Competitive advantages of HAB species under changing environmental conditions in the coastal waters of the Bohai Sea, Yellow Sea and East China Sea

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ABSTRACT

Harmful algal blooms (HABs) have become a severe ecological problem in coastal waters in recent decades. Under the enhanced anthropogenic disturbance, the Eastern Chinese coastal seas (ECCS), including the coastal waters of the Bohai Sea (BS), Yellow Sea and East China Sea, have been suffering environmental changes dramatically during the past 40 years. However, it is not clear how changes in coastal nutrient pollution, hydrodynamics and climate promote the succession of dominant HAB species simultaneously. In this study we used physical criteria (light availability, temperature and salinity) and chemical criteria (strategy of nutrient utilization) to quantify the competitiveness of the primary HAB species in the ECCS, i.e. *Skeletonema costatum, Noctiluca scintillans, Prorocentrum donghaiense, Karenia mikimotoi,* and *Aureococcus anophagefferens.* A risk assessment module has been developed and applied to this study based on the physical criteria of the main HAB species. Model result indicated a strong reliability on locating the potential physical habitat of blooms dominated by specific species. Imbalanced nutrient stoichiometry plays a vital role in HAB species succession in the ECCS, especially potential limitation of dissolved inorganic phosphorus. Due to long water residence time, persistence of nutrient imbalance and organic nutrient accumulation induce frequent blooms of *Aureococcus anophagefferens* in the BS. Observations and experiments have limitations when describing combining processes that influence HAB development, and need to be complemented with advanced mechanistic models for describing the hydrodynamics and biogeochemistry to allow for hindcasting and forecasting HAB risk under changing environmental conditions.

1. Introduction

There is increasing evidence that changes in climate and nutrients contribute to global eutrophication and the spreading and increasing frequency and areal extent of harmful algal blooms (HABs) (Glibert, 2020; Gobler, 2020; Wells et al., 2020). With severe ecological impacts, like losses of habitat, decrease in phytoplankton diversity and fish deaths, at present HABs are one of the most urgent global environmental problems (Berdalet et al., 2016; Grattan et al., 2016; Lewitus et al., 2012) and may prevent us from achieving Sustainable Development Goal 14 (Life below water) (SDG-14) (UN, 2022).

During the past four decades, HABs in the Eastern Chinese coastal seas (ECCS) (Fig. 1), including the Bohai Sea (BS), Yellow Sea (YS) and East China Sea (ECS), occurred more often in new and different locations, with changing HAB species that cover increasing areas. Before 1980, the frequency and areal extent of reported HABs were insignificant, and most algal blooms involved harmless diatom species such as *Skeletonema* spp (Greville, 1866). After 1980, both the frequency and areal coverage of reported HABs increased rapidly and the dominant species switched to dinoflagellates, although monitoring frequency also increased since the 1980s (Jiang et al., 2014). Globally, rising diatom/dinoflagellate ratios occurred earlier in coastal areas closed to

developed countries than in the ECCS (Sakamoto et al., 2021; Wasmund et al., 2017). However, changes of diatom/dinoflagellate ratio showed regional differences worldwide after initiatives were launched by local authorities to migrate terrestrial nutrient pollution (Hinder et al., 2012; Leterme et al., 2006; Sakamoto et al., 2021). Those inconsistent variations lead to the evolution of HABs in the ECCS more unpredictable.

Meanwhile, the number of different HAB species has been increasing (Yan et al., 2022; Yu et al., 2018), especially in the coastal waters of the ECS (Cui et al., 2021; Liu et al., 2013) (Fig. 1). *Prorocentrum donghaiense* (*P. donghaiense*) (Lu and Goebel, 2001) which is currently regarded as a synonym of *Prorocentrum obtusidens* (*P. obtusidens*)(Schiller, 1928), had become a dominant HAB species with circa 120 HAB occurrences in the coastal waters of the ECS between 2000 and 2006 (Wang and Wu, 2009). The large area covered and the long duration of *P. donghaiense* blooms severely impacted the marine ecosystem and caused loss of aquaculture production (Wang et al., 2020a) by inducing the oxygen depletion. *Karenia mikimotoi* (*K.mikimotoi*)(Miyake & Kominami ex Oda) Gert Hansen & Moestrup (Hansen et al., 2000) blooms in the ECS were first recorded in 1998 and have been recorded almost every year since 2002 (Chen et al., 2021b). *K.mikimotoi* is a typical ichthyotoxic species which through production of toxins caused the death of finfish, shellfish and other invertebrate species (Lu and Hodgkiss, 2004; Yamasaki et al., 2004). Besides dinoflagellates, the pico-sized species *Aureococcus anophagefferens* (*A. anophagefferens*)(Sieburth et al., 1988), leads to so-called brown tides in the BS every year since 2009 (Ou et al., 2018; Yao et al., 2019). *A.anophagefferens*, belonging to the Pelagophyceae, can reach cell densities of 10^6 cells ml^{-1} during blooms and leads to detrimental effects on the abundance of grazers (Bricelj et al., 2004; Gong et al., 2015; Huang et al., 2020a; Zheng et al., 2018). Blooms of the dinoflagellates *P.donghaiense* and *K.mikimotoi* and Pelagophyceae *A.*

