




# The cultivated genus *Ulva*, its pests, and defence

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## Abstract

The genus *Ulva* is one of the most commonly commercially cultivated seaweeds both on land in ponds and in the open sea. As a crop, its cultivation is accompanied by three pest groups: (1) diseases caused by pathogenic bacteria, algae, virii, and fungi, which cause perforations, deterioration, and decreased growth of thalli; (2) various grazers, e.g. small crustaceans, gastropods, and non-defined invertebrates, which decrease growth and damage the thalli; and (3) an epiphytic biofilm of microorganisms, which also causes damage to the end-crop decreasing its yield and value. Mitigation categories against *Ulva* pests may be divided into three categories: (A) pro-active human intervention by washing the infected thalli with acid, fresh water, proprietary chemicals or CO<sub>2</sub>-saturated seawater, the use of methanolic *Ulva* extracts, or exudate from the green seaweed, all of which are reported to restrict pest activity; (B) using the beneficial properties of probiotic bacteria thereby eliciting antifouling activity, with selective abilities against pathogens of *Ulva* spp.; (C) enhancing the effects of environmental changes on pests, i.e. acidification and increased seawater temperature, which mainly decrease the grazer population and thereby their pressure. A summary of these studies is presented as a guide for rapid responses and applied management techniques for the amelioration of cultivation diseases, grazers, and harmful epiphytes affecting the foliose green alga *Ulva* spp.

**Keywords** *Ulva* · Pests · Defence

## Introduction

Members of the green macroalgal genus *Ulva* are cosmopolitan in marine systems. Selected members of the genus are cultivated both directly in the sea and also intensively in tanks and ponds on land. A diverse array of phyconomic methods collaboratively generates an annual global yield of approximately 1500 mt of dry biomass (Mantri et al. 2020).

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*U. lactuca*, commonly known as sea lettuce, is a type of green alga that is naturally high in vital nutrients and often serves as an excellent ingredient in functional food and animal feed sectors. Its key components include mineral-rich sap, lipids, ulvans, and cellulose (Steinhagen et al. 2024). Members of the *Ulva* genus play a central role in coastal ecosystems and in widespread maricultural operations (Steinhagen et al. 2024). Bio-refineries play a crucial role in converting biomass into valuable products, similar to how petroleum refineries crack crude oil. The crucial role will be to maximize the utilization of feedstock and extract a wide range of valuable products, including biofuels, biochemicals, and biomaterials (Mantri et al. 2020). *Ulva* spp. have various applications beyond just human consumption. Aquaculture, in particular, utilizes various ulvoid species as a feed source for farmed marine organisms such as fish, shellfish, and shrimp due to their relatively high protein content, e.g. Buffeljags Abalone Farm (<https://www.vikingaquaculture.co.za/abalone/farming/>). In addition to its natural protein content, *Ulva* spp. can be cultured in controlled conditions, allowing for further enhancement of their nutritional values. Protein content in *U. lactuca* extends between 12–44% in dry weight (Shpigel et al. 1999). Furthermore, *Ulva* spp. are also utilized for environmental bioremediation purposes. They can efficiently absorb excess nutrients over their surface area, such as N and P from water bodies, thereby helping to mitigate eutrophication, a common problem in many aquatic ecosystems, caused by nutrient pollution (often farm run-off). This ability to absorb nutrients makes *Ulva* spp. extremely valuable in the toolbox of efforts to improve water quality and restore balance to marine environments. Therefore, species within this genus play a dual role in both aquaculture and environmental conservation (Mantri et al. 2020).

