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Ward, Georgia; Faisan, Joseph; Cottier-Cook, Elizabeth; Gachon, Claire; Hurtado, Anicia; Lim, Phaik-Eem; Matoju, Ivy; Msuya, Flower; Bass, David; Brodie, Juliet

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A review of reported seaweed diseases and pests in aquaculture in Asia

Georgia M. Ward[1] | Joseph P. Faisan Jr[2] | Elizabeth J. Cottier-Cook[3] | Claire Gachon[3] | Anicia Q. Hurtado[2,4] | Phaik E. Lim[5] | Ivy Matoju[6] | Flower E. Msuya[6] | David Bass[7] | Juliet Brodie[1]

[1]Department of Life Sciences, Natural History Museum, London, UK

[2]Aquaculture Department, Southeast Asian Fisheries Development Center, Iloilo, Philippines

[3]Scottish Association for Marine Science, Scottish Marine Institute, Oban, UK

[4]University of the Philippines Visayas, College of Fisheries and Ocean Sciences - Institute of Aquaculture, Iloilo, Philippines

[5]Marine Biotechnology Unit, Institute of Ocean and Earth Sciences (IOES), University of Malaya, Kuala Lumpur, Malaysia

[6]Botany Department, University of Dar es Salaam, Dar es Salaam, Tanzania

[7]Cefas, Dorset, UK

Correspondence
Juliet Brodie, Department of Life Sciences, Natural History Museum, Cromwell Road, London, SW7 5BD, UK.
Email: j.brodie@nhm.ac.uk

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Abstract

Seaweeds have been used as a food for centuries in Asia and are increasingly exploited as a source for dietary supplements, animal feed, chemicals, and biofuels. In recent years, there has been an increase in the prevalence of diseases and pests in these aquaculture crops, with a subsequent reduction in their quantity and commercial value. In this article, we review diseases that have been reported in the scientific literature for species of red and brown seaweeds. We have focused on the major seaweed crops grown in Asia, where much of this production is centered. We also provide information on disease management and biosecurity and some observations on future directions.

KEYWORDS

cultivated seaweeds, hydrocolloids, ice-ice, *Olpidiopsis*

1 | INTRODUCTION

The commercial production of seaweeds has expanded greatly over the past century, with various species exploited for food and dietary supplements, animal feed, chemicals, and biofuels (Tiwari & Troy, 2015). Much of this production is centered in Asia, where *Pyropia*, *Undaria*, and *Saccharina* spp. are cultivated for human consumption (J. K. Kim, Yarish, Hwang, Park, & Kim, 2017). Other species are grown for chemicals, including agar (*Gracilaria* spp.; Francavillla, Franchi, Monteleone, & Caroppo, 2013) and carrageenan (*Kappaphycus* and *Eucheuma* spp.) (Lim, Yang, Maggs, & Brodie, 2017). The total production of the main cultivated species in Asia, both in metric tons and value (US$), for the year 2016 as given by the United Nations Food and Agriculture Organization is summarized in Table 1 (Food and Agriculture Organization, 2018).

Seaweeds have been used as food for centuries in Asia, with records dating back as far as the third century in China (Yang, Lu, & Brodie, 2017), fourth century in Japan, and the sixth century in Korea (McHugh, 2003). Asian countries remain the largest consumers; however, products are increasingly exported to Europe, North America, and Africa as sushi consumption grows in popularity (Chen & Xu, 2005). The development of commercial cultivation of seaweeds for food began in Japan in the 1920s as demand began to outstrip natural yields (Chen & Xu, 2005). Today, China is the largest producer of seaweeds for human consumption (Food and Agriculture Organization, 2018), although large-scale production also occurs in both Japan and the Republic of Korea (G. H. Kim, Moon, Kim, Shim, & Klochkova, 2014). The exploitation of seaweeds for hydrocolloids also dates back centuries. It was commercialized in Japan in the 1930s, before rapidly expanding into surrounding countries following the Second World War to meet rising demand (McHugh, 2003). The eucheumatoid species *Kappaphycus* spp. and *Eucheuma denticulatum* are most commonly used in hydrocolloid production because of their high kappa- and iota-carrageenan content, with Indonesia, Malaysia, and the Philippines being major producers of these species in Southeast Asia (Food and Agriculture Organization, 2018).

