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RESEARCH

Do toxic epiphytic microalgae compromise the consumption of edible macroalgae?

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Abstract

The growing global demand for farmed macroalgae highlights the need to better understand potential contaminant loads, including toxins from harmful algal blooms, and their implications to human health. In this study, the green macroalga *Ulva rigida* was co-cultivated with the epiphytic dinoflagellate *Prorocentrum lima* to determine whether toxins produced by the toxic dinoflagellate accumulate in the macroalgae and assess the efficacy of post-harvest processing techniques to reduce or eliminate the risk of toxins contamination. *Ulva rigida* (60 g wet weight) was maintained under controlled laboratory conditions in sterile F/2 medium and in co-culture with *P. lima.* Macroalgae were divided into two treatments: a) no processing; b) processing. Samples were analysed by LC-MSMS to detect okadaic acid (OA) and dinophysistoxin-1 (DTX1). High toxins levels were detected after 7 days of exposure to *P. lima.* Contrastingly, the post-harvesting process of washing and scrubbing was efficient in reducing toxins loads, indicating that lipophilic toxins were surface bound and can be easily eliminated using efficient post-harvest processes. The results indicate that epiphytic toxic microalgae may jeopardize the consumption of macroalgae, particularly if appropriate post-harvest processes are not applied to ensure the safety of farmed macroalgae for consumers.

Keywords *Ulva rigida* · Harmful algal blooms · Marine biotoxins · Aquaculture · Post-harvest processing · Food Safety

Introduction

Aquaculture has a crucial role in global food production, supplying the demand for ever-increasing nutrient requirements, due to population growth and environmental challenges (FAO 2024). For many decades, macroalgae products have been traditionally used as food alongside many applications in various sectors. In recent years, the demand for macroalgal products has been rising, with the global market expected to increase 9.1% until 2027 (Khan et al. 2021). Macroalgae aquaculture is also growing amidst this demand, as a standalone production, co-production, or part of integrated multi-trophic aquaculture (IMTA) where species from different trophic levels, such as fish, bivalves, and macroalgae, are produced together for efficient nutrient recycling and diversification of production (Soto 2009; Araújo et al. 2016; Chopin 2018; Correia et al. 2020; Nederlof et al. 2022; Glauco et al. 2024).

Macroalgae aquaculture has several advantages, as macroalgae counteract the process of eutrophication given their bioremediation potential, provide raw materials for human

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and animal nutrition and health, with potential application across pharmaceuticals, cosmetics, green chemical processes (e.g., surfactants), bioplastics, construction materials and textiles (Queirós et al. 2021; Massocato et al. 2022; Moreira et al. 2024; Corrigan et al. 2025). However, the global macroalgae aquaculture currently faces ecological pressures driven by environmental factors, such as increasing seawater temperatures due to climate change (Zhang et al. 2023; Veenhof et al. 2024). Additionally, ocean warming tends to influence the frequency and abundance of harmful algal blooms (HABs) that potentially compromise food safety in aquaculture production (Aquino-Cruz et al. 2018; Ibghi et al. 2024).

Traditionally, HABs are associated with the contamination of shellfish that may act as phycotoxin vectors to humans and cause several types of poisoning, many times described according to their symptoms, such as diarrhetic, paralytic and amnesic shellfish poisoning (Braga et al. 2023). In addition to filter-feeding shellfish like mussels, clams and oysters there is growing evidence that macroalgae may also harbour toxic epiphytic microalgae and act as toxin vectors to humans through their consumption (Gharbia et al. 2017; Díaz et al. 2022).

While there is an established regulatory limit for marine biotoxins in bivalves by Codex Alimentarius and European Union standards, corresponding guidelines for macroalgae do not currently exist (Banach et al. 2020; Lähteenmäki-Uutela et al. 2021). Several toxins have been reported in macroalgae, notably palytoxins and cyclic imines detected in species of brown and red macroalgae, and domoic acid detected in red macroalgae including *Chondria armata* (Banach et al. 2020). Kainic acid, a neurotoxic compound that has been detected sometimes in *Palmaria palmata*, appears in varying concentrations, but standards related to human health remain undefined (Banach et al. 2020). Lack of occurrence data, undefined regulatory thresholds, variability in production and accumulation of these toxins emphasize the need for scientific monitoring and risk assessment to ensure the safety of macroalgae for human consumption and feedstock for animals.

