



Advances in Research on the Habitat-Disturbing Effects of *Ulva Prolifera* and Their Consequences for the Ecology of *Apostichopus Japonicus* Aquaculture Ponds

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Abstract: The sustained outbreaks of *Ulva prolifera* green tides in the Yellow Sea have become one of the most severe ecological disasters in China's coastal waters. During large-scale senescence and decomposition, substantial amounts of ammonia nitrogen, sulfides, and dissolved organic matter are released, triggering hypoxia, acidification, and sediment deterioration, thereby imposing significant stress on semi-enclosed *Apostichopus japonicus* aquaculture ponds. At present, systematic studies on how green tides across their entire life cycle—especially during senescence—specifically perturb the pond's benthic environment and, in turn, affect *A. japonicus* physiological homeostasis and health remain relatively weak. This paper systematically reviews the occurrence characteristics of Yellow Sea green tides, the biogeochemical processes during *Ulva* senescence and their potential impacts on the aquaculture environment, and integrates findings from *A. japonicus* ecology and physiological ecology. The aim is to elucidate the stress mechanisms by which green tide disasters affect pond aquaculture systems for *A. japonicus*, and to provide theoretical support for establishing ecosystem-health-based risk warning and control strategies in aquaculture.

Keywords: *Ulva prolifera*; *Apostichopus japonicus*; environmental stress; aquaculture ponds; water quality degradation

1 INTRODUCTION

Currently, the *Ulva prolifera* green tide in the Yellow Sea has evolved into a recurrent ecological crisis. Previous scholarly work has primarily focused on the provenance mechanisms, spatiotemporal succession patterns, and the associated hydrological and physicochemical characteristics[1, 2]. However, environmental responses triggered by the decay and decomposition of large macroalgae are often difficult to observe directly, resulting in a relatively weak systematic assessment of the biogeochemical processes during the senescence phase. Each year from July to August, the large algal bloom enters its senescence stage, with millions of tonnes of algal biomass accumulating in the nearshore waters of Shandong. Among them, more than a million tonnes of *Ulva* ultimately settle to the seabed and continue to decompose and mineralize there. The accumulation and transformation of these organic residues not only reshape local habitats but also impose significant economic impacts on coastal tourism and nearshore aquaculture industries[3, 4].

Massive accumulations of *Ulva* and other vigorous green-tide macroalgae continuously release ammonia nitrogen, reactive phosphorus, and sulfur-containing constituents into the water column during mineralization. These dissolved substances markedly accelerate coastal water quality deterioration, imposing prolonged toxic stress on planktonic communities as well as fish, crustaceans, and mollusks. In enclosed habitats where water exchange is constrained, high biomass loading can even trigger mass mortality among cultured organisms[5-7]. Relative to the water column, the oxygen depletion and drastic habitat modification induced by *Ulva* deposition exert more severe impacts on benthic communities[8, 9]. Yet, for the full bloom-senescence cycle, how these processes regulate the physiology and succession of benthic economically important species remains poorly understood, and empirical data on benthic invertebrate groups are particularly scarce. In light of this, it is urgent to delineate the disturbance characteristics of *Ulva* dynamics on the physicochemical conditions of pond sediments and the pathways by which these disturbances perturb the metabolic homeostasis of benthic fauna, thereby providing

theoretical support for assessing the impacts of green-tide outbreaks and senescence on marine aquaculture.

As a typical representative of the Holothuroidea class within the phylum Echinodermata, *Apostichopus japonicus* is phylogenetically classified in the family Stichopodidae and the genus *Apostichopus*[10]. A growing body of empirical evidence confirms that this species primarily relies on deposited organic detritus as its core nutritional base[11, 12]. Owing to its notable edible medicinal value and pharmacological potential, *A. japonicus* holds an important position in the development of aquaculture resources[13, 14]. Its mobility is relatively limited, mainly due to the functional characteristics of its podia as the primary locomotor organs[15][15]. The species favors shallow marine rocky reef habitats, with distribution hotspots in areas of dense macroalgal proliferation; populations can also be found in macroalgae-covered sandy–mud composite substrates, whereas occurrence in homogeneous sandy mud environments is significantly reduced[16]. Microscopic analyses of its digestive contents reveal diverse components, including microbenthic invertebrates, microbial communities, bacterial aggregates, and diatom remains[17, 18].

Currently, *A. japonicus* is predominantly cultured in pond systems; however, this farming modality is primarily threatened by aquatic vegetation and nuisance algae, with coastal Shandong farming bases severely affected by *U. prolifera* and other robust green-tide macroalgae. Consequently, systematically elucidating the disturbance mechanisms of green tides across their entire life cycle on the pond ecological environment for *A. japonicus* culture has become a critical scientific issue for safeguarding the sustainable development of the industry. Accordingly, this article begins with the occurrence characteristics and ecological effects of green tides, focusing on reviewing advances in understanding nutrient release and environmental-stress mechanisms during *Ulva* bloom outbreaks and senescence, and integrates findings from *A. japonicus* ecology and physiological ecology. It analyzes current gaps and future directions, with the aim of providing a theoretical basis for a deeper comprehension of the long-term impacts of green-tide disasters on benthic aquaculture ecosystems.

2 OVERVIEW OF GREEN TIDES

Green tides refer to the discoloration of the water body, usually in green, caused by the explosive proliferation or high aggregation of certain macroalgae (e.g., *U. prolifera*) in seawater under specific environmental conditions. Green algae in the green tides include a variety of macroalgae within the Phylum Chlorophyta, such as seaweed (*U. prolifera*), *Ulva lactuca* and *Chaetomorpha valida*[19] (Figure.1). These algae grow rapidly under suitable conditions and form a “green blanket” covering the water surface, greatly reducing the light transmission rate of the water body and affecting the living environment of other aquatic organisms[20].

