Mar. Sci. Tech. Bull. (2021) 10(3): 234-243
e–ISSN: 2147–9666
info@masteb.com

dergipark.org.tr/en/pub/masteb
www.masteb.com
DOI: 10.33714/masteb.917788

Marine Science and Technology Bulletin

REVIEW PAPER

Ice-ice disease in commercially cultivated seaweeds *Kappaphycus* spp. and *Eucheuma* spp.: A review on the causes, occurrence, and control measures

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ARTICLE INFO

Article History:
Received: 16.04.2021
Received in revised form: 26.05.2021
Accepted: 26.05.2021
Available online: 07.06.2021

Keywords:
Eucheuma
Ice-ice disease
Kappaphycus
Seaweed farming

ABSTRACT

Kappaphycus spp. and *Eucheuma* spp. are two economically significant seaweed species cultivated globally due to their carrageenan content with numerous commercial applications. They are mainly cultivated in the Philippines, Indonesia, Malaysia, and Tanzania. The culture of these seaweeds also provides income sources for many coastal dwellers. In 2018, the total global production from these seaweeds was about 11 million tonnes. One of the primary problems that affect seaweed production is the incidence of ice-ice disease. In this article, we reviewed the reported scientific journals on the ice-ice disease of two commercially cultured seaweed species (*Kappaphycus* spp. and *Eucheuma* spp.), focusing mainly on causes, occurrence, and control measures. The ice-ice disease is caused by both abiotic and biotic factors manifested by the presence of white and soft parts in the infected seaweeds. The occurrence of this disease varies from species, places, and seasons. Control measures may include proper farm management, polyculture with other seaweeds, pre-soaking with antibacterial substances and nutrient enrichment before out-planting, and possibly using genetic engineering.

Please cite this paper as follows:

Tahiluddin, A. B., & Terzi, E. (2021). Ice-ice disease in commercially cultivated seaweeds *Kappaphycus* spp. and *Eucheuma* spp.: A review on the causes, occurrence, and control measures. *Marine Science and Technology Bulletin*, *10*(3), 234-243. https://doi.org/10.33714/masteb.917788

Introduction

Commercial seaweed species like *Kappaphycus* spp. and *Eucheuma* spp. are significant seaweed species used as a carrageenan source, a phycocolloid, with various usage area in commercial applications as a thickening, gelling, and binding agents in food products and sauces, as well as in experimental medicine, pharmaceutical cosmetics, formulations, and

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industrial applications (Necas & Bartosikova, 2013; Loureiro et al., 2017a). Nearly 90% of the world's carrageenan comes from these seaweed species primarily cultured in Indonesia and the Philippines (Campbell & Hotchkiss, 2017). The annual global production of carrageenan is over 60,000 tons with a gross market value of US$ 626 million (Rhein-Knudsen et al., 2015). In many coastal tropical and sub-tropical countries, these seaweeds' farming is an essential livelihood source (Hayashi et al., 2017). The combined world production of these seaweeds in 2018 was around 11 million metric tons comprising 34% of the total seaweed production globally (FAO, 2020).

One of the main hurdles in the farming of these macroalgae is diseases, e.g., ice-ice disease and epiphyte infestation (Largo, 2002). These diseases developed due to increased farm size and culture practices intensification (Vairappan, 2006). These are responsible for many seaweed seedlings losses, influencing both biomass quantity and quality, which primarily affect marginalized coastal villages relying on seaweed farming as a sole income source (Loureiro et al., 2017b).

Ice-ice disease, in particular, is the most prevailing problem seen in the farming of eucheumatoids worldwide. This disease is caused primarily by stressful environmental conditions, as Largo et al. (1995a) demonstrated in laboratory experiments and likewise observed in the farm field (Arisandi & Farid, 2014). Pathogenic bacteria further degrade the diseased seaweeds lead to eventual thalli disintegration (Largo et al., 1995b). Marine-derived fungi also play an important role in ice-ice disease induction (Solis et al., 2010). This disease is characterized by the appearance of white and soft parts on the infected seaweeds' thalli.