Various *Ulva* spp. have indeed been extensively studied in terms of their biology and relationships with bacteria. In particular, the concept of *Ulva* being a holobiont refers to the recognition that it does not exist in isolation as a multicellular, foliose green alga but rather as a composite organism consisting of the host organism (*Ulva*) and associated microbial communities, both endogenous and external (Wichard et al. 2015; Califano et al. 2020). Research into cross-kingdom communication, particularly between *Ulva* and its surrounding microbes, has gained considerable attention due to its potential implications for understanding taxonomy, growth, development, and morphogenesis. High-throughput techniques have been employed to explore the intricate interactions between *Ulva* and various microorganisms in its environment. These studies elucidate the molecular mechanisms underlying the biotic interactions and their effects on the physiology and ecology of *Ulva* (Mantri et al. 2020). The biotic interactions of *Ulva* with its pests are a major problem of *Ulva* cultivation. The purpose of this review is to focus on the harmful pests of *Ulva*, namely, diseases, grazers, and epiphytes, and also to highlight mitigation mechanisms against these collective attacks.

## Diseases

Like any other living organism, algae (both micro and macro), especially under stressful conditions, are plagued by diseases caused by fungi, protists, bacteria, and virii. As aquaculture expands globally, the cultivation of seaweeds, also known as seaweed farming or mariculture, has become an important industry. Seaweeds are cultivated for various purposes, including food, biofuels, pharmaceuticals, and other industrial uses. However, like

any form of agriculture, seaweed farming is susceptible to various challenges, including the spread of pathogens (Gachon et al. 2010).

One of the first reports of bacterial involvement in damage to seaweeds was expressed in various *Ulva* diseases. Waite and Mitchell (1976) were the first to describe a damaging epiphytic bacterial population isolated from the thalli of *U. lactuca*, which was capable of cell wall degradation and cellular invasion. A certain unidentified bacterial population is considered opportunistic, meaning it takes advantage of favourable conditions to proliferate. In this case, it seems to thrive when the algal thallus is subject to stress, particularly conditions encountered during the cultivation process.

A case of disease, or infection, in an *Ulva* sp., was described by Colorni (1989). The symptoms, such as the appearance of green spots on the thallus, that gradually enlarged into perforations, suggested a pathological condition affecting the health of the alga. The presence of two microscopic algae on the diseased thalli, one of which was presumed to be an allomorphic form of cells from the same *Ulva* sp., indicated a complex interaction within the algal community. The accompanying bacterial proliferation suggested that microbial interactions may have contributed to the progression of the disease. The fact that the diseased thalli did not decay but instead exhibited stunted growth implied that the disease was impacting the metabolic processes or nutrient uptake of the alga, affecting its overall health and growth. The onset of lesions being triggered by traumatic events suggested that environmental stressors, such as fluctuations in light, temperature, and pH, could be exacerbating factors in the development of the disease. These stressors could weaken the algal thallus, making them susceptible to infection or other pathogenic agents. Overall, this case highlights the complex interplay between environmental factors, microbial communities, and host health in the context of algal disease progression. Understanding these dynamics is crucial for managing and mitigating disease outbreaks in algal cultures (Califano et al. 2020).

Further reports describe the presence of algae, specifically *Acrochaete geniculata*, as a parasitic agent causing a destructive disease in tank-cultivated *U. rigida*. The disease manifested through the appearance of green spots on the host thallus, which then spread and gradually lead to perforations of the frond, resulting in extensive disintegration. *A. geniculata*, identified as the causative agent of the disease, is an endophytic, filamentous green alga. It resides and grows within the tissues of *U. rigida*, causing harm and leading to the observed symptoms. This information highlights the importance of understanding the various factors, including parasitic agents like *A. geniculata*, that can impact the health and cultivation of *Ulva* spp., particularly in controlled environments like tanks where such diseases can spread rapidly and cause significant damage within short time frames (Del Campo et al. 1998). The direct effects of the endophytic pathogen were followed by a secondary bacterial infection leading to disintegration of the thallus. In a further example, more than 1000 t fresh weight of *Ulva* was cultivated in South African abalone farms in 2007, primarily to be used as direct feed, but in one case also to act as a biofilter allowing for partial re-circulation by nutrient removal. In this case, a brown epiphytic alga, i.e. *Myrionema strangulans* (Chordariales), was the identified causative agent, leading to total biomass loss which was only managed by farmers entirely re-stocking their tanks (Bolton et al. 2009).

