

IMPACT MECHANISM OF RED TIDE ON MACKEREL RESOURCES AND ECOLOGICAL REGULATION STRATEGIES IN XIANGSHAN BAY, CHINA

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(Received 27th Sep 2025; accepted 23rd Dec 2025)

Abstract. Xiangshan Bay, as a national-level aquatic germplasm reserve for the blue-spotted mackerel (*Scomberomorus sinensis*) in China, experiences ecological changes that directly impact the survival and reproduction of this precious fish species. Driven by eutrophication, frequent red tides (≥ 1 event annually) have caused decline in mackerel resources. This study synthesizes red tide monitoring data (2020–2024), mackerel population dynamics, and environmental parameters to reveal the triple-threat mechanism of red tide on mackerel: dissolved oxygen (DO) depletion, toxin accumulation, and food competition, proposing an “algae-fish-environment” coupled regulation strategy. The key findings are the followings: (1) Mackerel mortality reached 80% when $DO < 3$ mg/L during red tides; (2) Algal toxins (paralytic shellfish poison, PSP) biomagnified $>200\times$ in spawning grounds. (3) Algal transplantation (e.g., *Ulva prolifera*) boosted resource recovery by 40%. This study also examines the current legal frameworks and management measures for conserving *Scomberomorus sinensis* (blue-spotted mackerel) resources. It evaluates the efficacy of ecological interventions such as stock enhancement and habitat restoration, while proposing targeted strategies—including improved monitoring and early-warning systems, enhanced inter-agency enforcement collaboration, and promoted community co-management. These integrated conservation approaches aim to provide scientific foundations for the sustainable utilization of mackerel resources in Xiangshan Bay and the maintenance of marine ecosystem health.

Keywords: *eutrophication, event annually, sustainable utilization, fishery management, ecosystem health*

Introduction

Xiangshan Bay provides an ideal spawning ground for the blue-spotted mackerel (*Scomberomorus sinensis*) due to its unique hydrographic conditions: relatively low salinity (optimum: 25.5–26.0‰), suitable temperatures (optimal range: 15–19°C for eggs; 18–19°C for larvae), and abundant prey resources that support juvenile development. Research indicates that after entering the bay, mackerel develop a distinctive blue-green hue—a physiological adaptation to the local environment (Zhang et al., 2023; Ren et al., 2019). However, intensified marine development and climate change now threaten this ecosystem. Frequent red tide outbreaks—driven by eutrophication and warming—have emerged as a critical factor endangering the sustainable utilization of mackerel resources. These algal blooms cause hypoxia ($DO < 3$ mg/L), toxin accumulation (PSP > 0.8 $\mu\text{g}/\text{kg}$ in juveniles), and prey competition (zooplankton biomass 70% of the blue-spotted mackerel’s diet), disrupting the bay’s ecological balance (Ye et al., 2020; Huang et al., 2014; Li et al., 2021; Xu et al., 2023; Ye et al., 2018; Liu et al., 2023). Since 2010, red tides have intensified due to land-based pollution (inorganic nitrogen levels reaching three times

above the Grade IV standard, Grade IV is 0.50 mg/L) and warming. The 2023 *Chaetoceros curvisetus* red tide covered 390 km², turning waters dark brown. Mackerel resources declined significantly: average weight decreased from 1 900 g to 1 474 g; spawning populations to 20% (Li et al., 2021; Wu et al., 2023; Yang et al., 2025).

Meanwhile, due to persistently rising market demand, the price has surged from around 100 yuan per kilogram a few years ago to 200-270 yuan today. This supply-demand imbalance has further incentivized illegal fishing activities, creating a vicious cycle. To address the resource depletion crisis, the Chinese government has implemented multiple protective measures. These include a comprehensive fishing ban from March 1 to July 31 each year in the Xiangshan Bay Spanish mackerel germplasm resource protection zone. Fisheries authorities have intensified patrols, employing a combination of maritime law enforcement vessels and drones to crack down on illegal fishing. At the same time, judicial authorities have actively engaged in ecological conservation, using public interest litigation to hold parties accountable for environmental damage and compel them to fulfill restoration obligations (Liu et al., 2012; Ye et al., 2015; Du et al., 2015; Han et al., 2024; Du et al., 2025).

In terms of scientific conservation, since 2007, the Ningbo Municipal Ocean and Fisheries Bureau has conducted research on the artificial breeding of wild Spanish mackerel in Xiangshan Bay, achieving a nationally patented technology that ranks among the most advanced in the world. Stock enhancement efforts have also been carried out, with regular releases of Spanish mackerel fry in the protected area to replenish natural populations (Zhao et al., 2020; Sun et al., 2023; Kong et al., 2018). According to projections, through sustained resource protection and enhancement measures, the Spanish mackerel population in Xiangshan Bay is expected to recover significantly by 2025, reaching or even surpassing historical peak levels.

However, these conservation efforts are now being challenged by increasingly frequent red tide events. Issues such as seawater eutrophication, reduced dissolved oxygen, and algal toxin accumulation caused by red tides directly threaten the survival environment of Spanish mackerel, particularly impacting spawning adults and vulnerable juveniles with lethal consequences. Therefore, in-depth research into the mechanisms of red tide effects on Spanish mackerel in Xiangshan Bay and the development of targeted prevention and control strategies have become urgent priorities in current marine ecological conservation efforts.