In recent years, there has been a decline in yields of crops grown for both human consumption and hydrocolloid production. This decline has been attributed to an increase in the prevalence of diseases and pests because of the intensification of aquaculture activity (G. H. Kim et al., 2014; Loureiro, Gachon, & Rebours, 2015; Tsiresy et al., 2016). As the seaweed aquaculture sector expands, the importance of furthering our understanding of diseases and pests becomes more apparent. Intensive culture of macroalgae favors more frequent and damaging disease outbreaks (Gachon, Sime-Ngando, Strittmatter, Chambouvet, & Kim, 2010) as is the case in other aquaculture sectors, including finfish and shellfish (Petterson, Osmundsen, Aunsmo, Mardones, & Rich, 2015; Shinn et al., 2015). Table 2 lists published reports of disease incidence in major cultivated species in Asia and includes bacteria, protists, viruses, and other algae. Farmed seaweeds are also vulnerable to grazing pest species, including copepods (Tsukidate, 1991), amphipods (Kang, 1982), and fish (Mantri et al., 2017). Despite the economic importance of these crops on local, national, and international scales, only a few disease agents are well characterized, and little is known about effective treatment or mitigation strategies (G. H. Kim et al., 2014).

TABLE 1 Aquaculture production values for the main cultured species in Asia in the year 2016 as listed by the Food and Agriculture Organization of the United Nations

Species	Main producer(s)	Uses	Production in 2016 (metric ton)	Value (US$)
Pyropia spp.	Japan, Korea, China	Food (nori)	1,352,520	1,114,486,140
Undaria spp.	Japan, Korea, China	Food (wakame)	2,069,682	1,428,285,720
Saccharina spp.	Japan, China, Korea	Food (kombu)	8,219,210	4,084,176,750
Gracilaria spp.	China, Vietnam, Indonesia	Agar production	2,942,534	1,745,211,960
Eucheumatoids (*Kappaphycus* and *Eucheuma* spp.)	The Philippines, Malaysia, Indonesia	Hydrocolloid production	10,493,540	1,219,519,890

TABLE 2 Diseases and disease agents of red and brown seaweeds in aquaculture in Asia

Host	Disease	Disease agents	Taxonomy	Distribution	References
Gracilariopsis heteroclada	Rotten thallus syndrome	*Bacillus* spp.	Gram-negative bacteria	Philippines (in tank-held stocks)	Lavilla-Pitogo (1992), Martinez and Padilla (2016)
Kappaphycus alvarezii	Epiphytic filamentous algae	*Melanothamnus* (as *Neosiphonia) apiculata*	Rhodophyta (Eukaryota)	Philippines Indonesia Malaysia	Vairappan et al. (2008)
K. alvarezii* and *K. striatus	Ice-ice disease	*Cytophaga-Flavobacterium* complex, *Vibrio* sp.	Gram-negative bacteria	Philippines	Largo, Fukami, and Nishijima (1995)
		Alteromonas, Pseudoalteromonas, Aurantomonas	Gram-negative bacteria	Indonesia	Syafitri, Prayitno, Ma'ruf, and Radjasa (2017)
		Aspergillus ochraceus, A. terreus, Phoma sp.	Ascomycota (Eukaryota)	Philippines	Solis, Draeger, and de la Cruz(2010)
		Undetermined	Undetermined	India	Arasamuthu and Patterson Edwards (2018)
		Undetermined	Undetermined	China	Pang, Liu, Liu and Li (2015)
		Neosiphonia sp., *Polysiphonia* sp., *Gracilaria* sp., *Hypnea* sp., *Acanthophora* sp.	Rhodophyta (Eukaryota)	China	Pang et al. (2015)
	Epiphytic filamentous algae	*Cladophora* sp.	Chlorophyta (Eukaryota)	China	Pang et al. (2015)
Pyropia yezoensis	Red rot disease	*Pythium porphyrae*	Oomyceta (Eukaryota)	China	Ding and Ma (2005
				Korea	G.H. Kim et al. (2014), Lee et al. (2017)
				Japan	Kazama (1979)
		Pythium chondricola	Oomyceta (Eukaryota)	Korea	Lee et al. (2017)
				China	Qiu, Mao, Tang, Tang and Mo (2019)
		Alternaria sp.	Ascomycota (Eukaryota)	Korea	Mo, Li, Kong, Tang, and Mao (2016)
	Olpidiopsis disease ("Chytrid blight")	*Olpidiopsis* sp.	Oomyceta (Eukaryota)	China	Ding and Ma (2005)
				Korea	Kwak, Klochkova, Jeong, and Kim (2017)
		Olpidiopsis pyropiae	Oomyceta (Eukaryota)	Korea	Klochkova, Shin, Moon, Motomura, and Kim (2016)
	White spot disease	*Phoma* sp.	Coelomycete (Eukaryota)	China	Guan et al. (2013)
				Korea	G.H. Kim et al. (2014)