Among macroalgae, the genus *Ulva* has received much attention due to its relatively high protein content and potential for co-cultivation in Integrated Multi-Trophic Aquaculture (IMTA) systems (Queirós et al. 2021; Nederlof et al. 2022; Simon et al. 2022; Glauco et al. 2024). At the same time, the dinoflagellate *Prorocntrum lima* produces okadaic acid (OA) and dinophysistoxins (DTX) that accumulate in shellfish, leading to diarrhetic shellfish poisoning (DSP) (Ye et al. 2022), making it essential to understand how these organisms may interact in shared environments.

When toxin-producing dinoflagellates, like *P. lima,* grow within the vicinity of a macroalgae farm or IMTA systems, they can act as vectors for higher trophic levels (Gharbia et al. 2017; Brown et al. 2020). Thus, consumers' increasing interests in macroalgae in Europe and North America, as well as the traditional consumption in Asian countries, pose new questions whether there are food safety implications for consuming farmed macroalgae, when consumed fresh with inadequate processing (Rosa et al. 2020; Kumar & Sharma 2021; Lähteenmäki-Uutela et al. 2021). Monitoring dinoflagellates like *P. lima* is, therefore, an essential step in ensuring seafood safety (Sahraoui et al. 2013; Brown et al. 2020).

While numerous strategies are a potential solution to reduce toxin burdens in shellfish by means of washing or purging (Martinez-Albores et al. 2020; Bian et al. 2024), toxin removal strategies for macroalgae processing remain largely unexplored in view of growing concerns surrounding climate change, food security and its increased demand for food. To fill this gap, and in line with similar procedures in depuration strategies (Gémin et al. 2020), it was hypothesized that rigorous rinsing of macroalgae complemented with scrubbing could substantially reduce toxins levels, implying that even a simple handling procedure at harvest may be sufficient to lessen public health risks. The results will therefore give new insights to farmers and policymakers alike for post-harvesting and processing strategies.

In this study, the macroalga *Ulva rigida* was maintained under laboratory conditions and exposed to the epiphytic toxin-producing dinoflagellate *P. lima,* to understand if macroalgae accumulate *P. lima* toxins in the tissues and act as a potential toxin vector to consumers. Understanding the dynamics of toxins in macroalgae is crucial for a risk assessment and regulatory framework of the rapidly expanding macroalgae industry (Lähteenmäki-Uutela et al. 2021). This study also investigates the effect of a post-harvesting process to reduce toxins load and minimize the risks for consumers.

Materials and methods

Culture conditions

Ulva rigida (3 kg) were collected from AlgaPlus facility (Aveiro, Portugal; 40.6126° N, 8.6740° W), and transported to LABVIVOS- Live Marine Organisms Laboratory (IPMA, Algés, Portugal), thoroughly rinsed to remove debris, and acclimated for one week in F/2 medium (Guillard & Ryther, 1962) at 19 ± 1 °C under a 14:10 h light: dark cycle using an Aquabar T-series single blue LED lamp from Tropical Marine Centre Iberia (São Julião do Tojal, Portugal), providing a mean irradiance of 25 µmol photons m^{-2} s^{-1}.

Prorocentrum lima strain IPMA-PRMD07 from the microalgae culture collection of the Portuguese Institute for the Sea and Atmosphere (IPMA), isolated from Madeira Island (32°39′N 16°55′W) was used for this study. Clonal and non-axenic cultures were maintained in vented T-flask (50 cm^2) (Sarstedt, Germany) in enriched natural seawater F/2 medium (salinity 33 ppt), at 24 ± 1 ℃ under a 12:12 h light: dark cycle (Fitoclima 600 PL, Aralab, Portugal), and a photosynthetic photon flux density of 50–60 µmol photons m^{-2} s^{-1} (PPFD) (18W, Osram, Germany). The seawater used in all the experiments was from the same batch. Before use, it was pre-filtered in Whatman-GF/C glass fiber filters and 0.22 µm cellulose filters (Whatman, UK), followed by autoclave sterilization. Nutrients were added by filter sterilization (Whatman, UK).