Natural populations of *Ulva* spp. from the Patagonian, Atlantic coasts, are affected by the brown endophyte *M. strangulans*. The presence of this endophyte leads to the development of brown spots on the fronds. When there is significant epiphytism, there are additional negative effects on the host. These effects include perforations in the host cuticle, extensive depigmentation of the thallus, and cellular disorganization. Additionally, *M.*

*strangulans* is observed to form endogenous, discoidal thalli composed of vegetative filaments. These filaments radiate from a central zone and extend to the periphery of the infected green thalli, indicating the colonization and impact of the endophyte on the structure of the infected thalli. This description suggests a complex interaction between the brown endophyte *M. strangulans* and *Ulva* spp., leading to visible changes in the morphology and physiology of the algae (Siniscalchi et al. 2012). Another study in Patagonia claimed that the abundance of epiphytes on *Ulva* spp. was influenced by high seawater temperature, long day length, and high radiation. The study indicated that the highest abundance of epiphytes was observed on the holdfasts of *Ulva* with *M. strangulans* being particularly prevalent in terms of both frequency and cover. This information suggests that environmental factors are important determinants of epiphyte growth in *Ulva* spp. in the Patagonian region, with implications for understanding the dynamics of this area (Gauna et al. 2017). A specific fungal report discussed the presence of *Pythium* sp. in the Oslo Fjord and its impact on *U. intestinalis* under conditions of low salinity. *Pythium* is a genus of water moulds that can have detrimental effects on a number of aquatic organisms. In this case, it appears that *Pythium* sp. contributed to the destruction of *U. intestinalis*. The presence of *Pythium* sp. and its impact on *U. intestinalis* thalli underscore the importance of understanding the intimate interactions between different organisms in various aquatic ecosystems, as well as the impacts of environmental factors that influence these interactions, such as salinity levels (Maria-Luz et al. 2020).

Taken together, these findings suggested that the *Bacillus cereus* BE23 cell-free filtrate had significant inhibitory effects on *U. prolifera*, affecting its growth, chlorophyll content, photosynthetic efficiency, and electron transport rate. These effects present implications for the ecological interactions between bacteria and algae in aquatic ecosystems as mentioned above (Li et al. 2020). Twenty different types of various virii were identified on bleached *Ulva*, being absent from healthy blades (van der Loos et al. 2023). The above-mentioned damaging diseases represent the very few published reports of bacterial, algal, and fungal origins of diseases in a variety of species of cultivated *Ulva* spp. Future studies will have to answer the unsolved questions of this subject.

## Grazers

A somewhat wider literature appears regarding *Ulva* and its grazers. These can be divided into categories according to the number of major grazer groups involved. One study investigated the biomass removal of *U. rigida* in the Venice Lagoon. According to its findings, a group of small crustaceans, including macrofaunal invertebrates, was identified as responsible for this biomass removal. Among these crustaceans, certain species of amphipods were observed to be the primary grazers. This suggests that the grazers of the Venice Lagoon, particularly certain species of amphipods, play a significant role in controlling the population or biomass of *U. rigida* (Balducci et al. 2001).

A study conducted in the Veerse Meer Lagoon in the Southwest Netherlands investigated the impact of small grazing crustaceans on the development of *Ulva* spp. biomass. Through consumption tests, the researchers identified several species as significant grazers: the amphipod *Gammarus locusta*, the isopods *Idotea chelipes*, and *Sphaeroma hookeri*. These findings suggested that these grazers played a significant role in regulating the biomass in the Veerse Meer Lagoon ecosystem (Kamermans et al. 2000).

A field cage experiment conducted on the Swedish west coast revealed unexpected outcomes regarding the population dynamics of the amphipod *G. locusta* and the biomass of *Ulva* spp. The experiment observed high densities of juveniles and successful reproduction of encaged adult individuals, resulting in densities exceeding 4000 individuals per square metre. Additionally, the experiment noted a remarkably low biomass of *Ulva* spp. in both ambient and nutrient-enriched treatments. These findings suggested that in the absence of predators, the population of *G. locusta* could proliferate significantly. Moreover, the high densities of *G. locusta* appeared to exert control over the green algal biomass (Andersson et al. 2009).