(Continues)

TABLE 2 (Continued)

Host	Disease	Disease agents	Taxonomy	Distribution	References
	Diatom felt	*Fragellaria* sp., *Licmophora flabellata*, *Melosira* sp., *Navicula* sp.	Bacillariophyta (Eukaryota)	Korea	G.H. Kim et al. (2014)
	Cyanobacteria felt	Filamentous and coccoid blue-green algae	Cyanobacteria	Korea	G.H. Kim et al. (2014)
	Anaaki disease	*Pseudomonas* sp. *Vibrio* sp.	Gram-negative bacteria	Japan	Fujita (1990); G.H. Kim et al. (2014)
				Korea	G.H. Kim et al. (2014)
		Flavobacterium sp. LAD-1	Gram-negative bacteria	Korea	Suniari et al. (1995)
	Green-spot disease	PyroV1	Virus	Korea	G. H. Kim, Klochkova, Lee, and Im (2016)
	White blight disease	Unknown	Unknown	Korea	Lee et al. (2012); Cultured Aquatic Species Information Programme, FAO
	Unnamed disease	"*Pseudomonas*-like" bacteria	Gram-negative bacteria	Japan	Yamanoi & Takami (2008)
	Diatom blooms	*Eucampia zodiacus*	Bacillariophyta (Eukaryota)	Japan	Nishikawa, Hori, Tanida and Imai (2007)
		Coscinodiscus granii	Bacillariophyta (Eukaryota)	Japan	Nishikawa and Yamaguchi (2007)
		Asteroplanus karianus	Bacillariophyta (Eukaryota)	Japan	Shikata, Matsubara, Yoshida, Sakamoto and Yamaguchi (2015)
Pyropia tenera	Red rot disease	Undetermined	Undetermined	Japan	Arasaki (1947)
	Green-spot disease	PyroV1	Virus	Korea	G. H. Kim et al. (2016)
Pyropia dentata	Green-spot disease	PyroV1	Virus	Korea	G. H. Kim et al. (2016)
Saccharina japonica	Red-spot disease	*Alteromonas* sp.	Gram-negative bacteria	Japan	Yumoto, Ezura, and Kimura (1989); Sawabe et al. (2000)
		Pseudoalteromonas elyakovii	Gram-negative bacteria	Japan	Sawabe et al. (2000)
		Pseudoalteromonas bacteriolytica	Gram-negative bacteria	Japan	Sawabe et al. (1998)
	Hole-rotten disease	*Pseudoalteromonas, Vibrio, Halomonas*	Gram-negative bacteria	China	Wang et al. (2008)
		Macrococcus sp.		China	Wang et al. (2014)