Green tides, by virtue of their physical properties, can harm coastal ecosystems. They can inhibit photosynthesis by local primary producers, resulting in severe consequences such as

seagrass habitat deterioration[21]. In addition, if not removed in a timely manner, they can lead to the production of H₂S within the hypoxia[22], which will further exacerbate negative impacts on coastal ecology and adversely affect the tourism economy.

Green tides have, in recent years, become a global marine ecological disaster, predominantly occurring in nutrient-rich waters such as estuaries and lagoons, as well as along coasts with intense human activity[2, 23]. These large macroalgae are able to exhibit rapid growth when nutrients are abundant, water temperature is suitable, and light conditions are favorable[24]. In addition to favorable external conditions, their inherently short and diverse life histories, coupled with rapid reproductive rates, ensure their successful proliferation in the environment and confer a marked competitive advantage over other algae[25].

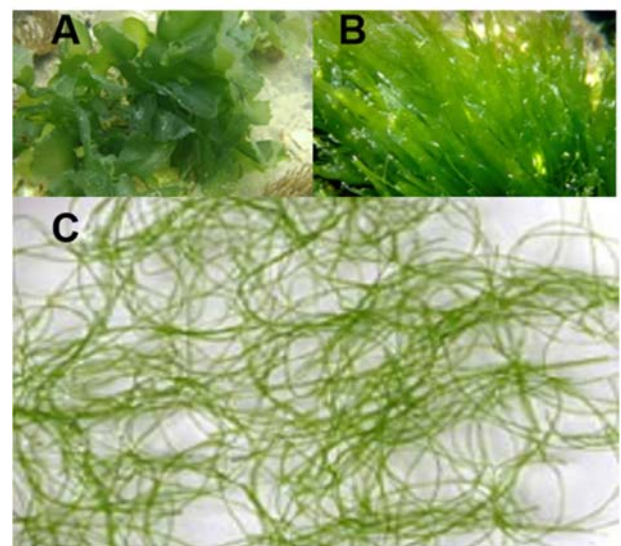


FIGURE 1 GREEN-TIDE ALGAE (A: *U. LACTUCA*, B: *U. PROLIFERA*, C: *C. VALIDA*)

According to studies, green tides are mainly caused by large macroalgae such as *Ulva*, *Enteromorpha*, *Cladophora*, and *Chaetomorpha*, which proliferate rapidly after detaching from substrata, constituting an algal disaster[26]. The outbreaks occur in late spring to early summer, typically persisting throughout the summer and completely subsiding before autumn[27]. Since 1970, this phenomenon has appeared along the coasts of numerous countries including the United States, Canada, Denmark, the Netherlands, France, Italy, Japan, Korea, and the Philippines[28](Figure.2). Synthesizing existing observations, the frequency and spatial extent of green tide events across the world's seas have shown a clear upward trend. From 2008 to the present, the Yellow Sea region has undergone sixteen consecutive years of large-scale algal blooms, inflicting far-reaching disturbances on neighboring marine ecosystems. Systematic surveys indicate that the dominant taxon within Yellow Sea blooms is *U. prolifera*[29]. This species ranges in color from olive green to vivid green, with thalli exceeding 1 m in length, a tubular morphology, a prominent main axis, and a multi-branched architecture; basal cells exhibit rhizoid-like

differentiation features[30]. *U. prolifera*, by virtue of its rapid proliferation, forms high-density surface aggregations that, through light-shading effects, disrupt the water column's

primary productivity and thereby trigger regional ecological crises[31, 32].

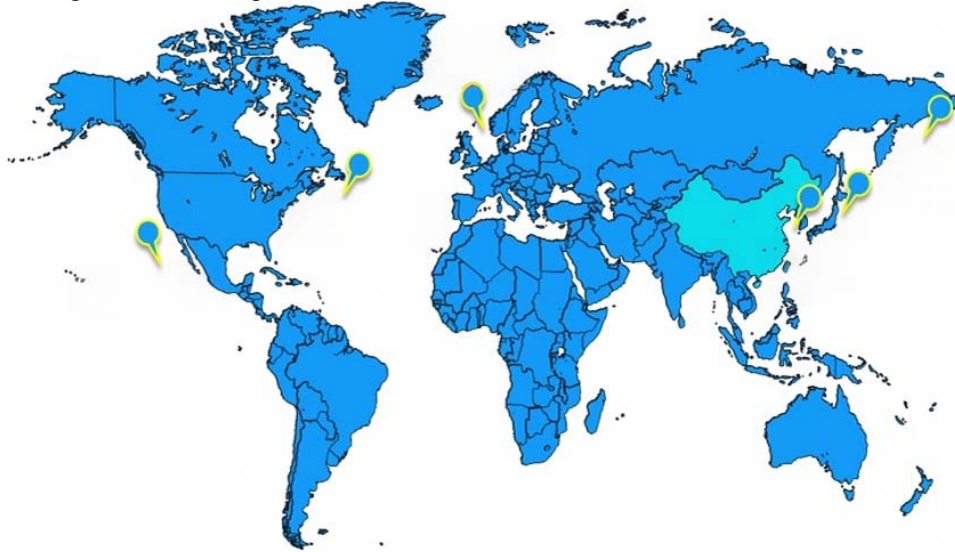


FIGURE 2 GLOBAL DISTRIBUTION OF GREEN TIDES[28]

As of 2024, data released by the National Marine Environmental Monitoring Center in the China Ocean Disaster Bulletin indicate that, from 2014 to 2023, with the exceptions of 2017, 2018, 2020 and 2022, the maximum coverage area of *U. prolifera* green tides in the Yellow Sea exceeded 500 square kilometers[33]. The recurrent occurrence of algal blooms in the Yellow Sea has inflicted multifaceted economic losses across multiple sectors, including mariculture, coastal recreation and tourism, shipping and logistics, and offshore sporting events[34]. More gravely, the metabolites released during the degradation of the algal biomass can trigger rapid depletion of dissolved oxygen, causing hypoxic mortality events among aquatic organisms, and thereby drive restructuring of community composition, imposing substantial perturbations on the stability of nearshore ecosystems[35].

