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Increased diversity and environmental threat of harmful algal blooms in the Southern Yellow Sea, China*

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Abstract Harmful algal blooms (HABs) in the Southern Yellow Sea (SYS) have shown a trend of increasing diversity and detrimental effects. While the Bohai Sea, East China Sea, and South China Sea have experienced a high incidence of HABs since the 1980s, the Yellow Sea provides a relatively healthy ecological environment in which fewer HABs have been documented before the 21st century. Yet large-scale blooms of the green macroalga *Ulva prolifera* (so-called "green tides") have occurred annually since 2007 in the Yellow Sea. Six people were poisoned and one person died in Lianyungang in 2008 due to ingestion of algal toxins. Moreover, the Yellow Sea experienced co-occurrence of harmful red tides, green tides, and golden tides in 2017. This combination of events, rare worldwide, indicates the potential for further deterioration of the marine environment in the Yellow Sea, which may be related to climate change, aquaculture, and other human activities. Using the SYS as an example, we collected data of the frequency and scale of HABs over the years, as well as that of marine algal toxins, and analyzed the trend in the diversity of HABs in the SYS, to explore the causes and impacts of HABs, as well as the interrelationships among different types of HABs, including harmful red tides, green tides, and golden tides. We also attempted to improve our understanding of HAB evolution under the influence of global climate change and intensified human activities.

Keyword: marine algal toxins; harmful algal blooms; red tides; green tides; golden tides; Southern Yellow Sea

1 INTRODUCTION

Harmful Algal Blooms (HABs) constitute exceptional ecological events caused by algae, which can attain high-biomass and/or result in proliferation of toxic cells (Hallegraeff, 1993; Kudela et al., 2017). Generally, HABs may include so-called 'red, brown, green, and golden tides', which can endanger ecosystem health and marine organisms survival through toxin production or by causing gill damage and water quality deterioration, although they are not always evidenced by water discoloration (Anderson et al., 2012; Kudela et al., 2017; Li et al., 2021). Moreover, they can contaminate seafood products, such as shellfish, with algal toxins that can be transferred through the food web, thereby harming human health (Reich et al., 2008). The frequency of HABs and the diversity of their causative species are on the rise in coastal China, and the modes of action

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of harmful algae that affecting the marine ecological environment and coastal human populations are becoming increasingly complex (Lu et al., 2014; Anderson et al., 2015).

In China, compared with the Bohai Sea, and the East and South China Seas, the Yellow Sea provides a relatively healthy ecological environment in which fewer HABs have been documented before the 21st century (Zhou et al., 2001). However, this changed in 2007 when large-scale blooms of the green macroalga *Ulva prolifera* (green tides) appeared and recurred annually thereafter (MNR, 2009–2020; Zhang et al., 2019). Furthermore, an unusual co-occurrence of green, golden (*Sargassum horneri*), and harmful red tides (*Kerenia mikimotoi* and *Heterosigma akashiwo*) was observed in the Southern Yellow Sea (SYS) in 2017 (Kong et al., 2018), while these HABs appeared individually in other sea areas. In addition to marine toxin concerns, HABs in the SYS have a greater diversity and ecological impact than those in adjacent seas. Over the past 30 years, algal toxins occasionally detected in shellfish and shellfish poisoning outbreaks, and sometimes were even associated with human fatalities, have been reported along the coast of the SYS (Liang et al., 2019). Manila clams, *Ruditapes philippinarum*, were contaminated with paralytic shellfish poisoning (PSP) toxins accumulated from *Alexandrium minutum* cells, resulting in six people poisoned and one person died in Lianyungang City, Jiangsu in 2008 (Yu and Liu, 2016; Yu and Luo, 2016). Furthermore, HABs formed by non-toxic species may also threaten the health and safety of coastal populations. For example, *U. prolifera*, which is non-toxic, can produce toxic gases such as hydrogen sulfide (H_2S) and ammonia (NH_3) during bulk deposition and decay along the coast (Yu and Liu, 2016), which can cause sea and atmospheric contamination, and endanger the health of coastal residents and tourists.

Harmful algal blooms in the SYS have also caused serious economic losses. A massive *U. prolifera* green tide occurred in the coastal area of Qingdao between May and July 2008 prior to the Qingdao Olympic Regatta. Motivated by the bloom, local government made a heroic effort to remove the green algae, costing an estimated 2 billion RMB (Ye et al., 2011), and caused economic losses of 640 million RMB in 2009 (Yu and Liu, 2016). Invasion of the brown macroalga *S. horneri* in the Subei Shoal resulted in a loss of more than 500 million RMB to *Neopyropia* farming in the winter of 2016 (Xing et al., 2017). Blooms of the dinoflagellates *Karlodinium veneficum* and *Takayama acrotrocha* occurred in Haizhou Bay off Lianyungang in North Jiangsu during summer 2020, and also harmed *Neopyropia* farming (Zhang et al., 2022).