(Continues)

TABLE 2 (Continued)

Host	Disease	Disease agents	Taxonomy	Distribution	References
	Malformation disease		Gram-positive bacteria		
	Twisted frond disease	*Mycoplasma*-like organisms	Bacteria	China	Wang et al. (2014)
	Green rot disease	*Pseudomonas* spp. and insufficient light	Gram-negative bacteria; environmental	China	Wang et al. (2014)
	White rot disease	Excessive light; insufficient nutrient availability; high water temperature	Environmental	China	Wang et al. (2014)
	Blister disease	Dilution of seawater with freshwater runoff following heavy rainfall	Environmental	China	Wang et al. (2014)
Undaria pinnatifida	Shot hole disease	*Aeromonas, Flavobacterium, Moraxella, Pseudoalteromonas, Vibrio*	Gram-negative bacteria	Japan	Tsukidate (1991)
	Spot-rotting disease ("Anaaki-sho")	Unknown	Bacteria	Japan	Kito, Akiyama, and Sasaki (1976)
	Green-spot rot	Unknown	Bacteria	Japan Korea	Kang (1982)
	Yellow hole disease	Unknown	Bacteria	Japan	Ishikawa and Saga (1989)
	Spot decay	*Halomonas venusta*	Bacteria	China	Ma, Zhang, Changfa et al. (1997); Ma, Zhang, Fan et al. (1997); Ma, Yang, Wan, Ge and Zhang (1998)
	Green decay disease	*Vibrio logei*	Gram-negative bacteria	China	Jiang, Ma, Zhang, and Xu (1997)
	Pin-hole disease	*Amenophia orientalis, Parathalestris infestus, Scutellidum* sp., *Thalestris* sp.	Copepoda (Eukaryota)	Japan Korea	Tsukidate (1991)
	Unnamed disease	*Ceinina japonica*	Amphipoda (Eukaryota)	Korea	Kang (1982)
	Brown endophytic disease	*Laminariocolax aecidoides*	Ochrophyta (Eukaryota)	Japan	Akiyama (1977)
		Laminarionema elsbetiae	Ochrophyta (Eukaryota)	Japan	Kawai and Tokuyama (1995)

Abbreviation: FAO, Food and Agriculture Organization of the United Nations.

2 | THE ECONOMIC IMPACT OF SEAWEED DISEASES AND PESTS

The occurrence of diseases and pests results in losses of 25–30% of harvested volumes of *Saccharina japonica* at a regional scale in China (Wang et al., 2014). Some of these diseases are known to be triggered by abiotic factors (Table 2), including either strong or insufficient light (white rot disease and green rot disease, respectively; Wang et al., 2014), while others are thought to result from the action of pathogenic microbes, often in combination with unfavorable environmental conditions.

Disease incidence is estimated to reduce the output of Korean *Pyropia* farms by up to 20% in some regions (G. H. Kim et al., 2014), with much of this loss attributed to the oomycete pathogen *Olpidiopsis pyropiae*. (Klochkova et al., 2016; Klochkova, Shim, Hwang, & Kim, 2012) and a condition known as green-spot disease, now known to be caused by the virus PyroV1 (G. H. Kim et al., 2016). Although disease-affected crops may still be harvestable and marketable, the lower quality and yield has a significant negative economic impact on these crops (G. H. Kim et al., 2014).

Losses of eucheumatoid stocks because of diseases and pests in the Philippines have resulted in a reduction of 15% of production yields, which is equivalent to almost $100 million on an annual basis (Cottier-Cook et al., 2016). In the Philippines, over 200,000 families work in seaweed aquaculture (Pedrosa, 2017); however, problems brought about by epiphyte infestations and ice–ice disease have resulted in diminishing culture stocks and reduced carrageenan quality, which in turn leads to low market value, loss of income, and loss of job opportunities, particularly for marginal seaweed farmers.