3 IMPACTS OF ULVA PROLIFERA BLOOMS

U. prolifera (Chlorophyta; Chlorophyceae; Ulvales; Ulvaceae; Ulva)[36] is the principal culprit species behind the Yellow Sea green tides[37]. This species leverages its thin-walled tubular morphology, buoyancy-enhancing adaptations, and efficient nutrient assimilation to rapidly accumulate biomass under multifactorial conditions, ultimately triggering regional algal blooms[38]. Morphological and molecular-systematic analyses describe *Ulva* thalli as filamentous, tubular, or flattened-tubular; the main branches are prominent, cells are arranged in a single layer and hollow, and branches are slender and densely branched[39]. Reproduction occurs sexually, asexually, and vegetatively, conferring strong tolerance to exposure[27].

Within aquaculture, *Ulva* exploits its remarkable environmental adaptability and diverse reproductive strategies to exert a pronounced competitive exclusion on cultivated economically important macroalgae[31]. Its explosive biomass growth can provoke precipitous declines in dissolved oxygen within cultivation waters, directly increasing the stress-related mortality of cultured stock. As *Ulva* enters the degradation-mineralization phase, the released reductive metabolites, including hydrogen sulfide and ammonia, exert demonstrable toxic effects on benthic economic species such as sea cucumbers (*A. japonicus*); simultaneously, the oxidative decomposition of organic matter continually depletes the dissolved oxygen reserves, further intensifying the risk of suffocation for cultured biota[40]. Historical disaster assessments indicate that in 2008 the Yellow Sea green tide invaded the Shandong Peninsula coastline, causing systemic shocks to enclosed-pond farming, bottom-seeded cultivation, raft culture, and seedling propagation systems in Rushan, Haiyang, Jiaonan, and Rizhao, with direct economic losses estimated at approximately 800 million yuan[19].

3.1 THE ENVIRONMENTAL IMPACTS OF *U. PROLIFERA* BLOOMS

Fan et al., through indoor experiments by collecting waters containing different *Ulva* decay liquids, found that *Ulva* decay significantly alters the aquatic environment. The decay process re-releases nitrogen and phosphorus absorbed by the thalli, markedly increasing nutrient biomass. Concurrently, the dissolved organic carbon (DOC) biomass in the water also changes significantly[8]. Feng et al. collected surface seawater from *Ulva* bloom-affected and *Ulva*-free areas in the Yellow Sea and conducted a 300-day DOC degradation experiment in the laboratory. The results show that DOC biomass in *Ulva* bloom



waters is significantly higher than in non-bloom areas, and after microbial degradation, refractory DOC (RDOC) accounts for 46% in bloom waters, much higher than 36% in non-bloom areas[41]. Cao et al., via static simulations of sea cucumber (*A. japonicus*) culture ponds, demonstrated that hair algae biomass markedly affects nutrient contents; with longer cultivation, total nitrogen, ammonium nitrogen, nitrate nitrogen, nitrite nitrogen, total phosphorus, and reactive phosphorus in the overlying water all follow a pattern of initial increase followed by decrease, peaking at 6–24 h of cultivation[42]. Feng et al. conducted laboratory studies and field surveys; results indicate that *Ulva* initially nearshore rapidly uptakes nutrients from seawater, driving dissolved inorganic nitrogen and phosphorus to minimum values at multiple stations; as *Ulva* accumulates and decays, nitrogen and phosphorus nutrients are released significantly, with Aoshan Bay being the most severely affected, the water quality even falling below Class II[43]. Ding et al. collected *Ulva* from the coasts of Jiangsu and the Shandong Peninsula and conducted laboratory simulations; they found that *Ulva* grows by absorbing large amounts of nitrogen and phosphorus from seawater, and during decay in the Shandong Peninsula, about 80 days, nearly all fixed nutrients are released back to seawater, driving total nitrogen biomass to over 80 $\mu\text{mol/L}$ (10 \times the eutrophication standard), with dissolved oxygen below 4 mg/L, indicating hypoxic conditions; the fraction of organic nutrients rises from 25% to over 90%, severely altering the nutrient structure and spatial distribution and threatening ecosystem stability[44]. Wang et al. collected *Ulva* decay liquids and algal mud extracts; results show that decay releases substantial ammonium and phosphates into seawater, suggesting decay may alter nutrient structure and release phyto regulators, affecting phytoplankton community succession and thus altering red-tide species composition and timing[45]. Zhang et al. conducted a synthesis of monitoring data on *Ulva* green tides in the Yellow Sea since 2007; results indicate that the decay phase consumes large amounts of oxygen, causing hypoxia and acidification (pH down to 7.6, DO drop up to 68%), releases high-biochemical-oxygen-demand and dissolved organic carbon, and may promote growth of red-tide algae, with lasting impacts on nearshore carbon cycling and the ecosystem[5].