Experimental design

The green macroalga *Ulva rigida* was selected as the experimental model due to it is relevance in aquaculture (Bolton et al. 2016; FAO 2024). Its high surface area to volume ratio makes it particularly efficient to test accumulation of toxins in tissues. The benthic dinoflagellate *P. lima* was used as the epiphytic toxin-producing dinoflagellate, being a well-documented producer of okadaic acid (OA) and dinophysistoxin-1 (DTX1) (Aquino-Cruz et al. 2018; Ye et al. 2022; Ibghi et al. 2024). Therefore, the *U. rigida* and *P. lima* system provides a biologically realistic framework for examining the dynamics of benthic phycotoxin accumulation and persistence in macroalgal tissues under natural exposure conditions.

At the time of collection, a baseline analysis was carried out to ensure the absence of *P. lima*. The analysis confirmed that the *U. rigida* collected were toxin-free. Samples were collected at three time points, in triplicate: T0 (start of the study, day 3); T3 (midpoint of the study, day 3); T7 (final day of the study, day 7). At each sampling point, 30 g of *Ulva* was removed from the beaker and the beaker was removed.

A total of 3 glass beakers (3 L capacity each) (Fig. 1) with 60 g of *Ulva* and 2040 cells mL^{-1} of *P. lima* each were randomly assigned to two treatments:

1) No Processing (NP): The algae were dried on paper towels and immediately stored at − 80 °C for freeze-drying.
2) Processed (P): The algae were vigorously shaken for 2 min in 50 mL seawater, followed by 10 min in sterile freshwater and by scrubbing with a cell scraper, dried on paper towels, and then frozen at − 80 °C for subsequent freeze-drying.

No medium renewal was performed during the 7-day experiment. Abiotic parameters (salinity 32 ± 1, pH 8.0 ± 0.1, and temperature 19 ± 1 °C) were monitored daily with a portable multiparameter (HI98494, Hanna Instruments, Italy), along with nitrogen compounds (nitrate, nitrite, and ammonium).

Additionally, 50 mL of the culture medium was sampled at day 3 and day 7 from each treatment. The samples were centrifuged at 5,200 × *g* for 10 min. Subsamples of culture medium were preserved in Lugol's solution (Karlson et al. 2010) and counted under a light microscope using a Palmer-Maloney counting chamber to verify *P. lima* cell densities.

Toxin analysis

Toxins extraction

A total of 1.0 ± 0.1 g of freeze-dried sample was placed into 50-mL polypropylene centrifuge tubes and 20.0 mL of 100% methanol was added and mixed thoroughly in a vortex for 5 min. Following this procedure, the tubes were centrifuged at ≥ 3600 × *g* for 10 min and supernatant was

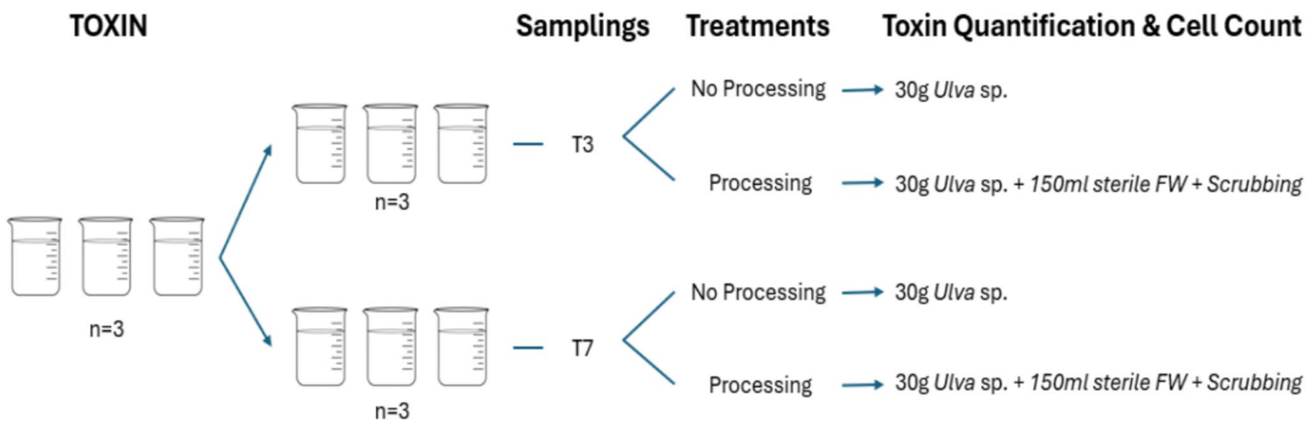

Fig. 1 Experimental design

filtered through a 0.2 µm syringe filter and stored at – 20 ℃ until LC–MS/MS analysis.