3 | SIGNIFICANT DISEASES AND PESTS OF CULTIVATED SEAWEEDS

Because of their detrimental impact on valuable *Pyropia* stocks, the oomycete pathogens *Pythium porphyrae* and *Olpidiopsis porphyrae* are perhaps the best-studied seaweed diseases. Red rot disease, attributed to *P. porphyrae* in 1977 (Takahashi, Ichitani, & Sasaki, 1977), has caused significant reductions in the yield and quality of *Pyropia* crops since it was first recorded in Japan in the 1940s (Arasaki, 1947). *Olpidiopsis* disease, initially thought to be caused by a chytrid pathogen (and therefore referred to as "chytrid blight"), was also first recorded in Japan (Arasaki, 1960) but has since been recorded in Korea and China (G. H. Kim et al., 2014). Interactions between oomycete pathogens and their *Pyropia* hosts have been subject to much study (Klochkova et al., 2012; Uppalapti & Fujita, 2002), although to date, these studies have offered little insight into biosecurity strategies that may limit the impact and spread of these diseases in culture environments. Recently, symptoms recognized as red rot disease have been attributed to other disease agents, namely, the closely related oomycete *Pythium chondricola* (Qiu et al., 2019) and the fungus *Alternaria* sp. (Mo et al., 2016). Similarly, *Olpidiopsis* disease has been linked to another *Olpidiopsis* species, *O. pyropia* (Klochkova et al., 2016), suggesting that the relationship between disease symptoms and disease agents may not be straightforward.

Several disease conditions listed in Table 2 have been attributed to the presence of one or more bacterial species. Ice–ice disease, affecting *Kappaphycus* and *Eucheuma* spp., is characterized by a whitening of the thallus in response to environmental stress and the action of opportunistic pathogenic bacteria (Ask & Azanza, 2002; Doty & Alvarez, 1975; Uyenco, Saniel, & Jacinto, 1981). Several bacterial species and complexes have been linked to ice–ice disease, including *Cytophaga-Flavobacterium* complex (Largo et al., 1995) and the presence of both *Alteromonas* and *Pseudoalteromonas* (Syafitri et al., 2017). Solis et al. (2010) also demonstrated the ability of marine fungi (*Aspergillus* spp. and *Phoma* sp.) to induce ice–ice symptoms in both *Kappaphycus alvarezii* and *K. striatum* under laboratory conditions. However, the exact mechanisms by which these organisms are able to cause the progression of ice–ice symptoms in *Kappaphycus* and *Eucheuma* spp. are as yet unknown, as is the role of environmental stress in inducing disease.

As knowledge of seaweed diseases and the range of micro-organisms associated with them increases, it becomes necessary to move beyond the one-disease-one-pathogen paradigm toward the pathobiome concept (Bass, Stentiford, Wang, Koskella, & Tyler, 2019). Pathobiotic systems are those in which multiple host-associated organisms (encompassing prokaryotes, eukaryotes, and viruses) are associated with reduced host health status as a result of interactions between members of that set, the host, and environmental factors. Even where a primary agent can be identified, its effect is often moderated by other symbionts. In seaweeds particularly, which are known to be associated with a wide diversity of microbial symbionts that influence their development, ecology, and evolution (Egan et al., 2013; Brodie et al., 2016 and refs therein), the potential for invasion by opportunistic pathogens, environmentally induced pathogenesis, and microbial dysbioses to initiate or exacerbate disease are diverse and omnipresent. Furthermore, a particular set of clinical signs of disease that might suggest a common cause by a primary pathogen may in fact have multiple etiologies, which present in similar ways (the "moving target" hypothesis; Sutherland et al., 2016).