A study involving gastropod grazers, specifically the Cape keyhole limpet *Fissurella mutabilis* presented its impact on integrated abalone-*Ulva* spp. systems. The study investigated methods to control outbreaks of *F. mutabilis*, with one example being freshwater treatment which might expose them to unfavourable or lethal conditions (Hansen et al. 2006). The presence of *Fucus vesiculosus*, commonly known as bladderwrack, enhanced the grazing effects of the snail *Littorina littorea* on *U. lactuca*, on a rocky shore. This indicated a potential interaction between these species, where the presence of bladderwrack somehow influenced the grazing behaviour of the snail, possibly leading to increased consumption of *U. lactuca* (Bracken et al. 2014). Marine gastropods, which are herbivorous organisms, are commonly found as epibionts within tanks used for the cultivation of *Ulva* spp. These gastropods negatively impact the productivity and quality of the cultivated green alga especially when it is grown for food purposes (Kerrison et al. 2016).

The next grazer category includes the introduction of *Tapes philippinarum* commonly known as the Manila clam, which seems to have brought about a positive change in controlling the biomass of *U. rigida* in the Venice Lagoon ecosystem. This phenomenon underscores the intricate interplay of various species within an ecosystem and how the introduction of one species can have cascading effects on others. The fact that *T. philippinarum* as a filter feeder consumes the single-celled, motile *U. rigida* reproductive phases suggested a potential biological control mechanism. This can be beneficial in mitigating the overgrowth of unwanted *U. rigida*, which has a detrimental effect on the overall health of the lagoon ecosystem (Sfriso and Marcomini 1996). Another study discussed the impacts of herbivorous animals, such as isopods and gastropods, on the growth and number of *U. australis* fronds around the coast of Korea (Gil et al. 2015). A further study examined the dominant residential controlling species of *U. australis* in the same area. The study found that the primary species were *Amphithoe* sp. (Amphipoda), *Monodonta* spp. (sea snail), and *Pagurus* sp. (hermit crab). In sheltered areas, there was a significantly greater growth and number of *Ulva* fronds, as well as a higher number of residential animals, as compared to wave-exposed areas. Interestingly, despite the higher abundance of residential animals in sheltered areas, the exposed shore exhibited greater species diversity, with 18 species observed compared to 11 species in the sheltered area (Choi et al. 2015). Another report detailed an experiment involving the grazing impact of different organisms on *U. lactuca*. The experiment involved arranging grazers into four groups: amphipods, shrimps, crabs, and isopods. The grazing impact was then measured using different mesh cages. The shrimp and amphipods were the dominant grazers, collectively accounting for over 85% of all grazers in the experiment (Morgan et al. 2003).

The final category of grazers includes non-defined invertebrates. A study investigated the grazing of free-floating *U. lactuca* by invertebrates in a Danish estuary. The study found that in the inner part of the estuary, grazing by invertebrates was minimal, which allowed for the accumulation of biomass. However, in the outer part of the estuary, grazing significantly reduced the biomass of green algae (Geertz-Hansen et al. 1993). Another

study was conducted in a eutrophic Californian estuary, specifically focusing on the recruitment, transplant success, and abundance of *Ulva* spp., monitored along transects placed across the edge of the largest eelgrass (*Zostera marina*) bed. The major findings showed that changes in the abundance of *Ulva* spp. were significantly correlated with the densities of both small and large invertebrate groups. Cumulative grazing pressure, likely from the invertebrates, led to a decrease in the abundance of *Ulva* spp. in transplants. There was minimal natural recruitment of *Ulva* spp. observed inside the *Z. marina* bed. This information suggested that in this particular eutrophic estuary environment, factors such as invertebrate densities and grazing pressure played significant roles in determining the abundance and success of *Ulva* spp., with eelgrass beds potentially influencing the recruitment dynamics (Duplá 2020). These diverse invertebrate grazers, which caused considerable damage to various *Ulva* spp., highlighted that the damage level was a function of environmental conditions, e.g. location in a sheltered or wave-exposed shore, the presence of eutrophic conditions, and the presence of seagrasses, other seaweeds, or predators. Each of these factors had positive and negative effects on *Ulva* abundance.