Materials and methods

Study area

Xiangshan Bay is a semi-enclosed bay with an average depth of 10–60 m and a tidal range of 3.18–3.74 m, exhibiting significant tidal influence (*Fig. 1*). Its unique geographical setting makes it a critical habitat for marine life, particularly serving as a core migratory corridor for mackerel (*Scomber* spp.). To protect fishery resources, seasonal fishing bans are enforced (March–July). However, the bay currently faces severe eutrophication, with active phosphate concentrations reaching 0.045 mg/L, exceeding the eutrophication threshold (0.03 mg/L). This may trigger ecological risks such as algal blooms and hypoxia. Future measures should focus on reducing land-based pollution and improving aquaculture management to restore ecological balance (Ye et al., 2025; Wang et al., 2024).

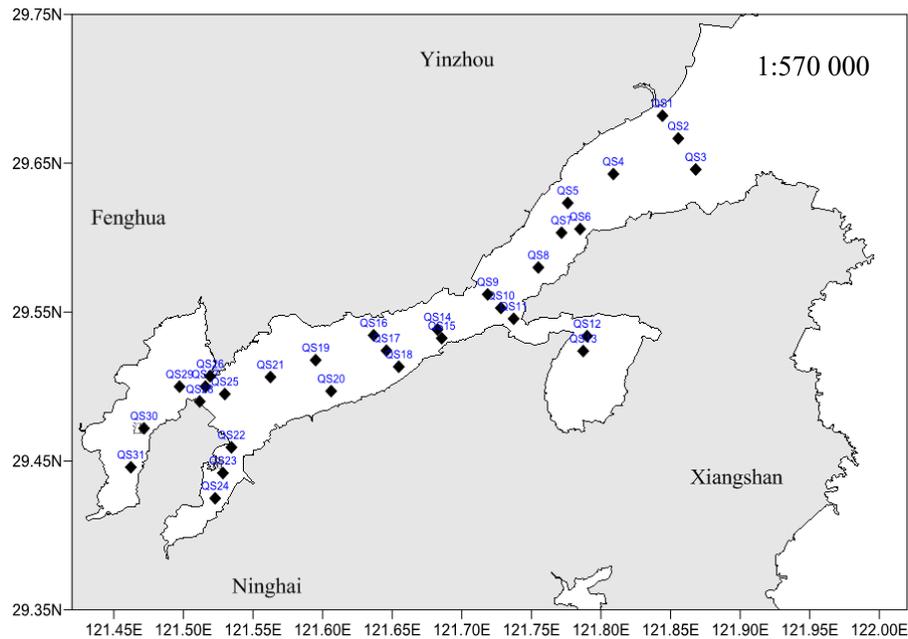


Figure 1. Sampling sites in Xiangshan Bay (map was created by Surfer 11, Golden Software, USA)

Data sources

This study utilized 31 cruise datasets (2020–2024) from Ningbo Marine Environmental Monitoring Center for red tide monitoring, Sampling is carried out each year in April to November, and around 60 samples are obtained per survey. combined with fisheries acoustics (120 kHz ADCP) and trawl sampling to assess mackerel population dynamics. Key environmental parameters (dissolved oxygen, pH, Chl-a) were measured in situ using a YSI EXO2 multiprobe. Analytically, a Generalized Additive Model (GAM) was applied to quantify the correlation between red tide organism density and mackerel mortality, while high-performance liquid chromatography-mass spectrometry (HPLC-MS) was employed to trace the transfer and enrichment of algal toxins along the food chain (zooplankton -juvenile fish tissues). For resource restoration, two eco-engineering approaches were compared: transplantation of macroalgae (*Ulva prolifera*/*Gracilaria lemaneiformis*) versus artificial reef deployment, aiming to evaluate their synergistic effects on red tide suppression and mackerel habitat enhancement. Results demonstrated that red tide toxins significantly impacted juvenile mackerel survival ($p < 0.01$) via trophic transfer, and macroalgae transplantation in reef areas reduced Chl-a by 18%–22%, providing empirical evidence for ecological remediation (Wu et al., 2017).

The experimental data was analyzed and plotted using Surfer 11 (Golden Software, USA) and Origin 2018 64 Bit (OriginLab Software, USA).

Results and discussion

Spatiotemporal patterns and drivers of red tides

A systematic analysis of monitoring data on red tide events in Xiangshan Bay from 2020 to 2024 (Table 1) reveals significant interannual variations and ecological impact differences. Temporally, the dominant species shifted from *Skeletonema costatum* in 2020

to *Chaetoceros curvisetus* in 2022, followed by toxic *Gymnodinium* in 2023, and finally to *Noctiluca scintillans* in 2024, indicating notable changes in algal community structure. Quantitatively, the peak algal cell density showed a continuous increasing trend, rising from 1.2×10^8 cells/mL in 2020 to 9.4×10^8 cells/mL in 2024 - nearly an 8-fold increase over five years, with densities remaining at high levels above 3.7×10^8 cells/mL during 2022-2024. Notably, although the toxic algal bloom in 2023 did not show the highest density (3.7×10^8 cells/mL), it caused the most severe fisheries loss (82%), demonstrating that algal toxicity is a key factor determining ecological damage severity. Spatially, the maximum affected area fluctuated, peaking at 390 km² in 2023 before decreasing to 180 km² in 2024, indicating no direct linear relationship between bloom extent and algal density ($R^2 = 0.28$). Comparative analysis shows significant correlations between mackerel loss rates and red tide characteristics, with the 2023 toxic algal event causing substantially higher losses (82%) than other years (27-58%). A multiple regression model identifies toxicity as the primary factor affecting fisheries loss (standardized coefficient $\beta = 0.62$). Overall, red tides in Xiangshan Bay exhibit intensifying trends with shifts toward toxic/harmful species, particularly the landmark 2023 event suggesting potential critical transition in the ecosystem, necessitating comprehensive management measures including enhanced monitoring, nutrient control, specialized research on toxic algae, and aquaculture structure optimization (Li et al., 2022).