In the SYS, different types of algal blooms co-occur; therefore, more attention should be paid to this unique sea area. This appears to be the result of the combined effects of economic development and global climate change in recent decades (Anderson et al., 2012; Trainer et al., 2020).

This paper comprehensively reviews the current status and trends of HABs appearance along the coast of China, with particular focus on the SYS, to document the history of HAB events that have occurred in the water mass over the years. It describes the pattern of increasing HAB diversity in the SYS, and analyzes their formation characteristics to better understand the associated threats to the environment and human health.

2 BACKGROUND AND HAB DIFFERENTIATION

Algal blooms, often referred to as red tides, are exceptional ecological events during which some marine microalgae or even protists proliferate resulting in discoloration at high concentrations (Zhou et al., 2001). However, this description is inadequate for toxic or harmful algal blooms that are not red, or that are toxic despite their occurrence at relatively low concentrations. The definition of HAB is often a societal concept rather than a scientific definition. Generally, HABs in the sea may include red, brown, green, and golden tides.

2.1 Harmful red tides and algal toxins

As a natural phenomenon, red tides have existed since ancient times. In this study, the term "harmful red tides" is used to distinguish them from green and golden tides that are all herein referred to as harmful algal blooms. The production of toxins is frequently responsible for the harmful effects of marine microalgae. As harmful red tide causative species, most *Alexandrium* species produce a variety of saxitoxin derivatives that are responsible for PSP syndrome (Caruana and Amzil, 2018). Shellfish are the main vectors for the transfer of algal toxins to humans. Of the global poisoning incidents caused by the consumption of contaminated seafood, 35% have been attributed to PSP and 30% to diarrhetic shellfish poisoning (DSP) (Hallegraeff et al., 2021).

2.2 Brown tides

Brown tides are caused by picoplanktonic (2–3 μm) microalgae that can attain extremely high cell densities (up to 2–3 million cells/mL) (Sieburth et al., 1988), and can last up to 8 weeks (Probyn et al., 2001); they exhibit a brown color at high cell densities, differentiating them from other HABs (Cosper et al., 1990). The main causative species of brown tides worldwide are the pelagophytes *Aureococcus anophagefferens* and *Aureoumbra lagunensis* (DeYoe et al., 1997). When concentrations exceed ~2×10^5 cells/mL, brown tides can result in mass mortalities of wild and cultured shellfish populations; alter the structure and function of marine ecosystems; and affect the reproduction, recruitment, and survival of bivalve species (Gastrich and Wazniak, 2002). Due to their broad ecological effects, they have been referred to as ecosystem disruptive algal blooms (Sunda et al., 2006).

2.3 Green tides

Generally, green tides are caused by the rapid and large-scale proliferation or aggregation of macroalgal chlorophytes after they break away from the attachment base to form aggregations of their thalli (Yu et al., 2018). They usually occur in semi-enclosed sea areas such as estuaries or inner bays, and are mostly caused by the genera *Ulva*, *Cladophora*, and *Chaetomorpha* (Ye et al., 2011). Green tides can harm coastal ecosystems by virtue of their sheer physical mass. They can block the photosynthesis of local primary producers via shading and lead to negative effects such as degradation of seagrass habitat (Valiela et al., 1997; Barnes, 2019). Additionally, if not removed in time, they may result in H_2S production from their anoxic interior (Smetacek and Zingone, 2013), which will have further detrimental effects on coastal ecology and tourism economy (Fletcher, 1996).

2.4 Golden tides

Golden tides are formed by the floating macroalga *Sargassum*, when it detaches from the sea bottom (Yoshida, 1963). They grow rapidly and accumulate on the sea surface over large areal scales, and have previously been mainly restricted to the beaches between the Gulf of Mexico and Bermuda (Smetacek and Zingone, 2013). However, due to the continuous expansion of Atlantic *Sargassum* in recent years, multiple blooms have occurred along the Brazilian coast in the South Atlantic, particularly from 2011 to 2015 (Sissini et al., 2017). Additionally, *Sargassum* is widely distributed along the coast of China, Japan, and Korea (Komatsu et al., 2014; Xu et al., 2018). Blooms of Sargassum in the Atlantic, extending from the West Indies across to West Africa, have been found to contain high concentration of toxic arsenic (Devault et al., 2021).

In the SYS, *Sargassum* attains high biomass, but toxin production has not been recorded. Before 2012, floating *Sargassum* in the East China Sea was mainly distributed in the open sea causing no major harm, and therefore did not attract much attention. However, the frequency and distribution area of floating and drifting *Sargassum* in the Yellow Sea and the East China Sea have significantly increased since 2015, thus, critically affecting the coastal social economy of Dalian Beach, Rongcheng aquaculture facilities, the Haiyang Nuclear Power Plant, and *Neopyropia* farming in Jiangsu Province. The impact on coastal social and economic development has greatly increased over the last decade.