Ulva also exerts influence on the seawater sulfur cycle. It absorbs seawater sulfate and assimilatorily reduces it to synthesize dimethylsulfoniopropionate (DMSP), an important sulfur metabolite in algae[46]. DMSP can be cleaved to yield dimethyl sulfide (DMS) and acrylate[47]. During algal bloom senescence, the flux of bioavailable sulfur released from *Ulva* biomass into the water column increases markedly, causing the biomass of DMS and its precursor DMSP to remain elevated at specific times. The cell-wall matrix of this species is enriched with *Ulva* polysaccharides that contain a high proportion of organic sulfur functional groups; when subjected to microbial degradation, these can drive substantial release of sulfur-containing metabolites. In bottom waters under hypoxic conditions, sulfate reduction is activated, producing hydrogen sulfide and participating in the gas–liquid–solid multiphase transport and transformation of the sulfur biogeochemical cycle[48, 49].

3.2 *U. PROLIFERA* BLOOMS' IMPACTS ON

MARINE ORGANISMS

Research on *Ulva*'s effects on marine fauna remains relatively scarce. Fu and colleagues conducted experiments using *Ulva* decay liquid and fertilized eggs of the Pacific oyster, revealing that decay-liquid bioavailability (0.25–10 g/L) is positively correlated with bio-toxicity, and that toxicity (ranging from 10% to 97%) is significantly negatively correlated with the hatching rate of D-shaped larvae. High-biomass decay liquid also caused rupture of the chorion and dispersion of cleavage-stage cells, resulting in extremely low proportions of blastula–gastrula and trochophore stages[50]. Hu notes that *Ulva* outbreaks can induce disease and mortality in sea cucumbers, imposing substantial economic losses on sea cucumber aquaculture[51]. Wang et al., found that both fresh *Ulva* culture medium and *Ulva* decay liquid markedly inhibited fertilized eggs of the scallop *Chlamys farreri*[45]. Xu et al., observed that *Ulva*-induced stress significantly reduced the survival of the brown-spotted flatfish *Paralichthys olivaceus* and suppressed total antioxidant capacity in both serum and liver, as well as activities of superoxide dismutase and catalase, while hepatic malondialdehyde content rose markedly, indicating compromised antioxidant defenses. They also found *Ulva*-induced stress markedly upregulated pro-inflammatory cytokine genes (*tnf- α* , *il-1 β* , etc.) in the head kidney, activating the p38 and JNK MAPK inflammatory signaling pathways and endoplasmic reticulum stress responses[52]. Shi et al., using juvenile *P. olivaceus* as the study subject and employing histopathology and transcriptomics, identified clear pathological lesions in the liver, spleen, and head kidney; they also found enrichment of steroid biosynthesis and the PI3K-Akt signaling pathway, with differential expression of immune genes *dusp1*, *dusp16*, *HSP90* and metabolism-related gene serotransferrin, thereby elucidating the detrimental mechanisms of *Ulva* decay on the fish immune system[53].

Yang et al., used the olive flounder (*P. olivaceus*) as the study subject and conducted a 60-day exposure using natural seawater from *Ulva*-bloom zones to investigate the effects of *Ulva* decay on fish growth and antioxidant capacity. Their results showed that metal elements Na, K, Mg, and Fe were significantly elevated in the decayed *Ulva* water, with the increased Fe potentially being the primary driver of the observed physiological changes. *Ulva* decay also markedly reduced the olive flounder's survival rate and specific growth rate, affected serum total antioxidant capacity, and altered transaminase and alkaline phosphatase activities, while inducing significant changes in antioxidant indices and gene expression in the liver and gills, including activities of catalase (CAT) and superoxide dismutase (SOD) and levels of glutathione (GSH) [54].

Uchida et al., using the Manila clam (*Ruditapes philippinarum*) as the study subject, conducted laboratory experiments simulating green-tide conditions with fresh *Ulva* to examine the effects on clam growth. Their results showed that when *Ulva* addition reached the amounts observed in natural seas, larval and spat shell-length growth was markedly suppressed (larval growth rate dropped to 33.7% of the control), while adults were not affected[55].

Consequently, *Ulva* has exerted numerous adverse effects on a variety of cultured organisms, leading to substantial economic



losses in nearshore and pond aquaculture. Since the large-scale *Ulva* blooms reemerged in the nearshore waters off Shandong in 2008, outbreaks of *Ulva* and other large macroalgae, have occurred with increasing frequency. Among them, the 2013 *Ulva* bloom was especially severe, triggering widespread physiological stress and even mortality in farmed *A. japonicus*, with a broad geographic reach and high mortality, causing a heavy blow to the *A. japonicus* aquaculture industry[51]. However, there remains a lack of systematic research on the full-process impacts and mechanisms of *Ulva* blooms and senescence on economically important benthic organisms like *A. japonicus*. Therefore, a thorough elucidation of how *Ulva* at different developmental stages perturbs benthic habitats and the stress pathways imposed on key economic species is of significant scientific importance and practical value for improving nearshore aquaculture risk-warning systems and for developing ecological prevention and control strategies.

4 ARTIFICIAL CULTIVATION OF APOSTICHOPUS JAPONICUS

A. japonicus, a key marine aquaculture species in the northern coastal waters of China[15], is rich in essential amino acids, bioactive polysaccharides, and trace elements, conferring nutritional and immunomodulatory benefits. Market demand has risen steadily in recent years, driving rapid expansion of cultivation[56]. Within the current *A. japonicus* industry system, pond farming has become the core production mode in Liaoning, Shandong, and other regions[57], with its yield and economic benefits providing substantial support to the regional marine aquaculture economy.

