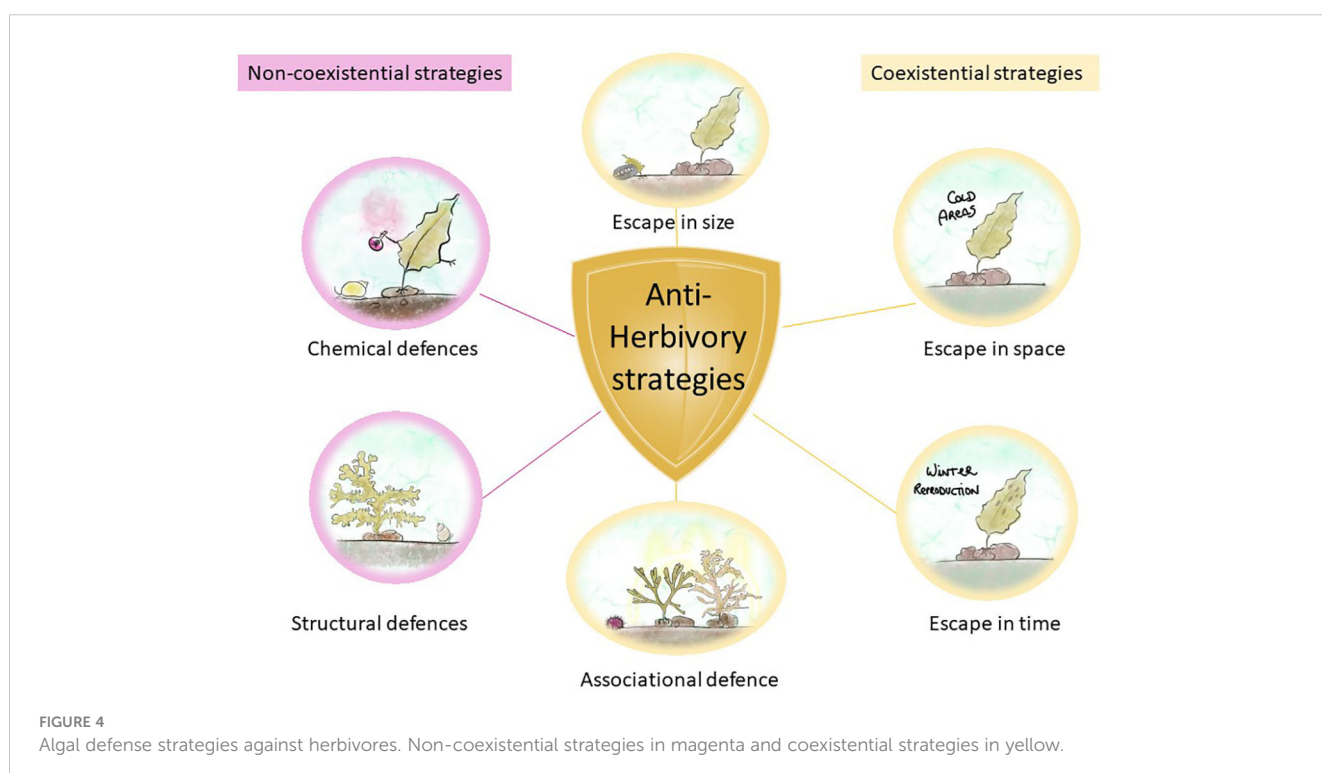
TABLE 7 Continued

Causative agents	Taxonomy	Host	Symptoms/effects	References
<i>Pugettia producta</i>	Crustacea Malacostraca Decapoda	<i>Egredia menziesii</i> <i>M. pyrifera</i> <i>N. luetkeana</i> and <i>Sargassum muticum</i>	Grazing damage	Ricketts and Calvin (1968); Andrews (1945); Morris et al. (1980)
<i>Strongylocentrotus droebachiensis</i>	Echinodermata Echinoidea	<i>Laminaria longicuris</i> & <i>L. digitata</i>	Destructive grazing	Breen and Mann (1976)
<i>Strongylocentrotus franciscanus</i> & <i>Lytechinus anamesus</i>	Echinodermata Echinoidea	<i>M. pyrifera</i> and <i>Pterygophora californica</i>	Destructive grazing	Dean et al. (1984)
<i>Sunamphitoe</i>	Crustacea Malacostraca Amphipoda	<i>Laminaria setchellii</i>	Establishment of two adult amphipods in the stipe where they produce multiple cohorts of offspring, which hollow and kill the plant.	Conland (1992); Chess (1993)

less susceptible to grazing, such as the chiton *Katharina tunicate*, which only grazes on sporelings but not on adult kelp *Hedophyllum sessile* (Markel and DeWreede, 1998). Associational defense occurs when macroalgae associate with other organisms that provide them with chemical or structural protection from grazers, such as the decreased consumption of *Sargassum furcatum* by sea urchin *Lytechinus variegatus* when protected by the chemicals of *Dictyota* sp (Pereira et al., 2010). These strategies are the result of chance or co-evolutionary processes (Iken, 2012).