Toxins determination by liquid chromatography with tandem mass spectrometry detection (LC–MS/MS)

The LC–MS/MS equipment consisted of an Agilent 1290 Infinity liquid chromatograph coupled to a triple quadrupole mass spectrometer Agilent 6470 (Agilent Technologies, Germany). The chromatographic separation was conducted as described in Braga et al. (2021) with a Zorbax SB- C8 RRHT column (2.1 × 50 mm, 1.8 µm), protected with a guard column (2.1 × 5 mm, 1.8 µm). The mobile phase A was water with 2 mM ammonium formate (Sigma-Alrich, USA) and 50 mM formic acid (LC–MS, Carlo Erba, Germany) and the mobile phase B was 95% acetonitrile (LC–MS grade, Carlo Erba) with 2 mM ammonium formate and 50 mM formic acid. An elution gradient at a flow rate of 0.4 mL min^{-1} was used as follows: 0–3 min, gradient from 88 to 50% eluent A; 3–6.5 min gradient 50 to 10% eluent A; 6.5–8.9 min 10% eluent A; 8.9–10 min, gradient 10 to 88% eluent A. The detection was carried out in Multiple Reaction Monitoring (MRM) acquisition mode. Two MRM transitions were monitored in negative polarity: m/z 803 > 255 and m/z 803 > 563 for OA and m/z 817 > 255 and m/z 817 > 563 for DTX1, quantification and confirmation, respectively. Five calibration standard solutions ranging from 2.0 to 22.0 ng mL^{-1} with a correlation > 0.990 was set up for quantification using a matrix match calibration and certified OA and DTX1 reference standards purchased from CIFGA (Lugo, Spain).

Statistical analyses

All statistical analyses were performed using R software (version 4.3.2; R Core Team, Vienna, Austria). Toxin concentrations of DTX1 and OA (ng g^{-1} fresh weight) were analysed using a two-way ANOVA to evaluate the main effects of sample processing (processed vs. non-processed), sampling day (Day 3 vs. Day 7), and their interaction. This approach was used to test whether sample processing influenced measured toxin concentrations differently across exposure times. Each treatment combination included three biological replicates (n = 3). Prior to analysis, data were $\log_1(x + 1)$ transformed to correct for right-skewness, stabilise variances, and allow inclusion of zero values. Model assumptions of normality and homogeneity of variances were verified by residual inspection, Shapiro–Wilk tests, and Levene's test (car package).

Results

DTX1 and OA content was detected only in the non-processed toxin-treated groups. In the TNP3 treatment (no processing treatment day 3), DTX1 averaged 64.9 ± 15.3 ng g^{-1} fresh weight (FW) and OA averaged 211.3 ± 17.2 ng g^{-1} FW (n = 3). In the TNP7 treatment (no processing treatment day 7), the values increased to 82.2 ± 12.3 ng g^{-1} FW for DTX1 and 301.5 ± 40.1 ng g^{-1} FW for OA (n = 3) (Table 1). For DTX1, processing was significantly efficient ($p < 0.001$), while there was no significant time-dependent accumulation ($p = 0.19$). For OA, processing also showcased statistical significance ($p < 0.001$) and in contrast to DTX1, displayed a significant time-dependent accumulation ($p = 0.005$).

Decrease in toxin concentration in the cell medium, was associated with a decrease in *P. lima* cells in *Ulva* sp. surface (Fig. 2).

Discussion

The present work shows that *U. rigida* when exposed to *P. lima* potentially poses a risk to food safety, however, it also shows a significant decrease of toxins when post-harvest

Table 1 Mean (± SD) concentrations of DTX1 and OA (ng g^{-1} fresh weight) in processed and non-processed samples of *Ulva rigida* on days 3 and 7, and corresponding p-values from the two-way ANOVA ($\log_1$-transformed data)

Toxin	Processing	Day	Mean ± SD (ng g^{-1} FW)	p (Processing)	p (Day)
DTX1	Processed	3	< LQ	**< 0.001**	0.186
		7	< LQ		
	Non-processed	3	64.9 ± 15.3		
		7	82.2 ± 12.3		
OA	Processed	3	< LQ	**< 0.001**	**0.005**
		7	< LQ		
	Non-processed	3	211 ± 17.2		
		7	301 ± 40.1		