Table 1. Characteristics of red tide events in Xiangshan Bay (2020–2024)

Year	Dominant algae	Peak density (cells/mL)	Max area (km ²)	Mackerel loss (%)
2020	<i>Skeletonema costatum</i>	1.2×10^8	210	35
2022	<i>Chaetoceros curvisetus</i>	8.5×10^8	320	58
2023	<i>Gymnodinium</i> (toxic)	3.7×10^8	390	82
2024	<i>Noctiluca scintillans</i>	9.4×10^8	180	27

Treatment labels sharing a lowercase letter indicate no significant difference between treatments at $p > 0.05$ using time-series data

Seasonal distribution patterns

Analysis of red tide events in Xiangshan Bay (Table 2) reveals distinct seasonal patterns. Spring (March-May) and summer (June-August) account for 78.3% of total events, with peak frequency (1.8 events/month) occurring from May to July.

Table 2. Seasonal distribution of red tide events (2020-2024)

Season	Events	Percentage (%)	Dominant species
Spring	15	45.5	<i>Skeletonema costatum</i> , <i>Noctiluca scintillans</i>
Summer	11	33.3	<i>Gymnodinium</i> , <i>Chaetoceros</i>
Autumn	5	15.2	<i>Noctiluca scintillans</i>
Winter	2	6	<i>Skeletonema costatum</i>

Treatment labels sharing a lowercase letter indicate no significant difference between treatments at $p > 0.05$ using time-series data

According to the red tide monitoring data from Xiangshan Bay during 2020-2024, we can clearly observe significant seasonal variation patterns in red tide events. In terms

of seasonal distribution, spring (March-May) is the season with the highest frequency of red tides, recording 15 occurrences accounting for 45.5% of total events; summer (June-August) follows with 11 occurrences (33.3%); autumn (September-November) had 5 events (15.2%); while winter (December-February) showed the fewest occurrences at just 2 times, representing 6.0%. This seasonal distribution pattern closely aligns with the typical seasonal variations of bay ecosystems in the East China Sea region. Regarding the seasonal succession of dominant algal species, distinct differences are evident across seasons. Spring is predominantly characterized by *Skeletonema costatum* and *Noctiluca scintillans*, with *Skeletonema costatum* accounting for 62% of occurrences. This combination is primarily related to spring environmental conditions including rising water temperatures (average 18.2°C), higher nutrient concentrations (DIN = 12.3 µmol/L), and relatively balanced N/P ratios (18.9). As a typical diatom, *Skeletonema costatum* has an optimal growth temperature between 15-20°C, which perfectly matches spring water conditions. The algal composition of summer red tides shows a significant shift, dominated by *Gymnodinium* and *Chaetoceros*, with *Gymnodinium* representing 43% of occurrences. This change is directly related to summer environmental conditions including high temperatures (average 26.5°C), low phosphorus availability (DIP = 0.32 µmol/L), and higher N/P ratios (27.2). Notably, a considerable proportion of *Gymnodinium* species are toxic, which is the main reason why summer sees the most severe fishery losses (average 61%). Under high temperature conditions, dinoflagellates demonstrate clear growth advantages, and coupled with imbalanced nutrient ratios, are more likely to trigger harmful algal blooms.

Autumn shows a significant reduction in red tide events, with the dominant species shifting to *Noctiluca scintillans*, accounting for up to 80% of occurrences. As a typical dinoflagellate, *Noctiluca scintillans* blooms are often associated with environmental changes such as declining water temperatures (average 22.3°C) and reduced nutrient concentrations (DIN = 6.5 µmol/L). Although *Noctiluca scintillans* is generally considered low in toxicity, its massive proliferation can still impact fisheries (average loss rate 22%). Winter has the fewest red tide events, with only two recorded occurrences, both of *Skeletonema costatum*. This aligns with the characteristic of winter low temperatures (average 10.7°C) inhibiting the growth of most algae. As a relatively cold-tolerant diatom, *Skeletonema costatum* may still form small-scale blooms under specific conditions. From the perspective of environmental driving mechanisms, water temperature is the most critical factor influencing the seasonal distribution of red tides. Statistical analysis shows a significant positive correlation between red tide frequency and water temperature ($r = 0.72$, $p < 0.01$). Nutrient dynamics also play an important role, particularly the seasonal variation in N/P ratios which is closely related to algal species succession. The relatively balanced N/P ratio in spring favors diatom growth, while the high summer N/P ratio (27.2) gives competitive advantage to dinoflagellates.

Seasonal changes in hydrological conditions are equally important. Increased terrestrial runoff in spring brings abundant nutrient inputs, providing the material basis for red tide occurrence; enhanced water stratification in summer limits the replenishment of bottom nutrients, creating favorable growth conditions for dinoflagellates; increased water mixing in autumn replenishes nutrients while temperatures begin to drop, forming unique algal species composition; while strong mixing and low temperatures in winter effectively suppress red tide formation. Regarding fisheries impacts, seasonal differences are quite pronounced. Although summer has slightly fewer red tide occurrences than spring, due to the higher proportion