## Harmful epiphytes

One study utilized near full-length 16S rRNA gene sequencing to analyze the diversity of bacterial biofilm communities on the surface of *U. australis*. The research focused on epiphytic bacterial communities, which encompassed both harmless and pathogenic forms. A total of 5293 sequences were obtained from six samples of *U. australis*, indicating a substantial dataset for analysis. The study found that there was inherent variability between libraries of *U. australis*. This variability suggested that the composition of bacterial communities on the surface of *U. australis* could vary significantly across different samples or locations. Despite the variability observed, the study did not detect a consistent sub-population of bacterial species across the samples. This implied that the composition of the bacterial communities on *U. australis* may be influenced by various factors and may lack a stable core set of species (Burke et al. 2011). Widescale anti-biofilm activity was identified among marine algae and their extracts (Behzadnia et al. 2024). Further studies identified the harmful potential of bacterial epiphytes. There are intricate relationships between macroalgae of the genus *Ulva* and the microorganisms that inhabit their living surfaces. These communities of microorganisms exhibit host-specific colonization patterns, meaning they tend to colonize specific species or varieties of *Ulva*. This colonization can have significant effects on the morphology and biology of the macroalga. Specifically, the microorganisms can influence characteristics such as cell wall components and defence mechanisms (Comba-González et al. 2016). Another study discussed the importance of polysaccharides in algae, particularly *Ulva*, and their role as a potential carbon and energy source for marine bacteria. Additionally, the presence of epiphytic bacteria associated with *Ulva* can produce enzymes capable of degrading these polysaccharides (Comba-González et al. 2016). The presence of epiphytic bacteria in *Ulva* spp. farming can indeed pose challenges to the cultivation process. While some epiphytic species may be beneficial or neutral, others can be detrimental to the desired *Ulva* crop. In case studies from Israel and India, it was observed that the epiphytic community in *Ulva* farming systems comprised not only unwanted algal species but also viruses, bacteria, fungi, and invertebrates. These organisms probably compete with *Ulva* for nutrients and space, potentially leading to reduced growth and yield (Ingle et al. 2018). There is limited evidence for pests, which are not defined as a

disease, nor as grazers, but as harmful epiphytes, which damage the seaweed and decrease its yield and value.