A. japonicus constitute a major nearshore aquaculture product in northern China, with Shandong Province as the primary production region. In the Jiaodong Peninsula's *A. japonicus* ponds, sediments are predominantly silty and sandy[58]. Over the past decade, *A. japonicus* aquaculture has expanded rapidly. The China Fishery Statistical Yearbook 2025 shows that in 2024 the total area of China's *A. japonicus* farming reached 4.03 million mu, with a production of 326,000 tons and a direct economic value of about 100 billion yuan[59]. The high added value of *A. japonicus* derives from their unique bioactive constituents: protein content in the body-wall dry matter reaches 60–70%[60], fucoidan sulfates (SC-FUC) exhibit anticoagulant and immunomodulatory functions[61], and saponin compounds (such as holotoxin A1) demonstrate notable anti-tumor activity[62]. These characteristics drive farming toward intensification and position *A. japonicus* as an important raw material source in the biomedical sector.

In China's artificial *A. japonicus* farming system, pond culture dominates[63]. As a typified anthropogenically regulated ecosystem, its hydrological exchange conditions and community structure cannot fully replicate those of natural marine environments, exhibiting pronounced semi-enclosed characteristics[64]. In such systems, the self-purification capacity is limited, nutrient retention is high; the continuous input of residual feed and metabolic byproducts leads to

accumulating organic load, triggering benthic hypoxia and markedly altering the forms of nutrients in the water column and in the sediments, as well as the biomass distribution[65]. Monitoring data indicate that more than 50% of nitrogen and phosphorus input fluxes in the ponds ultimately settle and accumulate in the sediment layer. Because the mineralization rate of sediments lags behind external inputs, the persistent accumulation of nutrients readily disrupts the water body's nutrient balance, thereby inducing harmful algal blooms. This ecological risk, arising from degraded aquaculture habitats, has become one of the central topics of concern in current aquatic environment management and healthy farming[66]. Among various harmful algal blooms, *Ulva* outbreaks are particularly prominent, constituting a frequent ecological anomaly in sea cucumber ponds[67]. The causes are: on the one hand, sea cucumber ponds are often located on nearshore tidal flats with weak water exchange, enabling nitrogen and phosphorus nutrients to accumulate within the pond and providing ample material for rapid *Ulva* proliferation[44]; on the other hand, *Ulva* exhibits high nutrient uptake efficiency, rapid growth, and can reproduce vegetatively through fragmentation, allowing it to quickly gain a competitive edge in eutrophic environments[31]. Each year in late spring to early summer, as water temperatures rise to 15–25°C, *Ulva* typically transitions from sparse distribution to large-scale blooms in ponds[68]. Abundant floating *Ulva* mats cover the water surface, not only hindering gas exchange between water and air and exacerbating bottom hypoxia, but also settling to the pond floor after senescence, thereby further deteriorating the sedimentary environment[44].

Sea cucumbers predominantly inhabit shallow marine environments, with their larval stages commonly found beneath rocks in the intertidal zone. Upon maturity, they migrate to crevices among gravelly substrates or to rocky, stone-rich shallow nearshore waters, which comprise their principal distribution zones. As a quintessential benthic organism, they favor waters rich in algal resources[69]. Extreme fluctuations in environmental parameters are clearly linked to disease incidence in sea cucumbers[70]. Therefore, research on the culture water and related environmental conditions within sea cucumber ponds is of great importance to us. Consequently, the frequent occurrence of *Ulva* green tides has emerged as a major destabilizing factor for sea cucumber pond culture systems, warranting urgent investigation into how *Ulva* affects the pond environment and the sea cucumbers' physiological state.

5 CONCLUSION AND FUTURE PROSPECTS

Frequent *Ulva*-green tides in the Yellow Sea pose a severe threat to nearshore aquaculture ecosystems. This study systematically delineates the disturbance pathways of the full bloom–proliferation–decay cycle on the pond habitats of *A. japonicus* and clarifies that the mineralization phase of *Ulva* decay is the critical period triggering environmental stress. During this phase, substantial releases of metabolites such as ammonium, reactive phosphorus, dissolved organic matter, and hydrogen sulfide into



the water column and sediments rapidly deplete dissolved oxygen and induce acidification and reductive deterioration at the benthic interface, directly undermining the microhabitat essential for sea cucumbers' survival. Sea cucumbers, as a classic benthic deposit-feeding economic animal, exhibit low mobility and a strong dependence on sediment physico-chemical conditions, making them particularly susceptible to immunosuppression, metabolic dysregulation, disruptions of summer dormancy rhythms, and even mass mortality under green tide disturbances. Existing research has preliminarily illuminated the basic pathways by which Ulva-decomposition products alter the water-sediment chemical environment and stress cultured organisms, thereby laying a theoretical foundation for aquaculture risk identification.

Nevertheless, several gaps remain in the current body of research. First, most studies focus on the origins, spatiotemporal distribution, and immediate water-environment effects of green tides; for the full Ulva cycle—from outbreak and proliferation to decay—there is a lack of systematic observation and assessment of the long-term, continuous impacts on sedimentary biogeochemical processes in aquaculture ponds, particularly during the decay phase when substantial organic matter settles. Second, toxicological mechanisms remain superficially explored. Research on sea cucumber stress has largely relied on macroscopic physiological indicators or simulations of single environmental factors, lacking integrated molecular toxicology evidence that spans tissue pathology, metabolic networks, and gene expression; key pathways and early biomarkers under combined stressors have yet to be established.