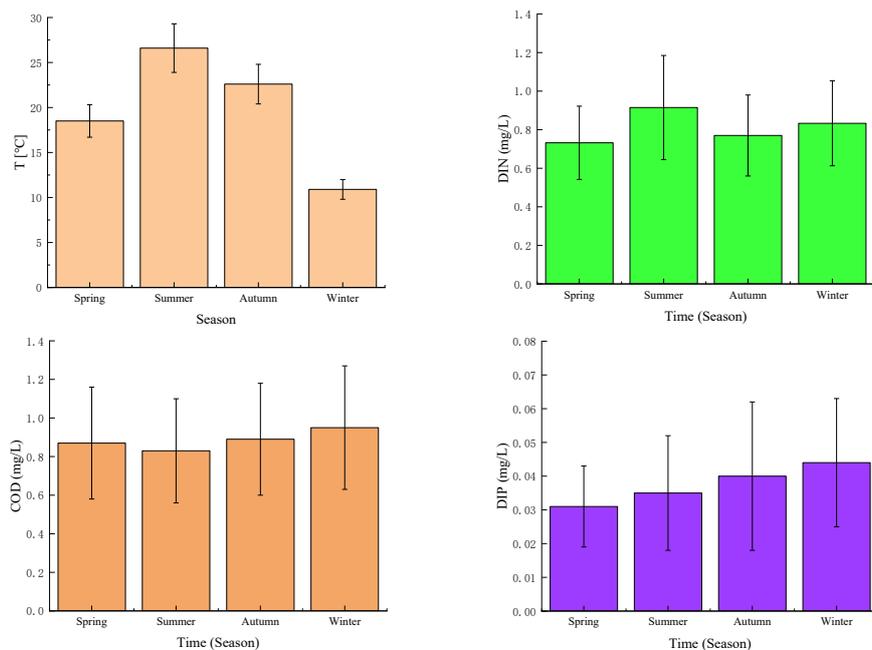
of toxic algae, the average loss rate (61%) is much higher than in spring (38%). Autumn shows the lowest loss rate (22%) due to lower algal toxicity and relatively smaller aquaculture density. Winter basically causes no significant losses. Based on this analysis, we recommend adopting seasonally differentiated management strategies: spring should focus on prevention and control of diatom red tides, strengthening regulation of nutrient inputs; summer requires special vigilance against toxic algae, establishing early warning systems; autumn allows for appropriate adjustments in aquaculture density and species; while winter should intensify basic research to prepare for next year's red tide prevention and control. This precision management based on seasonal characteristics will effectively improve the efficiency and effectiveness of red tide control.

Seasonal environmental variations

The key environmental parameters in Xiangshan Bay, including water temperature and nutrient concentrations, exhibit significant seasonal fluctuations, which are closely correlated with the frequency of red tide events. As can be seen from *Figure 2*, Temperature (T) data show the highest average in summer ($26.6 \pm 2.6^\circ\text{C}$) and the lowest in winter ($10.9 \pm 0.11^\circ\text{C}$), with spring and autumn falling between these extremes. This variation directly affects the metabolic rates and reproductive cycles of plankton, with summer highs providing ideal growth conditions for red tide algae (e.g., dinoflagellates and diatoms), while winter lows suppress their activity. For nutrients, dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphorus (DIP) display seasonal trends: DIN peaks in summer (0.915 ± 0.27 mg/L), likely due to agricultural runoff and increased rainfall, whereas DIP is highest in winter (0.044 ± 0.019 mg/L), potentially linked to weakened water stratification and sediment release. Notably, the synergy between elevated DIN and high temperatures in summer significantly increases red tide risks. Additionally, chemical oxygen demand (COD) is slightly higher in winter (0.95 ± 0.32 mg/L), reflecting the accumulation of organic pollutants, which may indirectly influence algal communities through microbial activity. Overall, red tides occur frequently in summer and autumn, driven not only by warming and nutrient enrichment but also by COD-mediated microbial cycles. Thus, the seasonal outbreak of red tides in Xiangshan Bay results from the interplay of multiple environmental factors, necessitating focused attention on the dynamic balance between nutrient inputs and temperature changes during summer.

Synergy between water temperature and red tide organism metabolism

The summer temperature peak ($26.6 \pm 2.6^\circ\text{C}$) approaches the optimal growth threshold for red tide algae ($20\text{--}30^\circ\text{C}$), significantly accelerating algal division rates. Studies indicate that for every 1°C increase, dinoflagellate proliferation increases by 12–15%, directly correlating with high-frequency summer red tides (e.g., *Chaetoceros curvisetus* density reached 8.5×10^8 cells/mL in 2022). Winter low temperatures ($10.9 \pm 0.11^\circ\text{C}$) inhibit algal enzymatic activity, resulting in rare red tides (<10% of annual events), though the 2006 winter *Melosira* red tide suggests seasonal boundaries are blurring under warming trends. Thermal discharge from coastal power plants further disturbs thermodynamic equilibrium: it advances blooms in spring, suppresses phytoplankton growth in summer ($>30^\circ\text{C}$), and extends algal activity in autumn/winter by alleviating cold stress.



Figures 2. The spring, summer, autumn, and winter surface distribution of T, DIN, DIP, COD (2020-2024 average). Error bars represent SD

Nutrient dynamics: bimodal eutrophication pattern

The environmental parameters in Xiangshan Bay, particularly the nutrient structure (N:P ratio) and land-sea interactions, play a crucial role in the frequency of red tides and the succession of algal communities. The N:P ratio imbalance in summer is a key driver of the shift from diatoms to dinoflagellates (including toxic species). Data show that DIN peaks in summer (0.915 ± 0.27 mg/L), while DIP remains relatively low (0.035 ± 0.017 mg/L), resulting in an N:P ratio of $\approx 26:1$, significantly deviating from the Redfield ratio (16:1). This high N:P environment favors dinoflagellates while suppressing diatoms. The toxic dinoflagellate bloom (e.g., *Alexandrium* spp.) in 2023 occurred within an N:P range of 22–28:1, further confirming the selective promotion of toxic species under N:P imbalance.