Coexistence strategies lower the herbivore's attraction to a seaweed because of the specific structural or chemical traits of the alga (Iken, 2012). There are two types of defenses: structural and chemical. The first are also known as mechanical or morphological

defenses, and they involve the inclusion of calcium carbonate into algal cells (Paul and Hay, 1986). For example, *F. distichus* produces adventitious branches after mechanical damage to the plant apices, preventing further grazing by the snails *Littorina sitkana* and *L. scutulata* (even if a chemical defense may also be present at the same time) (Van Alstyne, 1989). Chemical defenses are secondary metabolites that function as herbivore deterrents and mostly reduce the palatability or nutritional quality of the seaweed or can also reduce the fitness and survivorship of the herbivore through toxic effects (Iken, 2012), as explained in the previous section. For example, the snail *Lacuna vincta* avoids grazing on the intercalary meristem of *Laminaria longicuris* due to its high phenolic content (Amsler and Fairhead, 2005).



4 Disease breeding grounds

Marine ecosystems are currently threatened by global climate change. These climate-driven changes, especially ocean warming and acidification, alter species distributions and biodiversity and are expected to have profound ecological, social, and economic implications (Wernberg et al., 2016) (Figure 5). An alarming decrease in the density and biomass of canopy-forming kelps has been reported worldwide (Dayton et al., 1999); for instance, *S. latissima* beds were strongly reduced and partly replaced by filamentous turf algae along the southwest and Skagerak coasts of Norway, and between 2002 and 2018, approximately 80% of the populations disappeared (Moy and Christie, 2012). Temperature sets distributional limits for kelps and other macroalgae, and latitudinal range shifts in marine macroalgae have already been observed (Lima et al., 2007). Kelp decline and community structure changes have been linked to climate change and marine heatwaves (MHWs) in many studies overall (Wernberg et al., 2010; Raybaud et al., 2013; Arafteh-Dalmau et al., 2019). Filbee-Dexter et al. (2020) experimentally demonstrated a relationship between MHWs and high kelp loss in Southern Norway, where mortality was strongly linked to the physiological changes that kelp experiences when temperature goes beyond their lethal thresholds, that is, tissue damage, increased dislodgment, and reduced photosynthetic and reproductive performance (Filbee-Dexter et al., 2020).

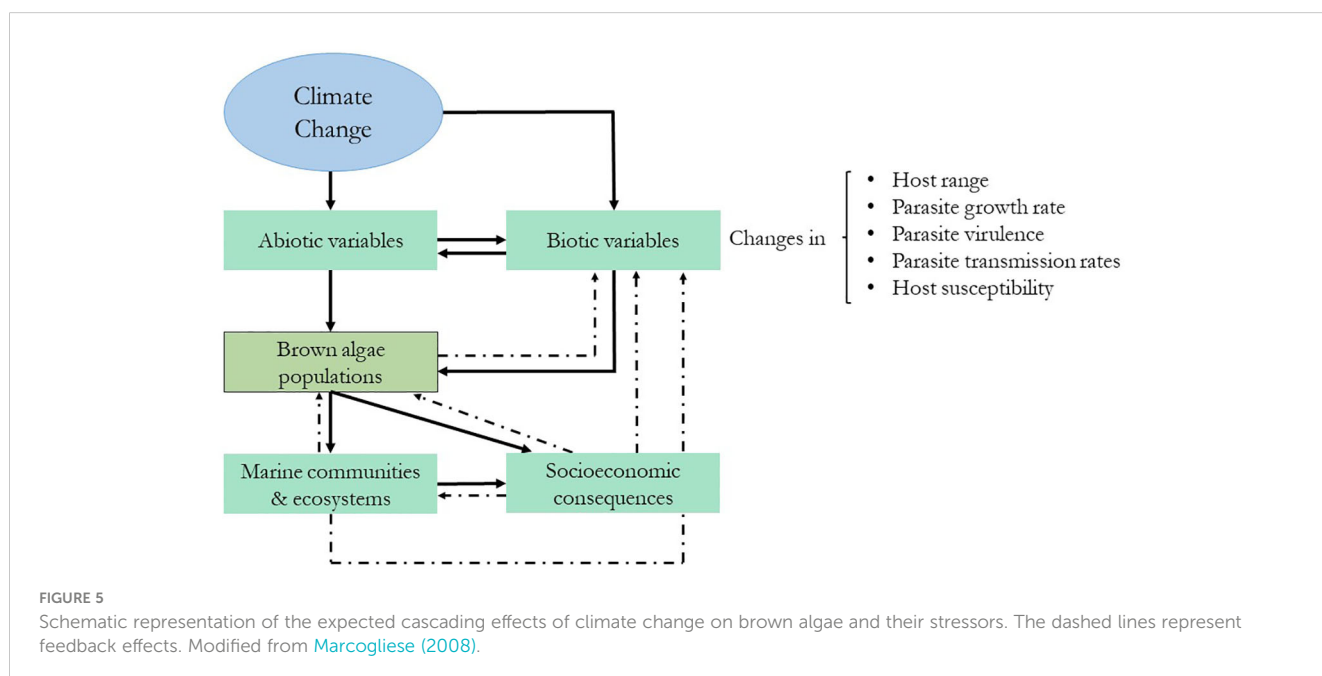
Abiotic changes can also affect pre-established biotic interactions between algae and their competitors, colonizers, grazers, and pathogens (Eggert et al., 2010) (Figure 5). Based on terrestrial ecosystems, Harvell et al. (2002) proposed that host-pathogen interactions will become more frequent and intense in the future and that they will be affected by (1) more rapid pathogen development owing to increased growth rates of the pathogen at higher temperatures, (2) increased winter survival of the pathogen, and (3) increased host susceptibility at higher temperatures. The