3 HAB DIVERSITY IN THE SOUTHERN YELLOW SEA

Harmful algal blooms in China are characterized by their species diversity, and have different sources and modes of action (Gu et al., 2021; Liu et al., 2021a; Xiao et al., 2021). In the spring and summer of 2017, a 35°N transect in the SYS documented a hitherto rare co-occurrence of green, golden, and harmful red tides (Kong et al., 2018), indicating degradation of the marine environment and severe ecosystem changes in this region. The interaction among HABs, and their succession and evolution, have thus become increasingly important and worthy of attention.

Previously, the SYS has attracted a great deal of attention due to the prevalence of green tides. In recent years, however, golden tides and harmful red tides have also raised considerable alarm, without diminishing the importance of green tides that have continued to occur in the region.

3.1 Characteristics of green tide formation in the SYS

Green tides in the SYS are mainly formed by *Ulva*, more specifically, a newly identified floating ecotype of *Ulva* (Zhao et al., 2015), that persists for many years. During early ontogeny, the living

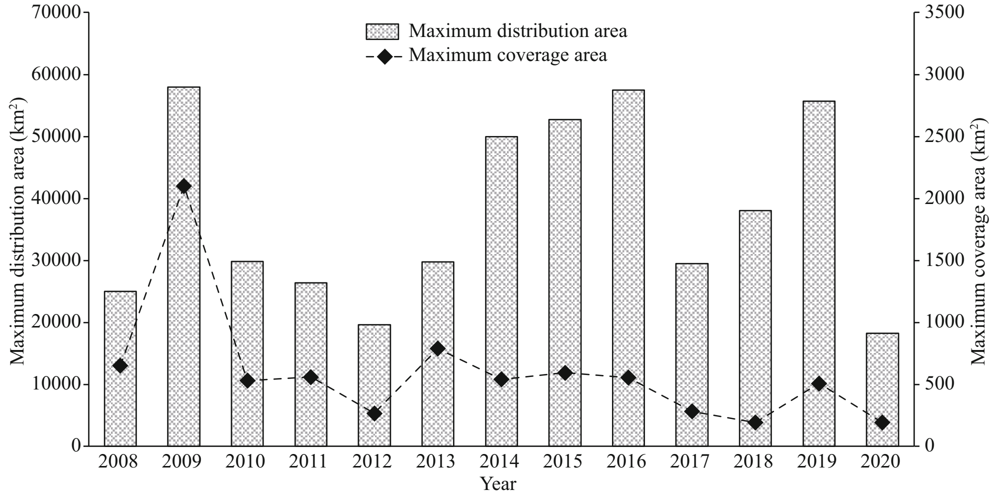

Fig.1 Variation on the maximum daily distribution and coverage area of the *U. prolifera* green tides in the SYS since 2008

Data source: the Bulletin of China Marine Disaster: 2009–2020 (MNR, 2009–2020).

environment of the floating *Ulva* is very similar to that of the intertidal stationary *Ulva*. However, during the former's later growth stage, it always floats at the sea surface. These algae occur both floating on the surface and in suspension below the surface, and therefore have different light adaptation strategies depending on where in the water column they occur (Zhao et al., 2016).

Green tides of the SYS originate every year from the sandbanks of the Subei Shoal, in April through May. *Neopyropia* culture rafts play a role in 'amplifying' the initial biomass of green tides by providing a substrate near the surface. After *Neopyropia* harvest, the attached green algae are removed from the rafts and fragments of *U. prolifera* fronds become floating (Zhou et al., 2015). Then, under the action of wind and currents at the surface, the floating chlorophytes drift northward during which rapid proliferation. The green tide area has progressively expanded, eventually affecting the south coast of the Shandong Peninsula. The distribution area, equal to the sum of the coverage area and the gap between the floating patches, reaches its maximum in June–July. Additionally, during June-July, green tides reach the mainland and successively affected a larger coastal area. Finally, in late July and August, they mostly disappear in the coastal waters off the Shandong Peninsula. The occurrence of green tides over the years is shown in Fig.1.

Ulva is a non-toxic green macroalgae that can be used for food, animal feed, fertilizer, and bio-energy production (Zhang et al., 2019). However, if green tides attain a large biomass of floating *Ulva* and cannot be effectively removed or harvested within a short time, they will also produce toxic gases from their anoxic interior, which pollute the sea and air, and negatively affect the health of coastal residents and tourists. During late green tide stages, the decomposition of this chlorophyte also leads to the release of high concentrations of nutrients that stimulate the growth of microalgae, and can thus cause secondary impacts such as harmful red tides (Kong et al., 2018).