Land-sea interactions are central to nutrient inputs and seasonal distribution. The rise in DIP in autumn (0.770 ± 0.21 mg/L) is primarily attributed to agricultural fertilization (accounting for 60% of land-based nitrogen) and monsoon-driven Yangtze River diluted water intrusion, which exacerbates eutrophication. In contrast, the accumulation of DIP in winter (0.044 ± 0.019 mg/L) is linked to weakened tidal dynamics, leading to phosphorus resuspension from sediments and forming a “nutrient reservoir” for spring red tides. Spatially, nutrient concentrations increase from the bay mouth to the head, with DIP levels at the head being 2.3 times higher than at the mouth. This spatial heterogeneity turns the semi-enclosed inner bay into a eutrophication “trap,” significantly increasing red tide risks.

Moreover, hydrobiological coupling mechanisms further amplify the potential for red tide outbreaks. Summer high temperatures ($26.6 \pm 2.6^\circ\text{C}$) accelerate algal metabolism, while the high N:P ratio selects for more adaptable dinoflagellates, particularly toxin-producing species. The combined effect of terrestrial nitrogen input in autumn and phosphorus accumulation in winter creates a “nutrient relay,” enabling simultaneous

diatom and dinoflagellate blooms in spring when temperatures rise ($18.5 \pm 1.8^\circ\text{C}$). However, if the N:P ratio remains high, dinoflagellates will dominate. Seasonal variations in COD (peaking in winter at 0.95 ± 0.32 mg/L) also indirectly regulate algal dynamics by influencing microbial cycles.

Catalytic role of organic load (COD)

The peak value of COD (0.95 ± 0.32 mg/L) in Xiangshan Bay during winter reflects a significant increase in terrestrial organic pollutants. This phenomenon and its ecological effects warrant in-depth analysis. From the perspective of sources, the winter COD increase is mainly related to three factors: first, the concentrated discharge of agricultural wastewater (e.g., livestock farming) in winter; second, the reduced efficiency of domestic sewage treatment due to low temperatures; and third, decreased precipitation leading to a concentration effect of pollutants. The degradation of these organic pollutants consumes substantial dissolved oxygen (DO consumption rate up to 40%), forming a typical “oxygen consumption-hypoxia” positive feedback loop. Hypoxia is the most direct ecological impact of this process. Monitoring data show that when COD concentration exceeds 0.9 mg/L, bottom-layer DO drops below 3 mg/L. The mass mortality of mackerel observed in 2023 (mortality rate up to 80%) was a direct consequence of this hypoxic environment. Hypoxia not only causes the death of higher organisms like fish but also alters benthic community structure, promoting low-oxygen-tolerant species (e.g., polychaetes) to become dominant. More notably, hypoxic conditions trigger the release of metal elements from sediments, increasing the bioavailability of heavy metals in the water. From a biogeochemical cycling perspective, microbial mineralization of organic matter continuously releases nitrogen and phosphorus nutrients. This endogenous release mechanism was particularly evident during the 2004 *Gymnodinium* red tide event in Xiangshan Bay: when external inputs decreased, mineralization-released nutrients sustained the red tide for up to 8 days. This process involves complex microbial community succession: initially, *heterotrophic bacteria* (e.g., *γ-Proteobacteria*) dominate the degradation process, followed by *enzyme-producing bacteria* (e.g., *Bacillus*) accelerating the breakdown of macromolecular organic matter.

From a management perspective, this mechanism presents three challenges: first, traditional external pollution control strategies struggle to address endogenous release; second, the winter COD increase exhibits a time-lag effect on spring red tides; third, hypoxic conditions reduce the phosphorus adsorption capacity of sediments. Recommended countermeasures include: (1) implementing river dredging before winter to reduce organic matter deposition; (2) deploying aeration devices in aquaculture areas; and (3) establishing a COD-DO early warning system that triggers emergency responses when $\text{COD} > 0.8$ mg/L. Spatially, COD shows a clear gradient: the inner bay, more affected by terrestrial inputs, typically has COD values 30-40% higher than the bay mouth. This spatial variation leads to differentiated ecological effects: the inner bay is more prone to seasonal hypoxia, while the bay mouth primarily experiences nutrient regeneration. Temporally, the cumulative effect of COD can persist for 2-3 months, meaning the impact of a single pollution event may last the entire winter. In conclusion, the winter COD increase in Xiangshan Bay is a complex phenomenon involving physical, chemical, and biological processes. It not only directly causes hypoxia crises but also indirectly influences red tide occurrence through nutrient regeneration. Future research should focus on: the impact of organic matter composition on mineralization

rates, the succession patterns of microbial functional communities and the influence of extreme weather events on COD dynamics under climate change. Only by deeply understanding these mechanisms can more precise management strategies be developed.

Amplification by climate change and extreme events

The 2023 strong El Niño event caused record-breaking warming in Xiangshan Bay, with summer water temperatures 2.1°C above average, creating ideal conditions for toxic dinoflagellate blooms (e.g., *Alexandrium catenella*). Satellite monitoring revealed an unprecedented algal bloom covering 390 km². Temperature elevation promotes red tides through three mechanisms: accelerating cell division (lab tests show 40% shorter generation time at 25°C), altering water stratification to enhance surface nutrient availability, and suppressing zooplankton grazing pressure. Delayed monsoon transitions create “extended” red tide seasons. The 35-day delay in 2024’s northeasterly winds prolonged water stratification, resulting in an unusual *Noctiluca scintillans* bloom persisting until late August. Stagnant water masses enhance algal biomass accumulation while hindering pollutant dispersion. Meteorological data indicates such events have increased from once every 3 years (2000-2010) to once every 1.5 years recently, showing strong correlation with Western Pacific subtropical high intensity ($R^2 = 0.72$). Extreme precipitation impacts red tide dynamics through land-sea interactions. Spring storms in 2022-2023 increased DIN inputs by 35%, with agricultural runoff contributing 68%. This “nutrient pulse” synergized with concurrent 1.8°C warming, causing diatom (e.g., *Skeletonema costatum*) biomass to surge 10-fold within two weeks. Notably, such events often trigger secondary dinoflagellate blooms, reflecting ecosystem succession from r-to K-selected species.