anophagefferens can be more harmful than that of many diatoms, and can lead to larger economic loss every year (Chen et al., 2021b; Zhou et al., 2008).

The focus of this study is the ECCS (Fig. 1), where dramatic changes in phytoplankton production and composition have occurred in response to environmental changes. During the past few decades, nitrogen (N) and phosphorus (P) discharge from land based-sources to coastal waters increased rapidly due to the excessive use of fertilizers, intensive freshwater aquaculture and increasing sewage pollution (Liu et al., 2018; Qu and Kroeze, 2010; Wang et al., 2019a, 2020b). Apart from the enhanced nutrient loading, there is an increasing stoichiometric imbalance between different nutrient forms in the ECCS (Liu et al., 2016a; Wang et al., 2019b, 2021; Wei et al., 2015; Yang et al., 2018b).

Under the umbrella of many international programs, the number of studies on HABs in the ECCS has been increasing since the 2000s (Furuya et al., 2018). Most studies explored the impact of one or more environmental factors, like temperature, light intensity and nutrient uptake and availability, on the specific species using lab culture experiments (Chen et al., 2005; Huang et al., 2020b; Wang et al., 2011; Wen et al., 2018, 2019; Yu et al., 2006), while other studies illustrated the linear relationship between phytoplankton community evolution and nutrient pollution (Chen et al., 2021a, 2021b; Li et al., 2014a; Lin et al., 2005; Liu et al., 2013, 2016a; Xin et al., 2019; Zhou et al., 2008) or warming (Chen et al., 2021a, 2021b; Lin et al., 2005; Xiao et al., 2018, 2019) covering time periods of decades. However, different HAB species have different physiological characteristics and strategies to adapt to changing environmental conditions (Brun et al., 2015). With specific competitive advantages, the evolution of one HAB species is a response to several simultaneous environmental changes (d'Ovidio et al., 2010). However,
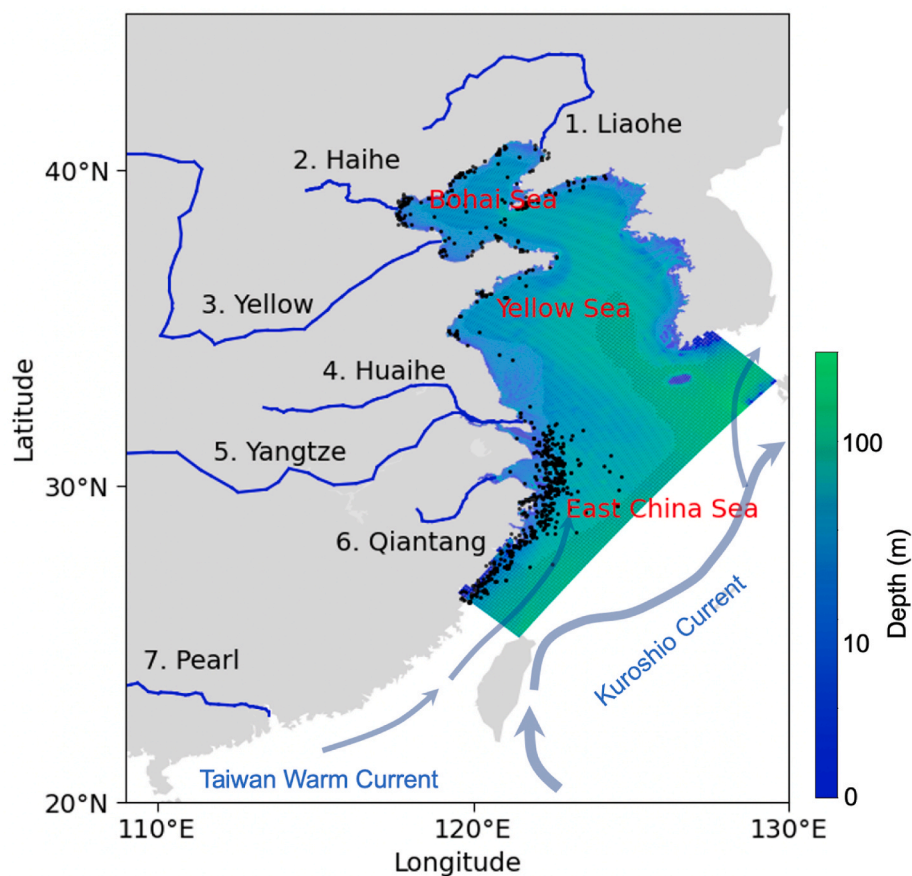