3.2 Characteristics of golden tide formation in the SYS

Sargassum has appeared in the Yellow Sea in China since 2000 (Komatsu et al., 2008). It occurred in the coastal waters of Zhejiang Province in 2012, and has reappeared almost every year in February to March since then (Qi et al., 2017). In recent years, *Sargassum*, accompanied by *Ulva*, has ravaged the southern coast of Shandong Peninsula and Dalian waters in the summer. After invading the *Neopyropia* farming area of the Subei Shoal, a large biomass has also damaged a large number of raft facilities. Taking 2016 as an example, the massive invasion of *S. horneri* resulted in a total direct loss of 500 million RMB (77 million US$) to the *Neopyropia* farming industry in Yancheng and Nantong, Jiangsu Province.

Habitats along the Jiangsu coast are unsuitable for the growth of benthic *S. horneri* populations, but adjacent regions may all provide a source (Huang et al., 2018). Using satellite imagery, Xing et al. (2017) found in 2016 that the floating path of *S. horneri* golden tides could be traced from coastal waters at the eastern end of the Shandong Peninsula to the Subei Shoal. Qi et al. (2017) focused on the drift path of the golden tide in 2017 and speculated that it originated in the coastal waters of Zhejiang Province. Ding et al.

Table 1 The Occurrence of Golden Tides in the SYS over the years (2013–2021)

Year	Region	Biom. (10^4 t)	Peak distr. area (km^2)	Peak coverage area (km^2)	Discovery time	Peak time	Impact	Reference
2013	SER	–	20	0.4	Jun., 20	–	Co-occurrence with *Ulva* in Qingdao littoral and biomass reached 20% of *Ulva* in some areas on June 23*	Kong et al., 2018
2015	ZL	–	–	–	Feb.	–	Coastal area of Jeju Island in total algal mass of 12 100 t and Dalian Beach with average daily cleanup of over 20-t algal mass	Qi et al., 2017
2016	WYS	–	20 000	50.1	Oct., 18	Dec.	Total lost >5×10⁸ RMB in *Neopyropia* farms in Subei Shoal, Nantong, and Yancheng	Xing et al., 2017
2017	JL	30	–	240.0	–	May 7	Lasted 233 days in Jiangsu	JSMFB, 2011–2017
	ZL	100	160 000	530.0	Mar., 1	May 18	–	Qi et al., 2017
2018	ZL	–	27 761	–	Apr., 29	–	–	Ding et al., 2019
2019	CRE	–	–	–	Mar.	–	–	Unpublished data
	SS	–	–	–	May	–	–	Unpublished data
2020	SS	~6.86	–	–	Apr.	–	–	Unpublished data
2021	SS	~1.29	–	–	Apr.	–	–	Unpublished data

*: data from North China Sea Environmental Monitoring Center, State Oceanic Administration; Biom.: biomass; peak distr. area: peak distribution area. SER: Sea area east of Rizhao; ZL: Zhejiang littoral; WYS: Western Yellow Sea; JL: Jiangsu littoral; CRE: Changjiang (Yangtze) River estuary; SS: Subei Shoal. – means no data.

(2019) believed that sessile *S. horneri* in the mussel, *Mytilus galloprovincialis*, farming area along the coast of Zhejiang may be one of the sources of golden tides. Thus, golden tides in the SYS may have a dual origin, although this remains unclear. Additionally, the *Sargassum* golden tide is known to influence the occurrence of *Ulva* green tides, indicating that the interaction between multiple HABs requires further attention. The occurrence of golden tides over the years is shown in Table 1.

3.3 Characteristics of harmful red tides formation in the SYS

Compared with other bodies of water off the coast of China, harmful red tides recorded in the SYS were previously much less important in terms of the toxic outbreak frequency and the geographic range of toxin influence (Yu et al., 2012); however, more recently an increasing trend has been documented. Several studies in 2020 showed that the coast of Lianyungang City experienced harmful red tides of the dinoflagellates *K. veneficum* and *T. acrotrocha*, *Heterocapsa* sp. (unpublished data). Based on the data in Table 2, we can draw the following conclusions. Harmful red tides in the Jiangsu sea area of the SYS have occurred mainly since 2000. The timing of the blooms varies from April to November, although they are most common in May, and are mainly located along the coast of Lianyungang and Nantong, Jiangsu Province. The area of harmful red tide outbreaks has ranged from hundreds to thousands of km^2, and the main causative species of these blooms have been the diatoms *Skeletonema* sp., *Thalassiosira* sp., and *Eucampia zoodiacus*, and the dinoflagellates *Gymnodinium catenatum*, *Heterosigma akashiwo*, *Amphidinium carterae*, and *Noctiluca scintillans*, and more rarely, raphidophytes. All these species have damaged the marine ecosystem due to their toxicity and/or high biomass. In the Shandong area of the SYS, there were eight records of harmful red tides in 2009, making it the year with the most frequent red tides in the history of this region. The causative species of harmful red tides since 2009 are mainly *N. scintillans*, while red tides of the ciliate *Mesodinium rubrum* were more prevalent before 2009. The locations of harmful red tide occurrence are concentrated in the water adjacent to Qingdao, Rushan, Rizhao, and Rongcheng. The initiation of red tides has shown a trend of earlier appearance over the years. The data by area is shown in Table 2.