Future research directions should focus on the following areas: Strengthening process-mechanism studies through in situ monitoring and controlled simulation experiments, quantifying the fluxes and transformations of key biogenic elements (C, N, P, S) at the sediment-water interface during Ulva decay, and clarifying their effects on the redox state of the benthic substrate and the restructuring of microbial community composition, thereby elucidating the sources and pathways of environmental stress. Deepening toxicological and physiological-effect research by integrating omics technologies, physiological indices, and histopathology methods to systematically reveal the stress-response network of sea cucumbers under Ulva-induced stress and identify key biomarkers to provide a scientific basis for early warning and health assessment.

REFERENCES

- [1]WANG G C, WANG H, GAO S, et al. Study on the biological mechanism of green tides[J]. *Oceanologia et Limnologia Sinica*, 2020, 51(4): 789-808.
- [2]ZHANG H B, WANG S, YIN H, et al. Development pattern of *Ulva prolifera* green tide in the South Yellow Sea in 2018 and the role of nitrogen components[J]. *Acta Oceanologica Sinica*, 2020, 42(8): 40-49.
- [3]LIU S, JIANG Z, DENG Y, et al. Effects of seagrass leaf litter decomposition on sediment organic carbon composition and the key transformation processes[J]. *Science China Earth Sciences*, 2017, 60(12): 2108-2117.
- [4]ZHANG T, WANG X. Release and microbial degradation of dissolved organic matter (DOM) from the macroalgae *Ulva prolifera*[J]. *Marine Pollution Bulletin*, 2017, 125(1-2): 192-198.
- [5]YONGYU Z, PEIMIN H, HONGMEI L, et al. *Ulva prolifera* green-tide outbreaks and their environmental impact in the Yellow Sea, China[J]. *National Science Review*, 2019, 6(4): 825-838.
- [6]TAKEMURA A F, CHIEN D M, POLZ M F. Associations and dynamics of *Vibrionaceae* in the environment, from the genus to the population level[J]. *Frontiers in Microbiology*, 2014, 5: 38.
- [7]YU F, YONG-AN Z, JINYU S, et al. Immunogenicity study of *OmpU* subunit vaccine against *Vibrio mimicus* in yellow catfish, *Pelteobagrus fulvidraco*[J]. *Fish and Shellfish Immunology*, 2021, 108: 80-85.
- [8]FAN Q X. Effects of *Ulva prolifera* decay on the living environment, intestinal microbiota and intestinal transcriptome of Japanese flounder (*Paralichthys olivaceus*)[D]. Qingdao: Qingdao University, 2022.
- [9]QU T F, HOU C Z, YU Z S, et al. Ecological effects of *Ulva prolifera* green tide on macrobenthic communities in the intertidal zone of Qingdao coast[J]. *Journal of Ocean University of China (Natural Science Edition)*, 2020, 50(12): 59-69.
- [10]LI B S. Effects of fucoidan, fucose and glucose on growth, digestive physiology and glucose metabolism of sea cucumber (*Apostichopus japonicus*)[D]. Shanghai: Shanghai Ocean University, 2024.
- [11]LIU C M. Effects of different coated lysine levels on growth, digestion, immunity and stress resistance of juvenile sea cucumber (*Apostichopus japonicus*)[D]. Dalian: Dalian Ocean University, 2016.
- [12]ZHAO J, XU T, YIN D-Q. Locomotor activity changes on zebrafish larvae with different 2,2',4,4'-tetrabromodiphenyl ether (PBDE-47) embryonic exposure modes[J]. *Chemosphere*, 2014, 94: 53-61.
- [13]LI J Q. Effects of different lipid sources on growth, physiology and lipid metabolism of juvenile sea cucumber (*Apostichopus japonicus*)[D]. Qingdao: University of Chinese Academy of Sciences (Institute of Oceanology, Chinese Academy of Sciences), 2025.
- [14]JOBSON S, HAMEL J F, HUGHES T, et al. Cellular, hormonal, and behavioral responses of the holothuroid *Cucumaria frondosa* to environmental stressors[J]. *Frontiers in Marine Science*, 2021, 8.
- [15]DING K. Molecular mechanisms of the neuroendocrine system in regulating locomotion and stress behaviors of sea cucumber (*Apostichopus japonicus*)[D]. Qingdao: University of Chinese Academy of Sciences (Institute of Oceanology, Chinese Academy of Sciences), 2019.
- [16]LI L H, CHEN Y, TIAN T, et al. Preliminary study on environmental suitability of sea cucumber (*Apostichopus japonicus*) based on habitat suitability index model[J]. *Journal of Dalian Ocean University*, 2016, 31(1): 80-84.
- [17]QIN C X. Study on pond culture structure and its optimization of sea cucumber (*Apostichopus japonicus* Selenka)[D]. Qingdao: Ocean University of China, 2009.
- [18]ZANG Y Q. Eco-physiological responses and mechanisms of sea cucumber (*Apostichopus japonicus* Selenka) to typical environmental stresses[D]. Qingdao: Ocean University of China, 2012.
- [19]YE N H, ZHANG X W, MAO Y Z, et al. 'Green tides' are overwhelming the coastline of our blue planet: taking the world's largest example[J]. *Ecological Research*, 2011, 26(3): 477-485.
- [20]GENG H X, YU R C, ZHANG Q C, et al. Tracing the settlement region of massive floating green algae in the Yellow Sea[J]. *Journal of Oceanology and Limnology*, 2019, 37(5): 1555-1565.
- [21]BARNES R S K. Context dependency in the effect of Ulva-induced loss of seagrass cover on estuarine macrobenthic abundance and