Among the most significant pests of commercially cultivated seaweed species are epiphytic algae. Epiphytic filamentous algae (EFA) are responsible for a significant decrease in both the production biomass and carrageenan quality of cultivated *Kappaphycus* and *Eucheuma* spp. in Southeast Asia and thereby affect both the income and job security of farmers in productive regions (Critchley et al., 2004; Hurtado & Critchley, 2006a; Hurtado & Critchley, 2006b). EFA are prevalent in all major eucheumatoid-producing countries and in countries with smaller, but developing, industries, including Madagascar and China (Pang et al., 2015; Tsiresy et al., 2016). Outbreaks of *Polysiphonia* have been reported as the cause of massive declines in *K. alvarezii* production in the Philippines and Malaysia (Hurtado & Critchley, 2006a; Vairappan, 2006), and die-offs of the same crop species have been attributed to the presence of *Melanothamnus* (as *Neosiphonia*) *savatieri*) in Chinese farms since 2009 (Pang, Liu, Liu, & Lin, 2011). Epiphyte infestations have been linked to abiotic stressors affecting host fitness, including the temperature, salinity, and current of seawater and intensity of light and nutrient availability (Hurtado & Critchley, 2006a; Korpinen et al., 2007; Pang et al., 2011). Heavy infections with epiphytic algae are known to cause damage to the cortex of *Kappaphycus* and thus leave the host vulnerable to infection by opportunistic bacteria (Vairappan et al., 2008).

4 | SEAWEED DISEASE MANAGEMENT AND BIOSECURITY

In order to attempt to eliminate or mitigate the impact and spread of disease and pest outbreaks on seaweed aquaculture, several treatments or mitigation strategies have been used. The washing of *Pyropia* blades in acid solutions is a widespread practice and is often used in an attempt to control all diseases (G. H. Kim et al., 2014). Sakaguchi, Park, Kakinuma, and Amano (2001) showed that washing thalli in an acid of pH 2.0 for 5 min was effective for suppressing the development of red rot disease, although exposure times are often closer to 30 seconds in practice and so are largely ineffective (G. H. Kim et al., 2014). This exposure to acidic conditions may, however, be partially effective for the treatment of green algae, diatoms, and cyanobacteria, the latter two of which are caused by the colonization of the blade surface by micro-organisms (Table 3). No effective treatment is yet available for either green-spot disease or *Olpidiopsis* disease, the two most severe diseases of *Pyropia* crops (G. H. Kim et al., 2014). However, there is evidence that fungal endophytes associated with brown algae produce bioactive metabolites that have the potential to protect against pathogen infection and have been shown to inhibit infection of *Pyropia yezoensis* by *O. pyropiae* and *P. porphyrae* (Prado, Vallet, Gachon, Strittmatter, & Kim, 2017; Vallet, Strittmatter, Murúra, Lacoste, Dupont, Hubas, Genta-Jouve, Gachon, Kim, & Prado, 2018; Qiu et al., 2019).

Changing cultivation conditions, particularly the repositioning of cultivation ropes to modify exposure to light and more favorable salinities, are effective measures that can be taken to reduce the severity of diseases caused by exposure of *S. japonica* to unfavorable abiotic conditions (Wang et al., 2014).

TABLE 3 Symptoms of diseases that have been reported in red and brown seaweeds in aquaculture in Asia