There are approximately 5 000 species of phytoplankton in the ocean, of which around 200 are toxic (Sournia, 1995; Du and Lu, 2008; Sarkar, 2018; Hallegraeff et al., 2021). Marine microalgae can produce a variety of toxins, most commonly including paralytic shellfish toxins (PSTs), diarrhetic shellfish toxins (DSTs), amnesic shellfish toxins (ASTs) or domoic acid, neurotoxic shellfish toxins (NSTs) or brevetoxins, and ciguatoxins (CTXs) (Egmond et al, 2004). The status of algal toxins in the SYS over the years, in terms of samples at various locations and their toxicities, is shown in Table 3.

The algal toxins in the adjacent sea area of Shandong in the SYS are dominantly DSTs, while both PSTs and DSTs have been detected in the seas adjacent to Jiangsu. The poisoning incidents caused by algal toxins along the SYS coast can mostly be attributed to PSTs. The toxic outbreaks caused by red tides in Lianyungang warrant further attention due to their high frequency. Real-time monitoring of shellfish poisoning, and parallel tracking of the occurrence of toxic HABs, will help provide a better scientific basis for developing suitable biotoxin management strategies.

4 CAUSES AND TRENDS IN HAB DIVERSITY IN THE SYS

While the evidence for increase in HABs worldwide is not clear (Hallegraeff et al., 2021), the diversity, frequency, and intensity of HABs in the SYS have clearly increased from 2000 to 2020. The ecological environment of the SYS has changed, as evidenced by the co-occurrence of diverse HABs, which is rare worldwide. Harmful algal blooms are becoming increasingly severe, resulting in intensification of the impacts to the ecological environment, mariculture and the coastal society and economy. As indicated earlier, they have also become more diverse and complex.

The diverse HABs in the SYS occur in the context of global warming and climate change, human activities, marine environmental conditions, and ocean dynamic processes. First, with regard to global warming, the water temperature in coastal China has increased significantly (Pei et al., 2017; Yu et al., 2019; Li et al., 2020), such that warm water HAB species now tend to extend northward. Secondly, the development of China's coastal industries and agriculture, sewage and

Table 2 Summary of harmful red tides in the SYS over the years

	Location	Period	Times	Total area (km^2)	Dominant species	Consequence	Reference
Jiangsu	Uncertain	2000	4	>200	Uncertain	–	MNR, 2009–2020; Liang, 2012
		May–Jun., 2001	4	>1 030	Uncertain	–	Liang, 2012
	Lianyungang	Aug., 2002	1	1	Uncertain	–	Liang, 2012
		May–Sep., 2004	2	100	*N. scintillans*, *Gonyaulax polygramma*	Marine ecosystem damaged	Zhang and Liu, 2009; Peng et al., 2010; Liang, 2012
		Sep.–Oct., 2005	4	1 275	*Skeletonema costatum*, *G. catenatum*	Direct economic loss of 5 million RMB	Zhang and Liu, 2009; Peng et al., 2010; JSMFB, 2011–2017; Liang, 2012
		Oct., 2006	1	600	*E. zoodiacus*, *G. catenatum*	Ecosystem severely damaged	Peng et al., 2010; JSMFB, 2011–2017
		May–Jul., 2007	3	582.4	*H. akashiwo*, *Thalassiosira* sp., *Chattonella* sp.	–	MNR, 2009–2020; Peng et al., 2010; Liang, 2012
		May, 2008	1	70	*H. akashiwo*, *A. carterae*	–	Liang, 2012
		Apr.–Jul., 2009	3	270	*Karenia mikimotoi*	–	Liang, 2012; Cao et al., 2019
		Apr.–Jul., 2010	2	220	*G. catenatum*	–	MNR, 2009–2020; Liang, 2012
		Sep., 2011	1	200	*S. costatum*	–	JSMFB, 2011–2017; Gao et al., 2017
		Jun.–Jul., 2012	2	350	*S. costatum*	–	JSMFB, 2011–2017; Cao et al., 2019
		May, 2013	1	450	*H. akashiwo*	–	JSMFB, 2011–2017; Peng et al., 2015; Gao et al., 2017
		May–Jun., 2017	3	>100	*S. costatum*, *G. catenatum*, *K. mikimotoi*, *H. akashiwo*	–	MNR, 2009–2020; JSMFB, 2011–2017; Kong et al., 2018
	Nantong	1997	2	Uncertain	Uncertain	–	Gao et al., 2017
		Jun., 2002	1	80	Uncertain	–	Liang, 2012
		Jul.–Aug., 2008	3	770	*Asterionella japonica*	–	Liang, 2012; Cao et al., 2019
		Jun., 2009	1	420	Uncertain	–	Liang, 2012
		May, 2010	1	400	*S. costatum*	–	MNR, 2009–2020
		May, 2012	2	137	Uncertain	–	JSMFB, 2011–2017; Cao et al., 2019