- biodiversity[J]. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 2019, 29(2): 163-174.
- [22]SMETACEK V, ZINGONE A. Green and golden seaweed tides on the rise[J]. *Nature*, 2013, 504(7478): 84-88.
- [23]HE Y. Molecular biological mechanisms of *Ulva prolifera* green tide outbreaks[D]. Suzhou: Soochow University, 2019.
- [24]LI R X, WU X W, WEI Q S, et al. Growth of *Ulva prolifera* under different nutrient conditions[J]. *Advances in Marine Science*, 2009, 27(2): 211-216.
- [25]YE N H, ZHANG X W, MAO Y Z, et al. Preliminary study on the life history of *Ulva prolifera* (*Enteromorpha prolifera*) in the Yellow Sea green tide[J]. *Journal of Fishery Sciences of China*, 2008(5): 853-859.
- [26]DING P Z. Assessment of ecological restoration capacity of green tide algae and study on green tide algae removal[D]. Shanghai: Shanghai Ocean University, 2017.
- [27]LIU X Q. Spatial and temporal distribution of floating green algae and micro-propagules during the formation of Yellow Sea green tides[D]. Qingdao: First Institute of Oceanography, State Oceanic Administration, 2014.
- [28]TANG Q S, ZHANG X W, YE N H, et al. Current status and problems of green tide research[J]. *Bulletin of National Natural Science Foundation of China*, 2010, 24(1): 5-9.
- [29]DING L P, LUAN R X. Taxonomy, habitat and distribution of *Enteromorpha prolifera*[J]. *Oceanologia et Limnologia Sinica*, 2009, 40(1): 68-71.
- [30]WANG X K, MA J H, YE D C, et al. Preliminary study on the life history of *Enteromorpha prolifera*[J]. *Marine Science Bulletin*, 2007(5): 112-116.
- [31]WANG Z L, FU M Z, XIAO J, et al. Research progress on *Ulva prolifera* green tide in the Yellow Sea[J]. *Acta Oceanologica Sinica*, 2018, 40(2): 1-13.
- [32]JIANG X L, ZHOU X J, LIN J N, et al. Research progress on ecological effects of *Ulva prolifera* green tide in the Yellow Sea[J]. *Marine Environmental Science*, 2021, 40(4): 647-652.
- [33]Bulletin of China Marine Disasters in 2022[M]. Beijing: China Natural Resources News, 2024.
- [34]NELSON T A, NELSON A V, TJOELKER M. Seasonal and spatial patterns of "Green Tides" (ulvoid algal blooms) and related water quality parameters in the coastal waters of Washington State, USA[J]. *Botanica Marina*, 2003, 46(3): 263-275.
- [35]GAO G, BEARDALL J, BAO M L, et al. Ocean acidification and nutrient limitation synergistically reduce growth and photosynthetic performances of a green tide alga *Ulva linza*[J]. *Biogeosciences*, 2018, 15(11): 3409-3420.
- [36]LIU X Q, WANG Z L, ZHANG X L. A review of the green tides in the Yellow Sea, China[J]. *Marine Environmental Research*, 2016, 119: 189-196.
- [37]HAO Y, GUAN C, HOU C Z, et al. Changes in the community structure of epiphytic green algae on rafts in the Subei Shoal and their correlation with environmental factors[J]. *Oceanologia et Limnologia Sinica*, 2021, 52(1): 123-131.
- [38]WANG Z L, XIAO J, FAN S L, et al. Who made the world's largest green tide in China? - an integrated study on the initiation and early development of the green tide in Yellow Sea[J]. *Limnology and Oceanography*, 2015, 60(4): 1105-1117.
- [39]LIU F, PANG S J. Research progress on *Ulva prolifera* green tide in the Yellow Sea and its source tracing[J]. *Advances in Marine Science*, 2012, 30(3): 441-449.
- [40]ZHANG G Z, WU M Q, ZHANG A D, et al. Influence of sea surface temperature on outbreak of *Ulva prolifera* in the Southern Yellow Sea, China[J]. *Chinese Geographical Science*, 2020, 30(4): 631-642.
- [41]FENG X T, LI J Y, WU W C, et al. Bioavailability of dissolved organic carbon and its carbon sink role during *Ulva prolifera* green tide outbreaks[J]. *Journal of Applied Oceanography*, 2023, 42(3): 442-449.
- [42]CAO X B, MA W W, LI Q, et al. Effects of *Cladophora* on nutrient concentrations in overlying water of a static simulated sea cucumber aquaculture pond[J]. *Marine Sciences*, 2018, 42(6): 88-95.
- [43]FENG L N, ZHANG H B, SUN Y Y, et al. Nutrient release during the decay of *Ulva prolifera* green tide and its impact on coastal environment[J]. *Acta Oceanologica Sinica*, 2020, 42(8): 59-68.
- [44]DING Y M. Migration and transformation of biogenic elements in the Yellow Sea *Ulva prolifera* green tide and their impacts on the ecological environment[D]. Qingdao: Graduate University of Chinese Academy of Sciences (Institute of Oceanology), 2014.
- [45]WANG C, YU R-C, ZHOU M-J. Effects of the decomposing green macroalga *Ulva* (*Enteromorpha*) *prolifera* on the growth of four red-tide species[J]. *Harmful Algae*, 2012, 16: 12-19.
- [46]TAN T T, LIU C Y, LIU T, et al. Effects of environmental factors on the growth and biogenic sulfur release of *Ulva prolifera*[J]. *Oceanologia et Limnologia Sinica*, 2018, 49(4): 793-801.
- [47]KATHRYN L V, et al. Environmental chemistry and chemical ecology of "Green Tide" seaweed blooms[J]. *Integrative & Comparative Biology*, 2015.
- [48]ZHANG X H, LIU J, LIU J L, et al. Biogenic production of DMSP and its degradation to DMS — their roles in the global sulfur cycle[J]. *Science China Life Sciences*, 2019, 62(10): 1296-1319.
- [49]HAN L, DENG X, LI P F, et al. Simulation study on the effect of seawater temperature on biogenic sulfur release from *Ulva prolifera* during the decline phase[J]. *Acta Oceanologica Sinica*, 2018, 40(10): 110-118.
- [50]FU P, HE J L, ZHANG X Z, et al. Biototoxicity of *Ulva prolifera* decomposition liquid and its effect on embryo development of Pacific oyster (*Crassostrea gigas*)[J]. *Ocean Development and Management*, 2019, 36(8): 13-17.
- [51]HU W, LI C L, HAN S, et al. Impacts of abnormal climate and environment on sea cucumber aquaculture and countermeasures[J]. *Marine Sciences*, 2018, 42(2): 159-166.
- [52]XU D, TANG Y Z, LI W L, et al. *Ulva prolifera* stress in the Yellow Sea of China: suppressed antioxidant capacity and induced inflammatory response of the Japanese flounder (*Paralichthys olivaceus*)[J]. *Animals*, 2023, 13(24).
- [53]SHI K P, FAN Q X, ZHAN M, et al. Exploring the effect of *Ulva prolifera* decay on the immune tissue of *Paralichthys olivaceus* based on transcriptomics and histopathological analysis[J]. *Marine Pollution Bulletin*, 2023, 194.
- [54]YANG Y M, LI W L, WANG R, et al. Effects of *Ulva prolifera* degradation on growth performance and antioxidant capacity of Japanese flounder (*Paralichthys olivaceus*) family[J]. *Fishes*, 2023, 8(12).
- [55]UCHIDA M, MIYOSHI T, NIIMURA Y, et al. Growth inhibitory effect of dissolved organic matter from fresh free-floating *Ulva* spp. fronds on asari clam *Ruditapes philippinarum*[J]. *Fisheries Science*, 2021, 87(2): 211-221.
- [56]PENG J X, ZHAO X N, SONG D R, et al. Comparative analysis of nutritional and functional components of sea cucumber (*Apostichopus japonicus*) from different culture modes and origins[J]. *Chinese Fishery Quality and Standards*, 2023, 13(2): 1-10.
- [57]ZHAO B, HU W, LI C L, et al. Characteristics of phytoplankton and benthic algal communities and water quality in sea cucumber