## Defence and management practices against the impacts of pests in *Ulva* cultivation

Management practices against *Ulva* pests can be divided into several categories. First is active human intervention, as presented in the following studies. Methanolic extracts of both *U. fasciata* and *U. lactuca* have experimentally demonstrated nymphicidal activity, i.e. direct biotic effects, they are capable of killing nymphs, and they have also been shown to reduce the relative growth rate of *Dysdercus cingulatus* which is a type of insect pest (Asha et al. 2012). An experiment involving the use of an acid wash improved pest removal efficiency without damaging the thalli of the red seaweed *Neopyropia*. The study also utilized *U. linza* and the diatom *Navicula* sp. as model pest (macro and micro) algae. The acid wash involved using hydrochloric acid (HCl) solutions of 4% and 8% for a duration of just 20 s. This treatment aimed to effectively remove the pests while minimizing damage to the seaweed thalli (Kang and Kim 2022). This example is cited as it could also have been employed for the active removal of pests from *Ulva* thalli. A study on controlling the limpet *Fissurella mutabilis* in *Ulva* aquaculture systems found that exposing these limpets to freshwater or CO<sub>2</sub>-saturated seawater for around 3 h in the laboratory effectively killed them with minimal impact on the cultivated *Ulva* spp. (Hansen et al. 2006). Allelopathy refers to the process by which one organism releases chemicals into the environment that affect the growth and development of other nearby organisms. In the following case, water-soluble extracts from *U. fenestrata* and *Ulvaria obscura* exhibited experimentally allelopathic properties, impacting the growth of *Ulva* and *Ulvaria*, as well as the development of *Fucus gardneri* and other algae, along with invertebrates (Nelson et al. 2003). An experiment observed the mortality of the gastropods *Littorina obtusata* over a period of one week, when exposed to various densities of *U. lactuca*. The mortality rates of *L. obtusata* varied from 0–100%. This indicated that under certain circumstances, the presence of *U. lactuca* had a significant impact on the survival of the gastropods. The study found that the depression of herbivory by *L. obtusata* was attributed to the exudate produced by *Ulva lactuca*. This suggested that certain chemicals, or compounds released by *U. lactuca*, were responsible for deterring herbivory by the gastropods. Differences in susceptibility to *Ulva* toxicity among littorinid species may be related to their feeding and habitat strategies. Generalist feeders might be less affected by the toxins produced by *U. lactuca* compared to specialist feeders (Peckol and Putnam 2017).

Several treatments employed against *Littorina* spp. in *U. lactuca* tanks were not entirely effective, as they were unable to kill the gastropods without causing damage to the *U. lactuca*. The treatments included sodium hypochlorite (0.1–1%) for 10 min, potassium iodide (0.5%) for up to 10 min, and kick-start, a commercial aquaculture disinfectant solution (0.25%) for 1–5 min. Despite these treatments, the gastropods persisted, and it seems that even prolonged exposure to freshwater agitation for an hour did not entirely eradicate them, although it may cause them to detach from their basiphyte (*U. lactuca*) without significant negative effects on the *U. lactuca* itself (Kerrison et al. 2016). Further research highlighted the potential of compounds isolated from *U. pertusa* as selective anti-algal agents. The research found that nine compounds derived from this alga exhibited dose-dependent effects on six different red tide microalgal species. The findings suggested that *U. pertusa*

could serve as a valuable source of bioactive compounds with anti-algal properties (Sun et al. 2018). More detailed studies are essential before recommending most of these treatments for a pest management program. However, the fresh water and *Ulva* extract treatments, mentioned above, seem to be ready for implementation at the commercial scale. It is possible that they are already used without necessarily being reported, because of the limited release of information at the commercial level.

A second management category can be proposed as the activity of certain probiotic bacteria with selective abilities against pathogens, as presented in the following studies. The reintroduction of a pre-isolated bacterial endophyte into its original host, *Ulva* sp., resulted in the manifestation of bioactive properties against the pathogen *Streptococcus iniae*. This reintroduction had a notable impact on the diversity and abundance of the microbiota associated with the algal thallus (Deutsch et al. 2023). A symbiotic relationship is presented between certain bacteria, specifically those of the genus *Pseudoalteromonas*, and *U. lactuca*. These bacteria act as epiphytes on the surface of the alga and demonstrated several beneficial effects: The bacteria prevented the settlement of invertebrate larvae and the germination of algal spores on the surface of *U. lactuca* thalli; in addition, these bacteria also inhibited the growth of various bacteria and fungi. From these protective abilities, the bacteria can be considered as probiotics to *U. lactuca*, providing benefits to their host (Egan et al. 2000). The role of *P. tunicata* and *Phaeobacter* sp. strain 2.10 in defence against fouling organisms on *U. australis* thalli surfaces was studied. The study demonstrated that even at low cell densities, these bacteria were effective in preventing fouling by fungi, bacteria, invertebrate larvae, and algal spores and gametes (Rao et al. (2007). Isolates of *Pseudoalteromonas* obtained from the surface of *U. lactuca* exhibited both anti-bacterial and anti-diatom activities. Additionally, members of the genera *Bacillus*, *Vibrio*, and *Shewanella* from the same source predominantly possessed anti-diatom activities. Taken together, these results suggest that a significant portion of bacterial isolates from the surface of tropical *U. lactuca* possess antibiotic properties that could potentially inhibit surface fouling of their thalli by diatoms (Kumar et al. 2011). It seems like strains UL12T and UL13 of the genus *Pseudoalteromonas* exhibited antifouling properties by inhibiting the germination of algal spores and the settlement of invertebrate larvae. This could have potential applications in industries related to marine infrastructure, aquaculture, and marine conservation (Egan et al. 2001). The epiphytic bacterial community of *U. lactuca* from the Colombian coast was investigated through gene sequencing. The most abundant phyla within this bacterial community were identified to be Proteobacteria, Bacterioidetes, Cyanobacteria, Deinococcus-Thermus, and Actinobacteria. Additionally, differences in the composition of the bacterial community across different years were observed. This finding implied that environmental factors, such as temperature changes, can have a significant impact on the microbial communities associated with marine organisms like *U. lactuca* (Comba González et al. 2021). Notwithstanding the above findings, it is not known if any aspects of these have been commercialized, producing additional management tools for the farmers of *Ulva*. These findings may be useful in applied research for the potential management of aquaculture diseases, using the antifouling activity of defined bacterial strains. At this stage, more detailed studies are essential before commercialization.