To be continued

Table 2 Continued

Location		Period	Times	Total area (km^2)	Dominant species	Consequence	Reference
Shangdong	Uncertain	Jun., 2012	1	10	*N. scintillans*	–	SDDOF, 2001–2017
	Rizhao	May, 2009	1	580	*N. scintillans*	–	MEE, 2009–2017
		May–Jun., 2012	1	780	*N. scintillans*	–	SDDOF, 2001–2017
		Mar.–Apr., 2017	2	0.000 92	*N. scintillans*	–	SDDOF, 2001–2017
	Qingdao	Jul., 1998	1	9	*S. costatum*, *Biddulphia regia*	–	Huo et al., 2001b; Liang, 2012
		Jun.–Jul., 1999	3	>86	*N. scintillans*, *S. costatum*, *M. rubrum*	–	Huo et al., 2001a; Lu et al., 2001; Yao, 2004; Liang, 2012;
		Jul., 2000	2	12	*N. scintillans*, *S. costatum*, *Actinocyclus ehrenbergii*, *E. zoodiacus*	–	Yan et al., 2001; Liang, 2012
		Jul., 2001	2	>9.8	*M. rubrum*	–	SDDOF, 2001–2017
		Jun.–Aug., 2002	2	>60	*M. rubrum*, *Dinophysis fortii*	–	SDDOF, 2001–2017; MEE, 2009–2017
		Jun.–Aug., 2003	3	>451	*S. costatum*, *M. rubrum*, *Gonyaulax spinifera*	–	Yao, 2004; MEE, 2009–2017; Liang, 2012
		Feb.–Aug., 2004	3	>120	*Thalassiosira nordenskioldii*, *Skeletonema* sp., *M. rubrum*, *K. mikimotoi*	–	Liang, 2012; Yao, 2004
		Jun., 2005	1	80	*H. akashiwo*	–	Liang, 2012
		Jun.–Sep., 2007	2	78	*H. akashiwo*, *G. spinifera*, *Alexandrium Tamarense*	–	Liang, 2012; Liang et al., 2019; SDDOF, 2001–2017
		Jun.–Aug., 2008	2	106	*Heterocapsa* sp., *M. rubrum*, *Chattonella marina*	–	Liang, 2012
		Apr., 2009	2	0.003 5	*N. scintillans*	–	Liang, 2012
		May–Sep., 2012	2	10.4	*N. scintillans*, *Cochlodinium* sp.	–	SDDOF, 2001–2017
		May, 2013	1	~0.039	*N. scintillans*	–	SDDOF, 2001–2017
		Apr., 2014	1	~0.01	*N. scintillans*	–	SDDOF, 2001–2017; JSMFB, 2011–2017
		Mar., 2017	2	0.000 33	*N. scintillans*	–	QOFA, 2017
		Mar.–Sep., 2020	3	~0.001	*N. scintillans*	–	NCSB, 2020
	Yantai to Weihai	May–Jun., 2009	1	550	*N. scintillans*	–	MEE, 2009–2017, 2009–2020
	Weihai	Aug., 2003	1	3	*C. marina*, *D. fortii*	–	Liang, 2012
		2008	2	>9	*Akashiwo sanguinea*	–	SDDOF, 2001–2017; Liang, 2012
		Apr., 2009	1	20	*N. scintillans*	–	SDDOF, 2001–2017
		May–Aug., 2009	3	180.45	*N. scintillans*, *C. marina*, *Katodinium glaucum*	–	SDDOF, 2001–2017; Liang, 2012
		May–Aug., 2011	2	Uncertain	*A. anophagefferens*, *K. veneficum*	A large amount of fish and shrimp died	Kong et al., 2012; Xu et al., 2012, 2014

– means no obvious economic loss or no reports.

waste discharge activities have led to eutrophication of coastal waters, and exerts great pressure on the local marine ecology as well as providing a basis for the occurrence of HABs. Furthermore, China has a well-developed marine aquaculture industry; the scale of *Neopyropia* farming in coastal cities, such as Nantong, Yancheng, and Lianyungang in Jiangsu, has also been expanding (Zhang et al., 2014) and this massive increase in coastal aquaculture facilities has greatly changed the marine ecological environment. Finally, the appearance and transport of HABs are closely related to the physical environment and dynamic processes in the sea area, especially wind-driven currents caused by the southward winter monsoon and northward summer monsoon that can drive HABs northward and southward, respectively.