- aquaculture ponds[J]. Journal of Guangxi Academy of Sciences, 2020, 36(4): 399-405.
- [58]SONG H X, XING R L, WANG H Y, et al. Distribution characteristics of nitrogen and phosphorus nutrients in water of two types of substrate sea cucumber ponds[J]. Jiangsu Agricultural Sciences, 2015, 43(5): 336-340.
- [59]Bureau of Fisheries, Ministry of Agriculture and Rural Affairs, National Fisheries Technology Extension Center, China Society of Fisheries. China Fishery Statistical Yearbook[M]. Beijing: China Agriculture Press, 2025.
- [60]YI-ZHEN H, YI-SHA X, YAN-XIN L, et al. Quality assessment of variable collagen tissues of sea cucumber (*Stichopus japonicus*) body wall under different heat treatment durations by label-free proteomics analysis[J]. Food Research International, 2023, 165: 112540.
- [61]JOKAR B N, MEHDI T, SANGGUAN Y, et al. Improved immunomodulatory and antioxidant properties of unrefined fucoidans from *Sargassum angustifolium* by hydrolysis[J]. Journal of Food Science and Technology, 2017, 54(12): 4016-4025.
- [62]ZHANG Y, FAN Y C, ZHANG Y C, et al. Antitumor activity and mechanistic study of steroidal saponins from the rhizomes of *Paris polyphylla* var. *yunnanensis*[J]. Phytochemistry, 2025: 114455.
- [63]YANG H S, SUN J C, RU X S, et al. Situation analysis and technological innovation prospects of sea cucumber seed industry in China[J]. Marine Sciences, 2020, 44(7): 2-9.
- [64]PEI H L, TAN B M, WANG L, et al. Structural characteristics of sediment bacterial community and its influencing factors in sea cucumber aquaculture ponds during freeze-thaw period[J]. Progress in Fishery Sciences, 2023, 44(4): 121-134.
- [65]LI J H. Ecological aquaculture technology in sea cucumber ponds[J]. New Rural Technology, 2024(11): 32-33.
- [66]YANG Y K L Y X Y S C Y. Dynamic monitoring and simulation of cyanobacteria bloom based on wireless sensor network and GIS[J]. Transactions of the Chinese Society of Agricultural Engineering, 2016, 32(24): 197-205.
- [67]SUN Y Y, YUAN Z X, XUE X L. Study on problems and countermeasures of sea cucumber industry development in China[J]. World Agriculture, 2018(3): 186-191.
- [68]WANG X J. Effects of algae on the culture environment and aestivation of sea cucumber (*Apostichopus japonicus*)[D]. Shanghai: Shanghai Ocean University, 2011.
- [69]MEI Y P, HOU Z S, GAO Q F, et al. Transcriptome analysis reveals new insights into the respiration metabolism mechanism of different feeding rations of sea cucumber (*Apostichopus japonicus*)[J]. Journal of Ocean University of China, 2023, 22(6): 1621-1634.
- [70]ZHAO B, ZHOU H X, LI C L, et al. Effects of ammonia nitrogen stress on non-specific immunity of sea cucumber "Luhai No.1"[J]. Journal of Northwest A&F University (Natural Science Edition), 2022, 50(2): 17-24.