Disease name	Host	Symptoms (for sources see Table 2)
Rotten thallus syndrome	*Gracilariopsis heteroclada*	White to pinkish discoloration and gradual disintegration of thallus. Causes erosion of the pericarp.
Epiphytic filamentous algae	*Kappaphycus* and *Eucheuma* spp.	Tiny black spots become visible on the cortex of the host, followed by the appearance of “goosebumps” as the epiphyte matures. At the end of infection, dark pits are left on the cortical surface, and the host is infected by opportunistic bacteria
Ice–ice disease	*Kappaphycus* and *Eucheuma* spp.	Bleaching of the thallus at the tips of the plant and close to site of “tie-tie” attachment to culture ropes, thought to be caused by environmental stress. Subsequent infection by opportunistic bacteria degrades the tissue of the thallus
Red rot disease	*Pyropia yezoensis*; *P. tenera*	Small, red patches on infected blades. The blade changes color to violet-red and numerous holes appear before the blade entirely disintegrates
Olpidiopsis disease (“Chytrid blight”)	*P. yezoensis*	Bleaching of infected blade sections, followed by the appearance of green lesions. Holes form in the blades, and the blades eventually disintegrate
White-spot disease	*P. yezoensis*	“Pinhole-like” white spots on the edge of shell-boring conchocelis, which gradually expand and form lesions
Diatom felt	*P. yezoensis*	A large number of epiphytic diatoms of various species colonize the blade, giving a dirty appearance and causing bleaching
Cyanobacteria felt	*P. yezoensis*	Often occurs simultaneously with green-spot disease. Bacteria and cyanobacteria attach to the cuticle in large numbers, causing it to degenerate. A distinctive “Bristle” appears on the surface at the edge of the lesion.
Anaaki disease	*P. yezoensis*	With *Pseudomonas* sp., *Vibrio* sp: formation of lesions with green borders; The blade rots, and holes are formed. With *Flavobacterium* sp. LAD-1: Pinhole lesions form in the center of the thallus, which gradually widen. The thallus eventually becomes detached from the culture bed.
Green-Spot Disease	*P. yezoensis*; *P. tenera*; *P. dentata*	Similar to Anaaki disease: green chains of fused dead cells develop on wounds of the thallus, followed by rows of pink cells and central green cells around the developing lesion.
White-blight	*P. yezoensis*	Bleaching of the blade, followed by cell lysis and blade disintegration
Unnamed disease	*P. yezoensis*	The appearance of tiny “reddish-brown” spots on conchocelis life stages grown on scallop shells. The diseased area eventually turns yellowish-white
Diatom blooms	*P. yezoensis*	Blooms of diatoms deplete nutrients in the water column, resulting in bleaching of *Pyropia* blades
Red-spot disease	*Saccharina japonica*	Swelling of gametophyte cells, followed by filamentous fading and decaying of the thallus
Hole-rotten disease	*S. japonica*	Alginase-secreting bacteria decompose host cell walls, causing rotting and forming holes in the blade
Malformation disease'	*S. japonica*	Malformation of various life stages, including gametophytes, sporelings, and eggs inside the oogonium, thought to be caused by saprophytic bacteria and poor culturing practices
Twisted frond disease	*S. japonica*	Fronds appear twisted, with swollen stipes and shortened holdfasts
Green rot disease	*S. japonica*	The stipes of sporelings become greenish, soft, and decayed and fall from nursery ropes

(Continues)

TABLE 3 (Continued)

Disease name	Host	Symptoms (for sources see Table 2)
White rot disease	*S. japonica*	Starting from the apex and spreading toward the lower part of the blade, fronds fade in color from brown to yellowish to white. Eventually, fronds decay and detach from culture ropes
Blister disease	*S. japonica*	Blisters form across the fronds. Disruption of these blisters results in decaying of the blade
Shot hole disease	*Undaria pinnatifida*	Brown spots appear in the middle of the thallus blade. These spots fuse and spread the pinnate part of the blade.
Green-spot rot	*U. pinnatifida*	Green spots form on the blade and start to rot, resulting in small holes with green margins. These enlarge, and the frond decays.
Yellow hole disease	*U. pinnatifida*	Bacteria enter the thallus through abrasions and digest cells, forming holes
Spot decay	*U. pinnatifida*	Formation of discolored spots on the thallus, followed by decaying of host tissue.
Pin-hole disease	*U. pinnatifida*	Copepods damage the surface of the frond, causing small, pinhole-like lesions
Unnamed disease	*U. pinnatifida*	Amphipods burrow through the holdfast of the blade, which may result in longitudinal separation of the frond. Heavily damaged blades can detach from the substrate.
Brown endophytic algae	*U. pinnatifida*	Epiphytized thalli become thicker and stiffer and so are less economically valuable

The current technique for decreasing the impact of pest epiphytes on eucheumatoid stocks is to monitor cultivated populations and remove the pests by hand as quickly as possible before they can reproduce and spread (Ask & Azanza, 2002; Pang et al., 2015). The removed material is then taken to land and disposed of. Plants infested with EFA are harvested immediately and replaced with uninfected propagules from a separate location (Ask & Azanza, 2002).