The offshore waters of the SYS in China mainly include the seas south of the Shandong Peninsula

Table 3 The overview of marine biotoxins in the SYS from 1994 to 2015

Toxin type	Sampling area	Sampling date	Sample	No. of sample	Detection rate (%)	Toxicity level	Maximum	Reference
DSTs	Jiaozhou Bay	1994	Bivalve	308	2.9	–	–	Li et al., 2000
		1995	Bivalve	219	7.7	–	–	Li et al., 2000
		May–Jul., 1995	Bivalve	2	100	>0.05 Mu/g*	–	Li et al., 2000
		1996	Bivalve	278	6.8	–	–	Li et al., 2000
	Coastal Qingdao	Mar.–Aug., 1997	*R. philippinarum*	1	100	542.9 μg/kg	–	Li, 2005
		Mar.–Aug., 2010	Seawater	5	100	6–311 pg/m³	311 pg/m³	Luo, 2011
	Lianyungang	Jan. 19, 1996	*Scapharca subcrenata*	1	100	15.7 μg/kg	–	Zhou et al., 1999; Li, 2005
		Jul. 30, 1996	*R. philippinarum*	1	100	71 μg/kg	–	Zhou et al., 1999; Li, 2005
		Nov. 20, 1996	*S. subcrenata*	1	100	99 μg/kg	–	Zhou et al., 1999; Li, 2005
		Dec. 20, 1996	*R. philippinarum*	1	100	102.9 μg/kg	–	Zhou et al., 1999; Li, 2005
		Feb.–Aug. 1997	*S. subcrenata*	3	100	42.9–130 μg/kg	130 μg/kg	Zhou et al., 1999; Li, 2005
		Mar.–Apr., 1997	*Mactra veneriformis*	2	100	94.3–160 μg/kg	160 μg/kg	Zhou et al., 1999; Li, 2005
		Nov. 2007–Aug., 2008	*Pinna inflata*	21	33.3	–	–	Huang et al., 2013
		Aug. 25, 2010	*Ostrea* sp.	5	80	30.1–39.8 μg/kg	39.8 μg/kg	Song et al., 2013
		Sep. 13, 2010	*Ostrea* sp.	12	83.8	20.9–74.5 μg/kg	74.5 μg/kg	Song et al., 2013
		May–Aug., 2011	*Ostrea* sp.	18	66.7	20.3–52.5 μg/kg	52.5 μg/kg	Song et al., 2013
		Apr.–May, 2012	*Ostrea* sp.	7	57.1	15.8–35.6 μg/kg	35.6 μg/kg	Song et al., 2013
PTXs**	Jiaozhou Bay	Jul.–Aug., 2006	Seawater	1	100	40–107 μg/kg	107 μg/kg	Li et al., 2010
	Coastal Qingdao	Apr.–Dec., 2010	Seawater	5	100	90–7 400 pg/m³	7 400 pg/m³	Luo, 2011
PSTs	Jiaozhou Bay	Sep., 1994–Jan., 1996	Bivalve	805	0	0	0	Li et al., 2000
	Coastal Qingdao	Nov.–Dec., 1997	*R. philippinarum*, *Crassostrea gigas*, *M. galloprovincialis*, *Chlamys farreri*	7	0	0	0	Guan et al., 1999
	Lianyungang	Aug. 15, 1997	*S. subcrenata*	1	100	17 μg/kg	–	Li, 2005
		Dec. 4, 1997	*S. subcrenata*	1	0	0	–	Guan et al., 1999
		Dec. 4, 1997	*Neverita didyma*	1	–	6.4 Mu/g	–	Guan et al., 1999
		Apr. 6, 2003	*S. subcrenata*	3	100	24.4–57.6 μg/kg	57.6 μg/kg	Li, 2005
		Jun.–Jul., 2003	*C. farreri*	10	100	2.8–380.8 μg/kg	380.8 μg/kg	Li, 2005
		Jun.–Jul., 2003	*C. farreri*	7	100	–		(Li, 2005)
		Nov., 2007–Oct., 2008	*P. inflata*	21	0	0	0	Du et al., 2013
		2008	*R. philippinarum*		6 people poisoned and 1 died			Yu and Luo, 2016
	The SYS	2006–2008	Shellfish	122	26.2	–	1 567 μg/kg	Liang, 2012
		2006–2008	Shellfish	122	0.8	–	341 μg/kg	Liang, 2012
		2013–2015	Shellfish	100	64	–	453 154 μg/kg	Liang et al., 2019

Most of the toxicity is expressed as μg/kg of soft tissue wet weight. *: A mouse unit (Mu) is the amount of toxin required to kill a 20-g mouse in 15 min via intraperitoneal injection. **: PTXs: pecteno-toxins that was once classified as DSTs. – means no data.