Significant effects ($p < 0.05$) are shown in bold. LQ, limit of quantification (0.0107 ng mL^{-1})

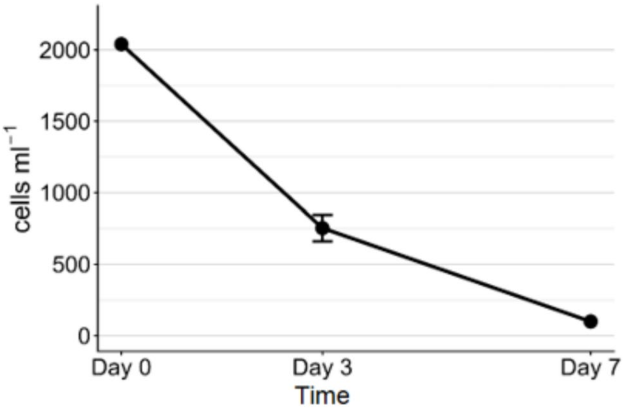

Fig. 2 Prorocentrum lima cell medium count (cells mL.$^{-1}$) at the 3 sampling points (T0, T3, T7) of the unprocessed treatment 3

processing is implemented. This is in accordance with recent evidence in other systems of macroalgae (Rhodes et al. 2014; Hachani et al. 2018; Gémin et al. 2020; Park et al. 2020) in which epiphytic microalgae pose potential threats to aquaculture operations. An important observation from our study was that toxins appeared primarily bound to macroalgae surface rather than accumulated internally within the macroalgae tissues. The significant reduction of toxins achieved through rigorous rinsing and mechanical scrubbing strongly supports the hypothesis of surface association.

In this study, the post-harvest technique applied is a simple, commercially applicable solution in the form of regular post-harvest rinsing plus scrubbing. This method and its wide-reaching applications could provide a roadmap to optimize macroalgae safety, ensuring that this quick-growing resource can meet food safety requirements sustainably around the planet, supporting the ever-growing world population.

Whilst in a previous study (Gémin et al. 2020) shaking and rising in filtered seawater were used to dislodge epiphytic cells without showing remarkable differences, our results indicate that adding a scrubbing step enabled a significant reduction in surface-associated toxins, showing significant differences between unprocessed and processed treatments.

Unprocessed samples at day 7 revealed significantly higher content of toxins compared to those at day 3 when looking into OA. Such time-dependent accumulation is in line with the evidence that epiphyte macroalga associations become more consolidated over time (Brown et al. 2020; Gémin et al. 2020). It is also worth considering that due to the culture medium not being renewed this likely promoted the accumulation of toxic metabolites. Moreover, studies indicate that *P. lima* can achieve higher production levels during the stationary phase (Aquino-Cruz et al. 2018). In open cultures or systems with medium renewal, the outcomes might therefore differ.

Due to the growing macroalgae aquaculture industry at a global scale (FAO 2024), our results indicate that standardized post-harvest processing procedure are relevant to address the reduction of potential toxin accumulation in the food-grade macroalgae, particularly when considered at risk for contamination. As consumer demand for macroalgae and marketplace competition increases, it is crucial to ensure food safety compliance and a consumer perception that macroalgae products are safe and toxin free. From a food safety perspective, novel post-harvest processes that reduce toxin content can enhance regulator, business, and consumer confidence. In established macroalgae economies, such as France, Japan, and China, the current regulatory agencies already set limits for heavy metals and non-safe chemical substances (Lähteenmäki-Uutela et al. 2021; Guo et al. 2023; CEVA n.d.). With maximum allowed limits for toxin (such as OA or DTX), combined with explicit requirements for post-harvest rinsing, the sector can proactively take action to prevent not only algal toxin's introduction to human or animal food streams, but also contribute to create a more robust food safety network. Such strategies hold high marketplace rewards.

Compared to bivalves, where complex depuration procedures need to be employed owing to lipophilic penetration of toxins into tissues (Braga et al. 2023), macroalgae take advantage of easy-to-implement, yet highly efficient, mechanical, or freshwater rinsing procedures.