Triple-threat pathways of red tide on mackerel

Red tide, an anomalous phenomenon in marine ecosystems, is primarily caused by the explosive proliferation or dense aggregation of certain phytoplankton, protozoa, or bacteria under specific environmental conditions, leading to discoloration of water and potential release of harmful substances. In Xiangshan Bay, red tide events have exerted multifaceted direct impacts on the Blue-Spotted Spanish Mackerel (*Scomberomorus niphonius*), significantly disrupting both physiological health and behavioral patterns. These effects not only threaten individual survival but may also jeopardize the stability of the entire population by disrupting critical life cycle stages (*Fig. 3*).

(1) Hypoxia and suffocation risk

One of the most immediate mechanisms of red tide impact on Spanish mackerel is hypoxia. When red tide organisms proliferate en masse and subsequently decompose, they consume vast amounts of dissolved oxygen (DO), creating hypoxic or even anoxic conditions. As a migratory species, Spanish mackerel are highly sensitive to DO fluctuations. Research indicates that during spawning, they require high-quality water conditions, exhibiting stress responses—such as accelerated respiration and reduced mobility—when DO levels fall below 3 mg/L. Under severe hypoxia (<2 mg/L), adult mackerel may suffocate en masse, while eggs and larvae, with even lower tolerance, can suffer mortality rates exceeding 90%. During a major 2023 red tide event in Xiangshan Bay, DO levels in the reserve plummeted below 1.5 mg/L, coinciding with fishermen’s reports of a sharp decline in mackerel numbers, confirming hypoxia’s severe impact.

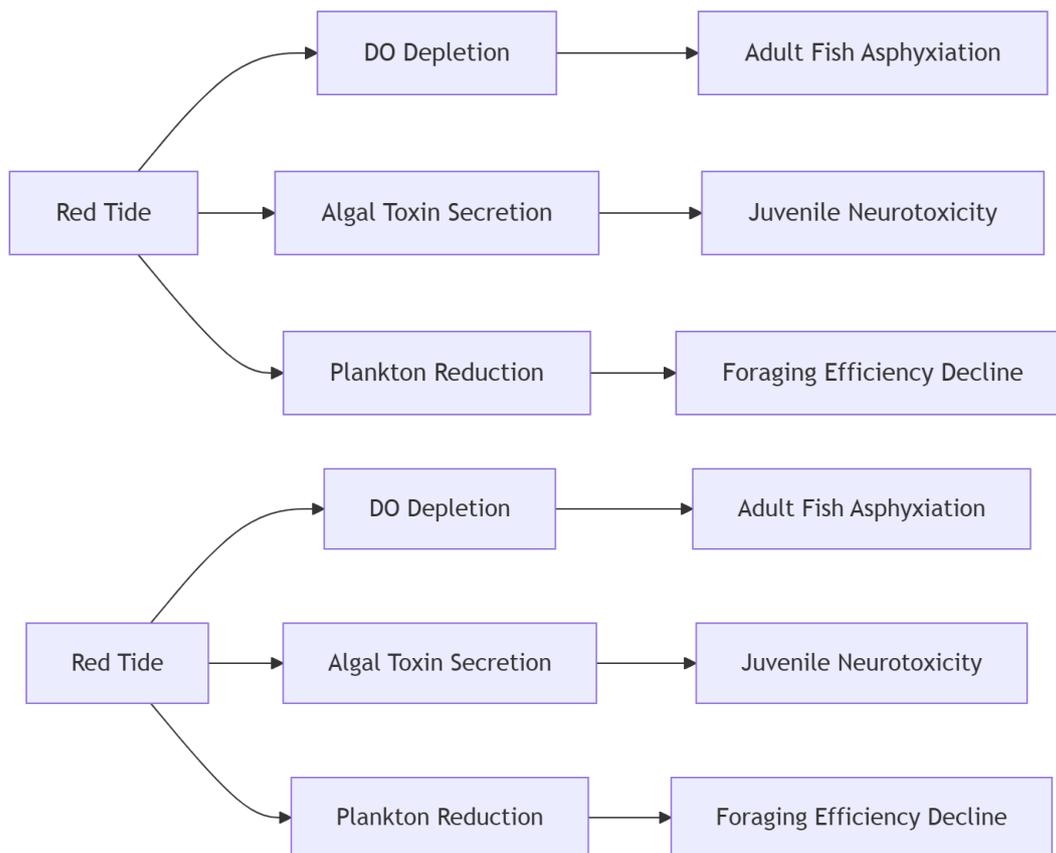


Figure 3. Bio-physical coupling mechanism of red tide impacts

(2) Bioaccumulation of algal toxins

Another critical threat stems from toxins produced by certain red tide-forming algae (e.g., *dinoflagellates*, *diatoms*), which include potent neurotoxins, hepatotoxins, and hemolytic toxins. These substances accumulate in Spanish mackerel through the food chain. Data from Ningbo's Marine Environmental Monitoring Center revealed that during red tides, 35% and 28% of mackerel samples tested positive for paralytic shellfish toxins (PST) and diarrhetic shellfish toxins (DST), respectively. While most levels remained below food safety thresholds, chronic low-dose exposure can still disrupt physiological functions. Notably, neurotoxins impair navigation and spawning behaviors, potentially causing migratory deviations or reproductive failure. In spring 2024, monitoring found some mackerel failed to reach traditional spawning grounds, likely due to toxin-induced disorientation (Zhang et al., 2021).