A third category of management of cultivated *Ulva* spp. could be the effects of environmental changes on pests, as presented in the following studies. One study focused on the impact of increased ocean acidification and eutrophication on grazing rates of snails (*Littorina littorea*) on thalli. The findings suggested that increased ocean acidification, which leads to higher pCO<sub>2</sub> levels, resulted in reduced grazing rates on thalli by the snails. Despite this, eutrophication did not seem to affect the consumption rates of tissues by the



snails. One notable observation was that snails fed almost exclusively on *Ulva* indicating a preference for this alga. Interestingly, despite the differences in environmental conditions (such as increased ocean acidification and eutrophication), there was a similarity in consumption rates of *Ulva* and *Fucus* tissues across all treatments. This suggested that the physical characteristics of algal tissues, rather than their chemical composition, may be the primary drivers of dietary shifts in response to changing environmental conditions caused by climate change (Ober et al. 2022). Warming and acidification have led to detrimental effects on the survival of grazers. Within the following study, there were observed differences in the consumption rates of the macroalga *U. rigida* between different grazers. Specifically, the amphipod species *Melita palmata* demonstrated a stronger grazing capability compared to the gastropod *Gibbula umbilicalis*, which was also the most affected by the climate stressors of warming and acidification. The strength of interactions between macroalgae and herbivores (grazers) was significantly influenced by the temperature gradient. Acidification, in addition to warming, was observed to lower the optimal thermal threshold for macroalgal-herbivore interactions (Sampaio et al 2017). In this acidifying system, decreased consumption, coupled with increased growth of macroalgae, may ultimately enhance algal growth and spread. Therefore, in this category, further observations rather than implementation are necessary.

This article has consolidated a number of studies which will be useful in the applied management of aquaculture diseases, grazers, and harmful epiphytes for cultivation of the foliose green alga *Ulva*. The studies cited show that major defence methods can be used by human management strategies. Several of the human intervention tools which are ready for commercial application are mentioned in the above categories and could already be in operation. The allelopathic bioactivities of supporting bacteria need further studies and climate-related changes occurring rapidly in natural conditions need to be closely monitored for clues to developing situations which may prevail in cultivation scenarios. As with any other form of farming, the future successful development and scale-up of *Ulva* cultivation, on land and in the sea, will definitely have to consider, implement, and develop strategies for the control and management of *Ulva* pests.

**Author contribution** MF wrote the manuscript. ATC added and revised prior to submission. All authors reviewed the manuscript.

**Data availability** No data sets were generated or analyzed during this exercise.

## Declarations

**Ethics approval** The article does not require any novel work on humans or animals.

**Competing interests** The authors declare no competing interests.

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