Fig. 1. Location distribution of HABs in the Eastern Chinese coastal waters during the period 1933–2015. Black dots are locations where HAB occurred (HABs data source: Liang (2012); Xiao et al. (2019); and Wang et al. (2021)). Fig. 1 is modified from Wang et al. (2023).

it is poorly documented how changes in nutrient pollution, hydrodynamics and climate promote the succession of dominant HAB species simultaneously in the ECCS.

The aim of this study is to establish a series of criteria based on current understanding of the intrinsic competitive advantage of dominant HAB species in the ECCS under changing abiotic conditions. These criteria can be used as descriptive parameters for HAB risk assessment/predicting tools developed in future research. In this study, we first summarized the preferential environmental adaptation regarding to physical conditions (light, temperature and salinity) and chemical conditions (nutrient availability and nutrient ratios) for the blooms of major HAB species in the ECCS, i.e. the diatom species *S. costatum* (Greville) Cleve, 1866, the dinoflagellate species *N. scintillans* (Macartney) Kofoid and Swezy, 1921, *P.donghaiense* and *K.mikimotoi* and the Pelagophyceae species *A.anophagefferens*. Based on satellite-derived data and the global oceanic physical/biochemical database, the quality of physical criteria for the dominant species was verified by our algorithm. We then came up with a concept of how nutrients concentrations and compositions drive the HAB succession in the ECCS and explained the impact of the environmental changes that have occurred on the observed HAB occurrences.

2. Methods and data

2.1. Chemical/physical data summary

To summarize the light, temperature, salinity and nutrient availability adaptation by different HAB species in the ECCS, we collected observations during HAB events (temperature, salinity and nutrient concentration) and the parameters of the physiological characteristics determined through culture experiments (optimum light intensity, half saturation and maximum uptake velocity of different chemical N forms). In order to eliminate differences caused by habitat adaptability, all selected data were from in-situ observations in the ECCS and laboratory cultures with water and algal material collected from the ECCS. To ensure the comparableness of collected nutrient concentration data, we only used nutrient concentrations measured by spectrophotometry methods (Grasshoff et al., 2009) with consistent standard deviations of DIN, DIP and DSi (±0.05, ±0.02 and ±0.05 μM), respectively.

The ranges for optimum light intensity and temperature for different HAB species were obtained by reviewing 31 literature reports (Tables 1 and 2). The half saturation constant (K_s) and maximum uptake velocity (V_{max}) of different chemical N forms were obtained from 9 published papers (Table 3). The V_{max} can indicate a preference of absorbing N from different N forms and the K_s can reflect the algal competitive ability in an environment with low N concentration (Li et al., 2010).

The observed data of temperature, salinity and dissolved inorganic P (DIP), dissolved inorganic N (DIN) and dissolved silicate (DSi) concentrations during HAB events caused by different species were extracted from 34 published papers (Figs. 2–3) (Tables S1–S3). The physiological characteristics of nutrient utilization by different HAB species were analyzed on the basis of the daily variation of DIP, DIN and DSi concentrations during pre-/post-bloom and bloom periods in bloom events of diatoms, dinoflagellates and Pelagophyceae (Fig. 3). Details for the data sources are listed in the Supplementary Information (Tables S1–S3).

2.2. Physical criteria validation

Base on a suite of physical parameters summary (see sections 3.1-3.3), the physical habitat, including temperature, salinity and light intensity envelopes, for dominant HAB species in the ECCS have been defined (Table S4). Corresponding distributions of those physical parameters in the ECCS were collected from global oceanic database and satillate-derived dataset and the spatial resolutions of all parameters unified to $0.083 \times 0.083°$ (grid size). The algorithm we used to identify

Table 1

The optimum light intensity of the representative HAB species in relation to water temperature in studies performed in the ECCS.