effects of climate change on marine algae-pathogen interactions are poorly understood; however, herbivore/epiphyte studies predict cascading effects on primary producers (Harley et al., 2012) (Figure 5). For example, warmer sea surface temperatures are associated with increases in some herbivore populations and a concomitant decline in certain algal species (Hart and Scheibling, 1988; Ling, 2008). However, it is difficult to make general predictions, since these changes will not be homogeneous or affect all organisms equally. Indirect effects of climate change can also alter these expectations; for example, acidification can negatively affect calcified herbivores, and changes in nutrient availability can also alter algal palatability (Harley et al., 2012). Epiphytic bryozoans in eastern Canada have also increased in number due to sea warming events, leading to drastic reductions in the percentage cover of *Saccharina longicruris* beds (Saunders et al., 2010). Field observations from different parts of the world have documented massive rates of infection prevalence by endophytes (Eggert et al., 2010), viruses (Ruiz Martínez et al., 2023), and bacteria (Harvell et al., 1999).

With the worldwide intensification of seaweed aquaculture and climate change-driven changes, an increase in the prevalence of diseases and pests is expected (Ward et al., 2019). Disease outbreaks can also occur if infected algae are introduced accidentally, which is a potential treatment for natural algal populations, not to mention the economic impact of diseases on the seaweed industry (Sugumaran et al., 2022) (Figure 5).

5 A sustainable future for aquaculture

Without a coordinated global effort to support seaweed research, the investigation and knowledge transfer of technical capacities, protection of wild seaweed populations, and promotion of environmental, gender-responsive, and socially inclusive



approaches to upscaling the seaweed industry are not possible. To address this issue, the GlobalSeaweedSTAR team published an international policy brief with a list of eight recommendations for improving the resilience and sustainability of the industry (Cottier-Cook et al., 2021). The key to sustainable aquaculture practices relies on biosecurity and mitigation measures (based on the identification of diseases and pests, and reviewed in [Behera et al., 2022] and [Sugumaran et al., 2022]) that should be further (1) developed into clear international policies and regulations. However, without proper knowledge and training regarding pathogen diversity, host range, and interactions with their hosts, it will be more difficult to predict the potential ecological consequences of climate change on algae–pathogen interactions in the future. This requires the (2) Development of gender-responsive regional and national capacity-building initiatives. It is extremely important to (3) develop regional and national seed stocks and biosecuring nurseries, and (4) maintain the genetic diversity of wild stocks by preventing the introduction of non-indigenous species and encouraging the development of indigenous strains/varieties for commercial cultivation. (5) Advanced assessment tools should be used to perform risk-based analyses of management options at multiple scales and to enable economic diversification. (6) The integration of seaweed with other fed-aquaculture species and other maritime activities should be incentivized. At the same time, (7) channeling support for long-term investment in promoting the beneficial aspects of the industry may help farmers implement the previously cited practices that will help build resilience to the impacts of climate change. The final recommendation is to (8) establish a network of Regional Seaweed Research Networks, to obtain the necessary scientific knowledge in which all previous studies will be based. As researchers, we have this responsibility, and this review intends to consolidate all previous efforts made on the topic while keeping our focus on future progress.

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