Disease problems (ice-ice disease and epiphyte infestations) in eucheumatoid farming have resulted in shrinking culture stocks and decreased quality of carrageenan, resulting in low market value and income and job opportunities losses, especially for marginal seaweed farmers (Ward et al., 2020). In the Philippines, ice-ice disease occurrence and epiphyte infestations have a drastic effect, causing 15% *Kappaphycus* production losses between 2011 and 2013 (Cottier-Cook et al., 2016). In Zanzibar, Tanzania, these diseases and pests become a menace to the commercially cultivated eucheumatoids, affecting seaweed farmers (Largo et al., 2020). Ice-ice disease lowers the carrageenan quality of *Kappaphycus striatus* "sacol" strain; hence, removing the diseased portion is recommended before drying (Mendoza et al., 2002).

Only a few reviews on cultivated seaweeds' pests and diseases are available (Largo, 2002; Ward et al., 2020). No recent review articles are available that focus on ice-ice disease, particularly the causes, occurrence, and treatments. Thus, this paper reviewed all the reported papers on the ice-ice disease, its causes, occurrence, and control measures, focusing on the *Kappaphycus* and *Eucheuma* species commonly cultivated worldwide.

Methods

This study reviewed the available articles from the literature by searching keywords such as ice-ice disease, *Kappaphycus,* and *Eucheuma* in Scopus and Mendeley databases published from 1977 to 2021. Online and printed theses related to this study were also considered. Articles published beyond the time of writing this review were not included.

Occurrence of Ice-ice Disease

The occurrence of the ice-ice disease varies from place to place and season. In Lian Bay, Hainan Province, China, the outbreak pattern in *Kappaphycus* spp. mostly occur from May to August, and October is the month where the outbreak pattern is the same with epiphyte *Neosiphonia savatieri* (Pang et al., 2015). Similarly, the month of April, October, and December noted the highest ice-ice incidence of *Kappaphycus alvarezii* and *Eucheuma denticulatum* in Bais Bay, Negros Oriental and Zamboanga del Norte, Philippines, which ranged from about 52 to 56% (Tisera & Naguit, 2009). Furthermore, in Zamboanga City and Zamboanga del Sur, Philippines, the ice-ice disease occurrence of *K. alvarezii* ranged from about 22 to 40% observed during July to September (Alibon et al., 2019). Farmed *K. alvarezii* in Mannar Gulf and Palk Bay, Southern India, also experienced ice-ice occurrence in March and April (Arasamuthu & Edward, 2018). Even in Zanzibar, Tanzania, the development of ice-ice disease was tremendous during February – March (hot, dry season) and typically diminished during May – June (wet season) by up to 99% (Largo et al., 2020). A month of May was also recorded a high ice-ice disease incidence ranging from 70% to 87% in Calaguas Is., Camarines Norte, Philippines (Hurtado et al., 2006). In South Sulawesi, Indonesia, the ice-ice disease occurred in September – October (dry season) after the emergence of epiphytic infestation (Badraeni et al., 2020). The occurrence of this disease indicates that most of the mentioned months are associated with environmental factors such as elevated temperature and low salinity, which are separately discussed below.

Environmental Factors Causing Ice-Ice Diseases Development

Temperature

It has been demonstrated in the laboratory experiment of Largo et al. (1995a) that stressful environmental conditions are detrimental to cultivated *K. alvarezii*. In their temperature experiments, seaweeds incubated on the weekly interval in two sets of temperature regimes starting from 25°C up to 35°C and from 20°C down to 15°C in a stepwise manner and revealed that extreme temperatures (33°C–35°C) caused extensive whitening resulting to total impairment of the thalli, and these damaged tissues resemble the ice-ice infected branches in seaweed farms. The recent paper of Largo et al. (2020) indicated that intense temperature (29.5°C–35.5°C) in seaweed farms in Zanzibar, Tanzania is one of the prime triggers of ice-ice development and epiphyte infestation. Whitening of the ice-ice infected thalli in *K. alvarezii* affects its photosynthetic efficacy due to the significant reduction in photosynthetic pigment concentration leading to sluggish growth before ice-ice occurrence (Ganzon-Fortes et al., 1993). Similarly, high surface temperatures have been associated with ice-ice disease and other pests (fouling and epiphytes), which caused a substantial decline in seaweed production in Song Song Island, Tanzania (Msuya & Porter, 2014).