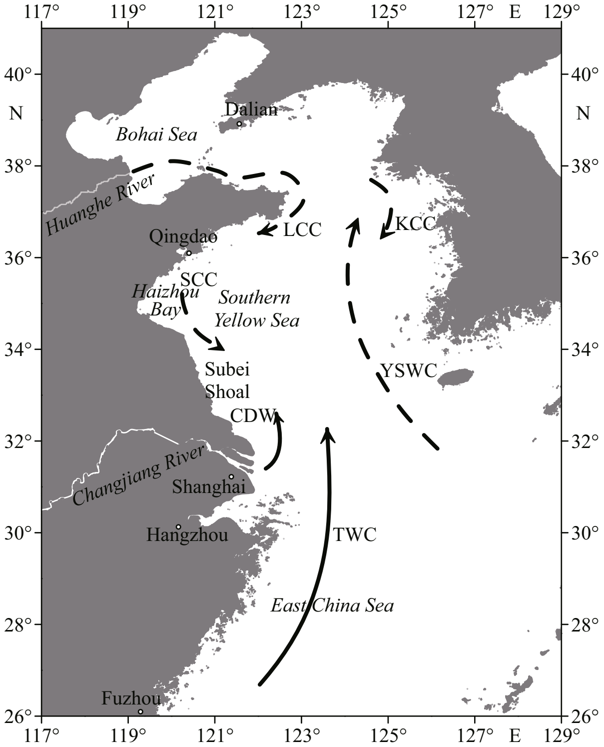

Fig.2 The location and currents of the SYS in China

CDW: Changjiang River diluted water; TWC: Taiwan Warm Current; YSWC: Yellow Sea Warm Current; SCC: Subei Coastal Current; LCC: Lubei Coastal Current; KCC: Korea Coastal Current. The arrowed solid lines and dashed lines mark the currents that predominated in summer and winter, respectively (modified after Guo et al. (2020)).

and those east of Jiangsu Province (Fig.2). As a part of a semi-enclosed continental shelf marginal sea in the Western Pacific, the SYS not only lies in the East Asian monsoon area, but is also affected by the Kuroshio Current and El Niño phenomenon (Wu et al., 2018; Liu et al., 2021b). The ecology of the region is affected by both climate change and intensive human activities, resulting in the increasing prominence of ecological problems such as HABs (Gu et al., 2021). Currents in various directions in different seasons have also contributed to the particular co-occurrence of diverse HABs in the SYS (Fig.2).

The diverse HABs in the SYS are also interconnected. Firstly, there is competition for nutrients and space among algal species, as well as mutual inhibition or promotion via allelopathy. Laboratory studies have found that the relationship between different HAB species is largely one of mutual inhibition (Liu, 2015; Cai et al., 2019), but the dominant species tend to change under different conditions. For example, *Ulva* plays a dominant role in its interactions with microalgae at different development stages (Liu, 2015). Both *S. horneri* decomposition medium and culture medium can inhibit the attachment and germination of microscopic propagules of *U. prolifera* at high concentrations but can promote them at low concentrations (Cai et al., 2019), and can also inhibit the growth of some causative species of harmful red tides (Cai et al., 2019). Field observations have indicated that there is also connection among HABs. As shown in Table 1 and Fig.1, the maximum distribution area of the golden tide in 2017 reached its peak (about 160 000 km^2), while the maximum distribution area of the green tide in the same year was relatively small (29 522 km^2). At the same time, the transport of nutrients and metabolites released during the decomposition of an organism may contribute to the occurrence of harmful red tides elsewhere. These interactions and their underlying mechanisms remain unclear and merit further investigation.

5 CONCLUSION

From a global perspective, once they appear, many HABs become recurrent in a given sea area, which gradually deteriorates the marine environment and negatively affects human health. The set of co-occurring complex and diverse HABs in the SYS is unique worldwide. It strongly indicates a deteriorating environment, and a potential threat to ecology and human health. Based on field observations and remote sensing, more data should be collected for further research on the early warning and prediction of diverse HABs to help develop comprehensive prevention and control measures. Furthermore, diverse HABs and aquaculture activities are interrelated. To some extents, human activities have intensified HABs in the SYS by affecting the marine environment. Moreover, interrelationships among diverse HABs under field conditions remain unclear. Therefore, there is an urgent need for the early warning and control of HABs based on the characteristics of diverse HABs, their environmental adaptability, the mechanisms of inter-specific competition, and their main controlling factors.

6 DATA AVAILABILITY STATEMENT

All data generated and/or analyzed during this study are included in this published article.

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