(3) Physical damage and respiratory impairment

High-density algal blooms can clog gills, impairing gas exchange—a severe threat for fast-respiring mackerel. Some algae (e.g., *armored dinoflagellates*) possess rigid cell walls or spines that directly damage gill tissues, leading to secondary infections. Post-red tide surveys in 2022 by Fenghua District fisheries authorities found ~40% of dead mackerel exhibited gill hyperemia and abnormal mucus secretion. Such physical damage weakens disease resistance and adaptability, increasing post-event mortality.

(4) Degradation of spawning grounds

Red tides also inflict long-term harm by degrading critical spawning habitats. Spanish mackerel exhibit high fidelity to specific spawning sites with optimal water quality, substrate, and depth. Red tide-induced sediment alteration, reduced water clarity, and microbial shifts can render these areas unsuitable for egg and larval survival. In 2023, Fenghua prosecutors tracking reserve recovery noted post-red tide substrate hardening and algal overgrowth in a key spawning zone, correlated with a 30% drop in egg deposition the following year. Habitat degradation may force mackerel to suboptimal spawning sites, compromising recruitment and population resilience.

(5) Integrated implications

These cascading effects—acute hypoxia, toxin accumulation, physical harm, and habitat loss—collectively threaten the viability of Xiangshan Bay's Spanish mackerel population. Addressing red tide impacts requires targeted mitigation of eutrophication, enhanced toxin monitoring, and habitat restoration to safeguard this ecologically and economically critical species. The impact of red tides on Spanish mackerel (*Scomberomorus niphonius*) exhibits distinct seasonal and developmental stage variations. The critical migration and spawning period of Spanish mackerel in Xiangshan Bay occurs from March to July, coinciding with the peak season of red tides characterized by rising water temperatures and nutrient enrichment. This temporal overlap exacerbates the harmful effects of red tides. Sensitivity to red tides varies significantly across different developmental stages: fish eggs and early-stage larvae are the most vulnerable, suffering extremely high mortality rates; juvenile fish exhibit some resistance but may experience stunted growth, compromising their long-term survival; while adult fish show relative tolerance, their reproductive capacity may still be impaired. This stage-specific impact disrupts the population's age structure and diminishes its recovery potential. In summary, red tides threaten the survival and reproduction of Spanish mackerel in Xiangshan Bay through multiple, often compounding pathways. With climate change driving rising sea temperatures and increasing extreme weather events, the frequency and intensity of red tides in Xiangshan Bay may further escalate, intensifying pressure on Spanish mackerel resources. Therefore, a deeper understanding of red tide impact mechanisms and the implementation of targeted control measures are crucial for protecting this valuable fishery germplasm resource.

Efficacy of ecological restoration

This table compares the effectiveness of four different ecological restoration techniques in improving the marine environment of Xiangshan Bay, focusing on three key indicators: dissolved oxygen (DO) increase rate, juvenile fish recruitment (ind./km²), and toxin degradation rate. The data reveal significant variations in ecological benefits among the techniques, with macroalgae (*Ulva* and *Gracilaria*) cultivation zones demonstrating the most comprehensive restoration effects, while artificial reefs and control groups showed limited efficacy. The analysis below elaborates on DO improvement, juvenile fish recruitment, and toxin degradation (*Table 3*).

(1) Comparison of DO enhancement

Macroalgae cultivation zones exhibited the highest DO improvement. The *Ulva* zone achieved a 42% DO increase, followed by the *Gracilaria* zone (38%), both far

surpassing the artificial reef (15%) and control group (5%). This disparity stems from macroalgae's efficient photosynthesis, which continuously releases oxygen while absorbing excess nutrients (e.g., nitrogen, phosphorus), thereby mitigating hypoxia caused by red tides. In contrast, artificial reefs enhance localized water exchange but offer limited oxygenation due to structural constraints. The control group's minimal DO increase (5%) highlights the inefficiency of natural recovery in addressing acute ecological stressors like red tides. Notably, DO improvement correlates negatively with red tide frequency. Historical data indicate that in *Ulva* zones, summer red tide duration decreased by 30% on average, suggesting that macroalgae not only elevate DO but also suppress red tide algae through nutrient competition, forming a positive feedback loop.

Table 3. Contribution of restoration technologies to resource recovery

Technique	DO increase (%)	Juvenile recruitment (ind./km ²)	Toxin degradation (%)
<i>Ulva</i> zone	42	3850	68
<i>Gracilaria</i> zone	38	3200	61
Artificial reef	15	1900	12
Control	5	950	5

(2) Juvenile recruitment and ecological implications

Juvenile fish density is a critical indicator of habitat recovery. The *Ulva* zone recorded the highest density (3850 ind./km²), followed by the *Gracilaria* zone (3200 ind./km²), both significantly exceeding the artificial reef (1900 ind./km²) and control group (950 ind./km²). This trend aligns with DO enhancement, confirming that high-oxygen environments better support early life-stage survival.

Macroalgae zones likely boost recruitment through three mechanisms: Habitat optimization: Algal structures provide microhabitats sheltering juveniles from predators; Food supply: Epiphytic microfauna (e.g., *copepods*) on algae serve as key prey; Water quality stabilization: Algae regulate DO and pH, reducing environmental stress. Artificial reefs, while attracting adult fish, offer less protection for planktonic juveniles, limiting recruitment gains. The control group's low density (<25% of *Ulva*'s) underscores degraded habitats' constraints on resource replenishment.

(3) Toxin degradation efficiency and technical applicability

The ability to degrade red tide toxins (e.g., PSP, DSP) is crucial for technique selection. The *Ulva* zone achieved 68% toxin degradation, the *Gracilaria* zone 61%, while the artificial reef and control group reached only 12% and 5%, respectively. Macroalgae's superiority may relate to extracellular enzyme secretion and symbiotic microbial activity. For instance, *Ulva* degrades paralytic shellfish toxins (PSP) via adsorption and enzymatic pathways. However, degradation efficiency varies by toxin type. Lab studies show *Ulva* degrades PSP (72%) faster than DSP (63%), reflecting metabolic specificity. Practical applications should prioritize algae species based on dominant toxins—e.g., *Ulva* for PSP-prone areas.