Salinity

Kappahycus and *Eucheuma* are true marine red seaweeds; hence, salinity fluctuations in the farms negatively affect cultured seaweeds, including the ice-ice disease development. Laboratory experiments of Largo et al. (1995a) showed *E. denticulatum* exposed to salinity 25‰ and 35‰ responded positively. In contrast, the salinity of 20‰ below within a week is considered deleterious, which led to the ice-ice ice disease development. The whitened parts have prominent similarities to those noted in the seaweed farms.

Light Intensity

The utmost significance of light to seaweeds is supplying the energy for photosynthesis and is considered the most important abiotic factor affecting seaweeds (Hurd et al., 2014). Light intensity has been suspected as one inducer in ice-ice disease development (Largo et al., 1995a). To elucidate the effects, the authors used an increasing light intensity beginning at 0, then elevated to 10, 20, 50, 100, and up to 125 mol photon m^{-2} s^{-1} at the seven-day interval and concluded that less than 50 mol photon m^{-2} s^{-1} light intensity led to ice-ice whitening. These conditions are comparable in the farms when the seaweeds are crowding due to overstocking of the branches in the lines and hindrance due to epiphytes presence, which may create an artificial effect that is lethal. Hence, ice-ice disease development in the farms is typically associated with epiphytes incidence (Trono & Ohno, 1989; Uyenco et al., 1977). In Zanzibar, Tanzania, seaweeds, farmed in shallow intertidal lagoons nearly in direct contact with seafloor bottom during low tides, received extreme levels of light intensity and temperature caused ice-ice disease outbreak (Largo et al., 2020).

Nutrients

Seaweeds require an extensive array of nutrients for growth. In the most natural environment, seaweed growth and yields are limited by the availability of two nutrients, nitrogen and phosphorus (Harrison & Hurd, 2001; Roleda & Hurd, 2019).

Kappaphycus cultivation depends chiefly on the sea's natural fertility (Luhan et al., 2015). Hence, extensive farming may result in the outbreak of ice-ice disease (Vairappan, 2006). Maryunus (2018) reported that nutrient deficiency is the primary factor triggering the ice-ice disease development, as shown by the relationship between nutrient deficiency (nitrogen and phosphorus) and the ice-ice disease outbreak.

Biological factors causing ice-ice disease

Pathogenic Marine Bacteria as Secondary Causative Agents

There are limited studies on the marine bacteria isolation and identification from ice-ice diseased seaweeds *Kappaphycus* and *Eucheuma* and undergoing into pathogenicity test. Table 1 summarizes the previously reported works on the associated and pathogenic bacteria isolated from the seaweeds infected with the ice-ice disease.

The mechanism of ice-ice disease-causing bacteria as secondary causative agents is still not fully clear and explored. Some studies (Largo et al., 1995b, 1998, 1999) have suggested that pathogenic bacteria *Vibrio* sp. (P11) took advantage of the host thalli using its motile ability hence can immediately attach and conquer seaweed tissue as an initial step of infection. Its ability to utilize carrageenan in the seaweed thalli as a carbon source by penetrating infected branches' medullary layer was another advantage that can cause ice-ice disease under stressful conditions.

Similarly, the ability of *Pseudoalteromonas carrageenovora* to produce kappa-carrageenase enzyme and degrade kappa-carrageenan in *K. alvarezii* indicated that this bacteria could trigger ice-ice disease symptoms like whitening of the thalli (Riyaz et al., 2020).

Table 1. Associated and pathogenic bacteria isolated from ice-ice infected seaweeds