However, it is important to carefully assess whether the toxin concentrations detected in macroalgae may represent a potential risk to human health. According to European Union regulatory standards (Regulation EC No. 853/2004), the maximum permitted levels of okadaic acid (OA) and related diarrhetic toxins in bivalve molluscs intended for human consumption are established at 160 ng OA equivalents g^{-1}. In the present study, toxin concentrations detected in unprocessed macroalgae samples exceeded this regulatory limit (Table 1). Nevertheless, it should be noted that this safety threshold was specifically established for shellfish consumption, and its direct applicability to macroalgae consumption remains uncertain due to differences in consumption patterns, exposure scenarios, and matrix effects. It is also important to note that diarrhetic shellfish toxins are thermally stable compounds that are not readily degraded during conventional cooking or processing procedures, which may increase the likelihood of dietary exposure when contaminated products, including macroalgae, are consumed. As this study was performed under controlled laboratory conditions, the findings should be interpreted within the scope of the experimental design and further studies are required to evaluate the toxicological relevance and public health implications of toxin levels in macroalgae intended for human consumption.

Conclusions

This study shows that *Ulva,* when exposed to *P. lima,* accumulates surface-bound lipophilic toxins, which can be removed through a simple post-harvest rinsing and scrubbing procedure. Since toxin levels in unprocessed samples exceeded EU limits, findings highlight both a food safety concern and the need for standardised post-harvest processing protocols in the expanding macroalgae industry.

To build on such promising observations, subsequent studies would need to undertake a range of key areas, such as systematic studies of varying durations of washing, temperatures, and even mild chemical treatments that would calibrate protocols to release maximum toxin without compromising algae integrity and environmental sustainability. Such knowledge would unlock more sophisticated, species-specific cleaning processes; interfacing dynamic rinsing processes to live surveillance systems for *P. lima* and other toxin producers' epiphytic dinoflagellates, which in turn would change large-scale macroalgae farms response to environmental variance. Such dynamic management would allow adjustment of cleaning processes, analogous to strategies used in shellfish depuration. With monitoring programs alongside effective processing methods, producers can ensure that their products are safe, boosting consumers' confidence in this ever-growing market.

Author contributions António Marques, Pedro R. Costa and Maria João Xavier contributed to the study conception and design. Material preparation, data collection, and analysis were performed by Tomás Chainho, Rui Cereja, Miguel Barbosa, Maria João Xavier, and Alícia Pereira. Resources were provided by Inês Oliveira and Madalena C. Mendes. The first draft of the manuscript was written by Tomás Chainho. Supervision, project administration, and funding acquisition were carried out by António Marques and Pedro R. Costa. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability All data supporting the findings of this study are available within the paper.

Declarations

Conflict of interests The authors declare no competing interests.

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References

Aquino-Cruz A, Purdie DA, Morris S (2018) Effect of increasing sea water temperature on the growth and toxin production of the benthic dinoflagellate *Prorocentrum lima*. Hydrobiologia 813:103–122

Araújo M, Rema P, Sousa-Pinto I, Cunha LM, Peixoto MJ, Pires MA, Seixas F, Brotas V, Beltrán C, Valente LMP (2016) Dietary inclusion of IMTA-cultivated *Gracilaria vermiculophylla* in rainbow trout (*Oncorhynchus mykiss*) diets: effects on growth, intestinal morphology, tissue pigmentation, and immunological response. J Appl Phycol 28:679–689

Banach JL, Hoek-van den Hil EF, van der Fels-Klerx HJ (2020) Food safety hazards in the European seaweed chain. Compr Rev Food Sci Food Saf 19:332–364

Bian Y, Feng X, Zhang Y, Du C, Wen Y (2024) Marine toxins in environment: recent updates on depuration techniques. Ecotoxicol Environ Saf 284:116990

Bolton JJ, Cyrus MD, Brand MJ, Joubert M, Macey BM (2016) Why grow *Ulva*? Its potential role in the future of aquaculture. Perspect Phycol 3:113–120

Braga AC, Marçal R, Marques A, Guilherme S, Vilariño Ó, Martins JML, Gago-Martínez A, Costa PR, Pacheco M (2021) Invasive clams (*Ruditapes philippinarum*) are better equipped to deal with harmful algal blooms toxins than native species (*R. decussatus*): evidence of species-specific toxicokinetics and DNA vulnerability. Sci Total Environ 767:144887