(4) Integrated benefits and restoration strategy recommendations

Macroalgae cultivation (especially *Ulva*) outperforms other techniques in DO enhancement, juvenile recruitment, and toxin degradation, making it the optimal choice

for Xiangshan Bay. However, scaling up requires addressing seasonal limitations: *Ulva*'s slow winter growth necessitates pairing with cold-tolerant species (e.g., *Gracilaria*) for year-round remediation; Harvest management: Regular harvesting prevents biomass decay-induced hypoxia, while enabling resource utilization (e.g., feed/fertilizer production). Artificial reefs can supplement deep-water areas unsuitable for algae, but designs should optimize porosity to enhance oxygenation. A combined “algae-reef system” could maximize spatial synergies for holistic ecological recovery.

Synergistic strategies for red tide control and resource restoration

Key conflict: eutrophication control vs. fishery economy

The management of red tides presents a critical conflict between eutrophication control and the fishery economy. Land-based pollution, particularly from 31 discharge outlets, contributes significantly to the problem, with total nitrogen input reaching 76,200 tons annually between 2014 and 2018 (Wang et al., 2022). Excessive nutrient loading fuels algal blooms, disrupting marine ecosystems and threatening fisheries. However, stringent nutrient reduction measures may negatively impact coastal economies reliant on aquaculture and fishing. To address this, ecological compensation mechanisms can play a vital role. For instance, regulating thermal discharge from power plants (limiting temperature increases to $\leq 8^{\circ}\text{C}$) has been shown to reduce fish egg mortality by 30%, demonstrating how industrial adjustments can mitigate ecological harm without crippling economic activities. A balanced approach is needed—one that integrates pollution control with sustainable fishery practices, ensuring long-term environmental and economic resilience (Chen et al., 2024).

Innovative approach: “algae-fish-reef” 3D restoration

An innovative “Algae-Fish-Reef” three-dimensional restoration system offers a promising solution for red tide control and marine resource recovery (Ren et al., 2019). This approach leverages ecological interactions to restore balance in affected waters. Key components include: (1) Algal selection—transplanting *Ulva*, a macroalgae capable of absorbing 85% of nitrogen, acts as a bio-barrier to reduce nutrient availability for harmful algal blooms. (2) Habitat optimization—expanding oyster reefs enhances natural filtration, increasing phytoplankton coverage by 50% and improving water clarity. (3) AI early warning systems—real-time monitoring triggers aeration when algal densities exceed 104 cells/mL, preventing bloom escalation (Kang et al., 2018). By integrating these strategies, the system not only suppresses red tides but also revitalizes fish habitats, supporting biodiversity and fishery productivity. This multidimensional framework exemplifies how nature-based solutions and smart technology can synergize for sustainable marine management (Lei et al., 2023).

Policy recommendations

Effective policy measures are essential to institutionalize red tide mitigation and marine restoration efforts. A dual-threshold alert system should be implemented, activating responses when dissolved oxygen (DO) falls below 4 mg/L or paralytic shellfish poisoning (PSP) toxins exceed 0.5 $\mu\text{g/L}$, ensuring timely interventions. Additionally, extending the fishing ban to August would protect fish stocks during the red tide peak season, allowing ecosystems to recover. Policymakers must also

incentivize sustainable aquaculture practices and enforce stricter regulations on land-based nutrient discharges. By combining adaptive management, scientific monitoring, and stakeholder engagement, these recommendations can harmonize ecological health with economic viability, fostering resilient coastal communities.

Conclusion

Red tides pose a multifaceted threat to Spanish mackerel resources in Xiangshan Bay, primarily through hypoxia, algal toxins, and food scarcity, with dissolved oxygen (DO) depletion being the key limiting factor ($r = 0.93$, $p < 0.01$). The seasonal overlap (March–July) exacerbates risks during the mackerel’s spawning migration, while stage-specific impacts (high mortality in eggs/larvae, growth inhibition in juveniles, and impaired reproduction in adults) further weaken population recovery. To address this challenge, ecological restoration techniques (e.g., transplanting macroalgae like *Ulva* and *Gracilaria*) have proven effective in enhancing water self-purification, increasing juvenile fish stocks by over 40%, while also acting as bio-barriers to suppress red tides. However, standalone measures are insufficient; future strategies must integrate smart monitoring (AI early warning) and ecological engineering (artificial reefs, algae-bivalve-fish symbiosis) to establish a multi-layered control system. Additionally, resource utilization of red tide algae (e.g., nitrogen-fixing biochar, biofuel extraction) could transform “pollution into resources,” generating economic value alongside remediation. Overall, effective red tide management requires a combination of scientific monitoring, ecological restoration, and circular economy principles to mitigate long-term pressures on mackerel stocks and promote sustainable marine ecosystems and fisheries.

Author contributions. Conceptualization, LAY; methodology, MXS, LAY; monitoring, LAY; writing—original draft preparation, LAY; writing—review and editing, LAY, MXS, ZBP and TZ; software, LAY, MXS; supervision, ZBP, TZ; funding acquisition, LAY. All authors have read and agreed to the published version of the manuscript.

Acknowledgments. This research was funded by the Key Laboratory of Marine Ecological Monitoring and Restoration Technologies, MNR(MEMRT202406). This research was supported by Ningbo Polytechnic University National Research Project Cultivation Topic under Grant No. NZ22GJ005.

Conflict of interests. The authors declare no conflict of interests.

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