Seaweed	Associated bacteria	Pathogenic bacteria (ice-ice disease promoters through pathogenicity test)	Method to confirm as ice-ice disease-causing bacteria	Location	References
Kappaphycus alvarezii and *Eucheuma denticulatum*	*Cytophaga-Flavobacterium* complex, *Vibrio* group	*Vibrio* sp. (P11), *Cytophaga* sp. (P25)	Pathogenicity test	Philippines	(Largo et al., 1995b)
K. alvarezii	*Pseudomonas cepacia, Vibrio alginolyticus, Pseudomonas diminuta, Plesiomonas shigelloides, Flavobacterium meningosepticum*	*V. alginolyticus*	Pathogenicity test	Indonesia	(Aris, 2011)
K. alvarezii	*Shewanella haliotis, Stenotrophomonas maltophilia, V. alginolyticus, Arthrobacter nicotiannae, Ochrobactrum anthropic, Catenococcus thiocycli, Pseudomonas aeruginosa, Bacillus subtilis* subsp. *spizizenii*	*S. maltophilia, V. alginolyticus*	Pathogenicity test	South Sulawesi, Indonesia	(Achmad et al., 2016)
K. alvarezii	*Alteromonas macleodii, Bacillus oceanisediminis, Pseudomonas stutzeri, Pseudoalteromonas issachenkonii, B. hunanensis, B. megaterium, Alteromonas marina, Aurantimonas coralicida, Rhodococcus rhodochrous*	*Alteromonas macleodii, Pseudoalteromonas issachenkonii, Aurantimonas coralicida*	Pathogenicity test	Karimunjawa island, Indonesia	(Syafitri et al., 2017a)
K. alvarezii	*Vibrio* sp., *Halomonas* sp., *Alteromonas* sp., *Aestuariibacter* sp., *Primorskyibacter* sp., *Thalassospira* sp., *Pseudoalteromonas* sp.	*V. alginolyticus*	Agarolytic analysis	Semporna, Sabah, Malaysia	(Azizi et al., 2018)
K. alvarezii	*Vibrio, Bacillus*	Not determined	Not confirmed	Kottapatinam, Rameswaram, Thondi, India	(Riyaz et al., 2019)
E. denticulatum	Dominant species: *Rivularia, Marinagarivorans, Lewinella*	Not determined	Not confirmed	Vietnam	(Kopprio et al., 2021)
K. striatus	Dominant species: *Vibrio, Cobetia, Marinomonas, Pseudoalteromonas*	Not determined	Not confirmed	Vietnam	(Kopprio et al., 2021)

Marine-Derived Fungi as Potential Causative Agents

Aside from marine bacteria, marine-derived fungi also play an essential role as ice-ice inducers. The only study that proved that marine fungi are also involved in this disease was Solis et al. (2010). They isolated 18 morphospecies of marine-derived fungi from *K. alvarezii* and *K. striatus* gathered from Calatagan, Batangas, Philippines. Ten marine-derived fungi were used in the ice-ice disease induction assay. The study showed that three isolates (*Aspergillus terreus, A. ochraceus,* and *Phoma* sp.) triggered ice-ice disease in healthy, non-axenic *K. alvarezii* cultures.

Control Measures

Proper Farm Management and Intervention

Malpractice of seaweed farming harms seaweed production, leading to ice-ice disease development in the seaweed farms. Thus, proper farm management could potentially eliminate or, if not at least, minimize ice-ice disease occurrence. These are the following management intervention as suggested in early studies;

a) Avoid overcrowding seaweeds in farming. Overstocking seaweeds in the farm offers pathogenic bacteria susceptibility and hinders light penetration (Largo, 2002).

b) Stick within optimum conditions for seaweed requirements. Changes drastically in water temperature and salinity must be avoided (Largo, 2002).

c) During summer, especially El Niño seasons where light intensity is extreme, planted seaweeds are advised to transfer to a deeper location where irradiance is enough to prevent photoinhibition (Largo, 2002).

d) For Lian Bay, China, the seaweeds are suggested to be planted in deeper areas from August- October during La Niña years (Pang et al., 2015) related to salinity fluctuations. This recommendation may apply to locations with similar weather conditions.

e) Identify and choose the species or strains that are resistant to ice-ice disease. According to Hurtado et al. (2008), *K. striatus* var. *sacol* is more resistant to ice-ice disease and even to epiphyte infestation than *K. alvarezii* var. *tambalang*. Brown varieties of *Kappaphycus* showed more resistance against ice-ice disease induced by *Vibrio* sp. pathogens than green varieties due to their higher antimicrobial compounds (Irmawati & Sudirjo, 2017). Tissue-cultured *K. alvarezii* produced from the laboratory is also unsusceptible to ice-ice disease and better resistant towards extreme temperatures of 30 and 35 °C than farmed seaweeds (Azizi et al., 2018). Also, *E. denticulatum* is more resistant than *K. alvarezii* against epiphyte infestation and ice-ice disease (Tisera & Naguit, 2009; Pang et al., 2015; Ndobe et al., 2020). Hence, these species/strains can be used as stocks for seaweed cultivation, especially in ice-ice outbreak times.

f) In areas where the ice-ice disease outbreak is already determined, avoidance of planting susceptible species/strains during the ice-ice outbreak can be done and instead engage in other livelihood sources for the meantime.