Braga AC, Rodrigues SM, Lourenço HM, Costa PR, Pedro S (2023) Bivalve shellfish safety in Portugal: variability of faecal levels, metal contaminants and marine biotoxins during the last decade (2011–2020). Toxins 15:91

Brown AR, Lilley M, Shutler J, Lowe C, Artioli Y, Torres R, Berdalet E, Tyler CR (2020) Assessing risks and mitigating impacts of harmful algal blooms on mariculture and marine fisheries. Rev Aquac 12:1663–1688

Chopin T (2018) Integrated multi-trophic aquaculture (IMTA): a responsible approach to farming our waters. Int Aquafeed 21:16–17

Correia M, Azevedo IC, Peres H, Magalhães R, Oliva-Teles A, Almeida CMR, Guimarães L (2020) Integrated multi-trophic aquaculture: a laboratory and hands-on experimental activity to promote environmental sustainability awareness and value of aquaculture products. Front Mar Sci 7:156

Corrigan S, Cottier E, Lim P E, Brodie J (2025) The State of the World's Seaweeds 2025. [Data set]. Nat Hist Mus. https://doi.org/10.5519/4ln9oqk7

Díaz PA, Álvarez G, Pizarro G, Blanco J, Reguera B (2022) Lipophilic toxins in Chile: history, producers and impacts. Mar Drugs 20:122

Edible algae—Regulatory update (n.d.) CEVA. Retrieved 3 December 2025, from https://www.ceva-algues.com/en/document/edible-algae-regulatory-update/

FAO (2024) The state of world fisheries and aquaculture 2024. FAO, Rome

Gémin M-P, Réveillon D, Hervé F, Pavaux A-S, Tharaud M, Séchet V, Bertrand S, Lemée R, Amzil Z (2020) Toxin content of *Ostreopsis* cf. *ovata* depends on bloom phases, depth and macroalgal substrate in the NW Mediterranean Sea. Harmful Algae 92:101727

Gharbia HB, Yahia O-D, Cecchi P, Masseret E, Amzil Z, Herve F, Rovillon G, Nouri H, M'Rabet C, Couet D, Triki HZ, Laabir M (2017) New insights on the species-specific allelopathic interactions between macrophytes and marine HAB dinoflagellates. PLoS ONE 12:e0187963

Glauco F, He P, Chen Z (2024) Combine effects of multiple environmental factors on growth and nutrient uptake of euryhaline seaweed growth in integrated multitrophic aquaculture systems. Algal Res 77:103347

Guo Y, Lundebye A-K, Li N, Ergon Å, Pang S, Jiang Y, Zhu W, Zhao Y, Li X, Yao L, Wang L, Aakre I (2023) Comparative assessment of food safety regulations and standards for arsenic, cadmium, lead, mercury and iodine in macroalgae used as food and feed in China and Europe. Trends Food Sci Technol 141:104204

Hachani MA, Dhib A, Fathalli A, Ziadi B, Turki S, Aleya L (2018) Harmful epiphytic dinoflagellate assemblages on macrophytes in the Gulf of Tunis. Harmful Algae 77:29–42

Ibghi M, Rijal Leblad B, L'Bachir El Kbiach M, Aboualaalaa H, Daoudi M, Masseret E, Le Floc'h E, Hervé F, Bilien G, Chomerat N, Amzil Z, Laabir M (2024) Molecular phylogeny, morphology, growth and toxicity of three benthic dinoflagellates *Ostreopsis* sp. 9, *Prorocentrum lima* and *Coolia monotis* developing in Strait of Gibraltar, Southwestern Mediterranean. Toxins 16:49

Karlson B, Godhe A, Cusack C, Bresnan E (2010) Microscopic and molecular methods for quantitative phytoplankton analysis. Intergov Oceanogr Comm Man Guides 55:5–12

Khan RM, Salehi B, Mahdianpari M, Mohammadimanesh F, Mountrakis G, Quackenbush LJ (2021) A meta-analysis on harmful algal bloom (HAB) detection and monitoring: a remote sensing perspective. Remote Sens 13:4347

Kumar MS, Sharma SA (2021) Toxicological effects of marine seaweeds: a cautious insight for human consumption. Crit Rev Food Sci Nutr 61:500–521