The development of ice–ice symptoms in *Kappaphycus* and *Eucheuma* is thought to be the result of stress to the host from abiotic conditions, such as temperature and salinity (Vairappan et al., 2008) and light intensity and water movement (Hurtado & Critchley, 2006a) in combination with the action of opportunistic bacteria (Largo et al., 1995; Uyenco et al., 1981). The triggers behind disease onset and progression are not well understood, and as a result, no effective management protocols that are cost effective have been developed to date.

The improvement of disease mitigation strategies in macroalgal aquaculture is reliant on increasing our understanding of the agents and abiotic factors influencing disease onset and progression and the subsequent development of biosecurity programs, including the use of quarantine procedures and improved farm management practices through capacity building (Campbell et al., 2019).

5 | FUTURE DIRECTIONS FOR SEAWEED AQUACULTURE

The continued and sustainable expansion of seaweed aquaculture is reliant on a number of factors. Perhaps the most pressing is the need for a greater understanding of the causes of pathogenic and physiological disease. Improvement in methodologies for the characterization of pathogens, such as the application of histopathological and molecular diagnostic techniques already routinely used in other aquaculture sectors, will lead to the development of rapid and robust diagnostic techniques. These in turn will allow for the early detection of pathogen (and pest) outbreaks and, when paired with disease surveillance programs and the monitoring of environmental conditions, will lead to a greater understanding of the abiotic and biotic factors influencing disease and pest outbreaks.

Several diseases affecting cultured algal species are known to be caused or exacerbated by abiotic stress as a result of unfavorable environmental conditions, particularly increased water temperature, light, and changes in water salinity (Arasamuthu & Patterson Edwards, 2018). As sea water temperatures continue to rise, as a result of climate change, such incidents may be expected to become more frequent and severe. Therefore, it is important to adapt farm management, such as culturing red algae in deeper water to reduce the impact of too much sun and potentially reduce the growth of epiphytes that may be optimum in higher light conditions, and to ensure biosecurity practices. It is also important to gain a greater understanding of the association between these abiotic factors and opportunistic pathogens, such as the role of bacteria in the development of ice–ice disease in *Kappaphycus* and *Eucheuma*. The microbial community associated with seaweeds is also known to have an important role in both their normal development and in disease (Egan et al., 2013). The composition of these pathobiotic communities and the factors influencing unfavorable shifts in community structure, however, remain largely unexplored (Bass et al., 2019).

Marine viruses are c. 10 times more abundant in marine environments than both bacteria and archaea (Fuhrman, 1999; Middelboe & Brussard, 2017) and are known to be drivers of both mortality and microbial community structure. Their role in health and disease is poorly understood, but evidence from the wild suggests that viruses will be an agent of diseases in cultivation (McKeown et al., 2017). However, improved surveillance and detection methods, particularly using unbiased molecular methods such as metagenomics on infected seaweed tissues will facilitate the discovery and characterization of novel viruses and lead to a greater understanding of their influence on seaweed aquaculture.

In addition to improving our understanding of disease-causing agents, it is important to also consider the role of the host in disease and pest susceptibility. The domestication of seaweeds has, in many cases, led to a reduction of the genetic diversity of seaweed crops, which in turn may result in an increased susceptibility to pathogenic and physiological disease (Valero et al., 2017). A greater understanding of the genetic diversity of cultured seaweeds and appropriate breeding strategies and crop selection are required to retain this genetic diversity and safeguard the disease and pest resistance cultivars for future use by the industry.

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ORCID

Georgia M. Ward https://orcid.org/0000-0002-9654-1228
Juliet Brodie https://orcid.org/0000-0001-7622-2564

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