Polyculture With Other Seaweeds

Some studies show that the polyculture of *Kappaphycus* and *Eucheuma* with other seaweeds exhibits potential control effects against ice-ice disease. These seaweeds are;

a) *Achantophota spiciformis. K. alvarezii* can be co-cultured with *A. spiciformis*- owing to its antimicrobial property, and this alga protects against the ice-ice disease with only 0.062% ice-ice incidence compared to 50% monoculture of *K. alvarezii* (Tokan et al., 2015).

b) *Laurencia majuscule*. Polyculture of *Kappaphycus* or *Eucheuma* with *L. majuscule* may be done since this species produce metabolites that can inhibit ice-ice disease-causing bacteria (Vairappan et al., 2010).

c) *Eucheuma denticulatum*. This species is readily available and economically farmed in many seaweed-producing countries. Pang et al. (2015) suggested that there was a reduction in ice-ice disease incidence and epiphytes *N. savatieri* in *Kappaphycus* species during July – August when co-cultured with *E. denticulatum* – a species with a more efficient defense mechanism against the diseases owing to its volatile halocarbons production when under intense irradiance and CO_2-lacking conditions (Mtolera et al., 1996).

Using Antimicrobial Substances Extracted From Plants

Few authors have investigated the effectiveness of extracts from some mangrove species against ice-ice disease-causing bacteria in laboratory experiments. For instance, extract from the *Avicennia marina* leaves using methanol solvent exhibited potential use as an antimicrobial against four ice-ice disease-causing bacteria, *S. maltophilia, S. haliotis, V. alginolyticus,* and *P. aeruginosa* (Rahman et al., 2020). Also, 500 ppm of flavonoids extracts obtained from the fruits of *Sonneratia alba* showed an antibacterial property against *V. alginolyticus* – one of the opportunistic pathogens that trigger ice-ice development in *K. alvarezii* (Sulistijowati & Karim, 2020). Furthermore, the extracts from the leave of *S. alba* at a concentration of 2.5 – 10 mg ml^{-1} have effectively hampered the growth of nine ice-ice disease-causing bacteria such as *Alteromonas macleodii*, *Bacillus oceanisediminis*, *Pseudomonas stutzeri*, *Pseudoalteromonas issachenkonii*, *Bacillus hunanensis*, *Bacillus megaterium*, *Alteromonas marina*, *Aurantimonas coralicida*, and *Rhodococcus rhodochrous* (Syafitri et al., 2017b).

The use of common lantana (*Lantana camara*) extracts to obstruct ice-ice disease and increase the growth of *K. alvarezii* has been evaluated by Patadjai et al. (2019) in the field experiment. Based on their results, pre-soaking the seaweeds in a 500 ppm solution of common lantana extract for 30 minutes before planting resulted in the absence of ice-ice disease compared to untreated seaweeds. Hence, it is recommended to apply this strategy as ice-ice disease control.

All plant extracts tested by different authors with promising results in inhibiting the growth of ice-ice disease-causing bacteria as well as those tested effective in the field reducing/eliminating ice-ice disease occurrence. This suggests that plant extracts may be useful and feasible as a treatment for the disease through short immersion of the seaweeds to the extract solutions before out-planting to farms.

Nutrient Enrichment

Since seaweeds are dependent on available natural nutrients in the farm, it is not deniable that seaweeds absorb these nutrients for growth and development. Once reach harvestable size, the farmer harvests, dries, and then markets them. Because of extensive farming here, nutrients are also being harvested and not return to the natural environment, in contrast to when the seaweeds are naturally rotting alone. These nutrients may become limited, resulting in low growth and even may result in ice-ice disease.