Lähteenmäki-Uutela A, Rahikainen M, Camarena-Gómez MT, Piiparinen J, Spilling K, Yang B (2021) European Union legislation on macroalgae products. Aquacult Int 29:487–509

Martinez-Albores A, Lopez-Santamarina A, Rodriguez JA, Ibarra IS, Mondragón A, Miranda JM, Lamas A, Cepeda A (2020) Complementary methods to improve the depuration of bivalves: a review. Foods 9:129

Massocato TF, Robles-Carnero V, Moreira BR, Castro-Varela P, Pinheiro-Silva L, Oliveira WdaS, Vega J, Avilés A, Bonomi-Barufi J, Rörig LR, Figueroa FL (2022) Growth, biofiltration and photosynthetic performance of *Ulva* spp. cultivated in fishpond effluents: an outdoor study. Front Mar Sci 9:981468

Moreira A, Cruz S, Marques R, Cartaxana P (2024) The underexplored potential of green macroalgae in aquaculture. Rev Aquacult 14:5–26

Nederlof MAJ, Neori A, Verdegem MCJ, Smaal AC, Jansen HM (2022) *Ulva* spp. performance and biomitigation potential under high nutrient concentrations: implications for recirculating IMTA systems. J Appl Phycol 34:2157–2171

Park J, Hwang J, Hyung J-H, Yoon EY (2020) Temporal and spatial distribution of the toxic epiphytic dinoflagellate *Ostreopsis* cf. *ovata* in the coastal waters off Jeju Island, Korea. Sustainability 12:5864

Queirós AS, Circuncisão AR, Pereira E, Válega M, Abreu MH, Silva AMS, Cardoso SM (2021) Valuable nutrients from *Ulva rigida*: modulation by seasonal and cultivation factors. Appl Sci 11:6137

Regulation (EC) (2024) No 853/2004 of the European Parliament and of the Council of 29 April 2004 Laying down Specific Hygiene Rules for Food of Animal Origin . http://data.europa.eu/eli/reg/2004/853/2024-11-09/eng

Rhodes L, Smith K, Papiol GG, Adamson J, Harwood T, Munday R (2014) Epiphytic dinoflagellates in sub-tropical New Zealand, in particular the genus *Coolia* Meunier. Harmful Algae 34:36–41

Rosa J, Lemos MFL, Crespo D, Nunes M, Freitas A, Ramos F, Pardal MÂ, Leston S (2020) Integrated multitrophic aquaculture systems – potential risks for food safety. Trends Food Sci Technol 96:79–90

Sahraoui I, Bouchouicha D, Mabrouk HH, Hlaili AS (2013) Driving factors of the potentially toxic and harmful species of *Prorocentrum* Ehrenberg in a semi-enclosed Mediterranean lagoon (Tunisia, SW Mediterranean). Mediterr Mar Sci 14:353-362

Simon C, McHale M, Sulpice R (2022) Applications of *Ulva* biomass and strategies to improve its yield and composition: a perspective for *Ulva* aquaculture. Biology 11:1539

Soto D (2009). *Integrated mariculture: A global review*. FAO Fisheries and Aquaculture Technical Paper 529. FAO, Rome

Veenhof RJ, Burrows MT, Hughes AD, Michalek K, Ross ME, Thomson AI, Fedenko J, Stanley MS (2024) Sustainable seaweed aquaculture and climate change in the North Atlantic: challenges and opportunities. Front Mar Sci 11:1483330

Wu D, Chen J, Wang J, He X, Xin M, Wang B (2020) Monitoring and warning of lipophilic marine algal toxins in mariculture zone based on toxin profiles of phytoplankton. Ecotoxicol Environ Saf 197:110647

Ye MH, Li DW, Cai QD, Jiao YH, Liu Y, Li HY, Yang WD (2022) Toxic responses of different shellfish species after exposure to *Prorocentrum lima*, a DSP toxins producing dinoflagellate. Toxins Basel 14:7

Zahir M, Su Y, Shahzad MI, Ayub G, Rahman SU, Ijaz J (2024) A review on monitoring, forecasting, and early warning of harmful algal bloom. Aquaculture 593:741351

Zhang YY, Yu SE, Wang WL, Yang LE, Lu QQ, Xie CT, Liu T, Dong YW (2023) Temperature sensitivity of marine macroalgae for aquaculture in China. Aquaculture 567:739262

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