Nutrient enrichment using both organic and inorganic fertilizers has been proven efficient in minimizing ice-ice disease occurrence. In particular, when seaweed *K. alvarezii* immersed to 10 ppm of sodium nitrate for 12 hrs before planting into the open sea for 45 days, not only growth and carrageenan yield was improved but also decreased the occurrence of ice-ice disease to 8.75% compared with untreated seaweed (97%) (Luhan et al., 2015). A similar study also revealed that *K. striatus* enriched with 8.82 g L^{-1} ammonium phosphate solution for about 5 seconds to 1 minute and left covered overnight using canvass before out-planting significantly reduced the occurrence of ice-ice disease of up to 42% compared to untreated (78%) during ice-ice disease season parallel to what the farmers practiced and observed in the study site (Tahiluddin, 2018). Acadian Marine Plant Extract Powder (AMPEP) as organic fertilizer enhanced growth and carrageenan and also not only efficient in reducing the epiphytes infestation (Borlongan et al., 2011; Hurtado & Critchley, 2013; Loureiro et al., 2017b; Ali et al., 2020) but also lessening the ice-ice disease occurrence (Hurtado & Critchley, 2013; Illud, 2020) in *Kappaphycus* cultivation. The mode of application for AMPEP in *Kappaphycus* varies, as demonstrated by studies. For example, to reduce epiphytic *Neosiphonia* infestation and increase growth rate, Borlongan et al. (2011) soaked the *K. alvarezii* seedling in 0.1 g L^{-1} AMPEP before out-planting. Illud (2020), on the other hand, used both 0.01 g L^{-1} and 8.82 g L^{-1} of AMPEP enriched by following the same method of Tahiluddin (2018). The action mode on the efficacy of AMPEP in ameliorating deleterious outcomes of disease outbreaks is thought to be via elicitation of seaweed's natural defense mechanism against pathogens (Hurtado & Critchley, 2013; Loureiro et al., 2017b). However, precautions must be taken into account as inorganic fertilizer such as ammonium phosphate at a concentration of 6–9 g L^{-1} significantly reduced the carrageenan yield and viscosity of *K. striatus* by 4.81% and 1.83 cPs, respectively (Robles, 2020).

Using Genetic Engineering

Nowadays, in improving the horticultural crops, genetic engineering approaches renders countless applications for abiotic (heat, drought, and salinity) and biotic (insect-pest and pathogenic organisms) stress tolerance by using several genes like in providing immunity against biotic stress (*Cry* genes, trypsin inhibitors, protease inhibitors, cystatin genes, chitinase, osmotin, glucanase, defensin, pathogenesis-related genes, and RNAi technique), and in giving protection against adverse environmental stresses (genes encoding for stress biosynthesis protecting compounds such as glycine, betaine, mannitol, and heat shock proteins, various transcription factors like mitogen-activated protein kinase (MAPK), WRKY, DREB1, etc.) (Parmar et al., 2017).

However, the application of genetic engineering in seaweeds for disease controls is still in its infancy. For instance, gene transformation to produce a seaweed resistant to abiotic stress as a potential solution for the ice-ice disease has been tested by Sulistiani et al. (2019) using the Gα gene extracted from soybean (*Glycine max* mar Slamet). Sulistiani et al. (2019) introduced this gene into the *K. alvarezii* callus using *Agrobacterium tumefaciens* and regenerated modified callus cells to transgenic plantlets. Results revealed that *K. alvarezii* transgenic plantlets with Gα genes were successfully created. Likewise, Handayani et al. (2014) established a binary plasmid bearing chicken lysozyme gene and transferred it to *K. alvarezii* thalli using *A. tumefaciens* and also successfully produced a transgenic *K. alvarezii.* According to the authors, the Gα gene encodes for the heterotrimeric G protein α subunit is a gene that has an essential role in biotic and abiotic stress tolerance. Also, chicken lysozyme is a significant constituent of immune defense against pathogenic bacterial diseases that can boost seaweed tolerance against pathogens.

However, the authors of these two experiments did not evaluate the transgenic plantlets' efficacy in protecting against ice-ice disease. But their findings are beneficial for further investigation in the level of tolerance against ice-ice disease-causing bacteria and abiotic stresses.

Conclusion

The ice-ice disease is a disease caused by drastic fluctuations of water parameters in the environment, further degrade the stressed branches by the attack of pathogenic microorganisms. The occurrence of this disease varies from species, places, and seasons (wet and dry). Control measures may include proper farm management, polyculture with other seaweeds, pre-soaking with antibacterial substances, nutrient enrichment, and possibly using genetic engineering. Knowledge of this disease may be helpful, especially for the farmers, to avoid production losses and improve the seaweed industry.

Compliance with Ethical Standards

Authors' Contributions

ABT and ET conceptualized the study, ABT wrote the first draft of the manuscript and then ET edited the manuscript. Both authors read and approved the final manuscript.

Conflict of Interest

The authors declare that there is no conflict of interest.

Ethical Approval

For this type of study, formal consent is not required.

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