Species	Method	Temperature (°C)	Light saturation (μE m^{-2} s^{-1})	Source
Skeletonema costatum	field culture	22.3 ± 1.8	272	Wang et al. (2008)
	lab culture	25	266	Tian et al. (2002)
Karenia mikimotoi	lab culture	18	81.5	Wen et al. (2019)
	lab culture	22	80.3	Wen et al. (2019)
	lab culture	25	79.3	Wen et al. (2019)
	field culture	22.3 ± 1.8	57.8	Wang et al. (2008)
	lab culture	25	>30	Xu (2006)
Prorocentrum donghaiense	lab culture	18	79.4	Wen et al. (2019)
	lab culture	22	78.2	Wen et al. (2019)
	lab culture	25	76.7	Wen et al. (2019)
	field culture	21.4 ± 2.7	76.4[a]	Sun et al. (2008)
	field culture	22.3 ± 1.8	57.8	Wang et al. (2008)
	lab culture		>60	Yu et al. (2006)
Aureococcus anophagefferens	lab culture	20	50	MacIntyre et al. (2004)

s^{-1}.

[a] The reported unit of light adaptation is W m^{-2}. The wavelength of the radiation is in the range of 400–700 nm according to Sun et al. (2008), and the conversion coefficient between total solar radiation (W m^{-2}) and photo active radiation is 0.47 μE m^{-2}
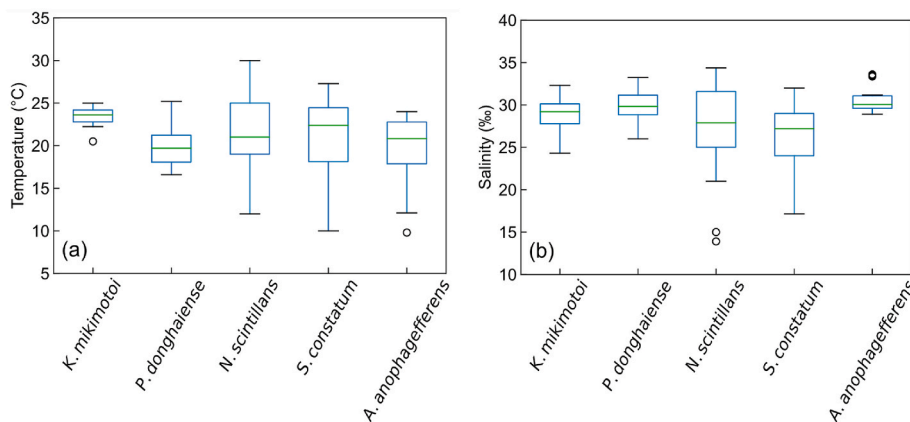
Table 2

The optimum temperature and range for the representative HAB species in ECCS.

| Species	Optimum temperature (°C)	Optimum range (°C)	Source
Skeletonema costatum	25.0		Suzuki and Takahashi (1995)
	22.0		Chen et al. (2005)
	25.0		Yu et al. (2006)
	25.0	20.0–25.0	Eppley (1972)
		24.0–28.0	Zhao et al. (2018)
Prorocentrum donghaiense	25.0	22.0–28.0	Deng et al. (2009)
	21.5	17.4–26.6	Wen et al. (2018)
	24.0	20.0–27.0	Zhao (2006)
	22.0		Chen et al. (2005)
	20.0	18.0–22.0	Wang and Huang (2003)
	20.3		Shen (2014a)
		22.0–28.0	Long (2005)
		23.0–26.0	You (2006)
Karenia mikimotoi	25.0	20.0–25.0	Dai et al. (2014)
	22.4	17.8–27.1	Wen et al. (2018)
	25.0	20.0–27.5	Si (2016)
	23.4		Shen (2014b)
	23.8		Ding and Zhang (2018a)
Noctiluca scintillans		12.0–30.0	Qi et al. (2019)
Aureococcus anophagefferens	20.0		Cosper et al. (1989)

Table 3
The half saturation (K_s) and maximum uptake velocity (V_{max} and ρ_{max}) of different chemical N forms of the representative HAB species in ECCS.

Species	Type of exp.	NO_3^-			NH_4^+			Urea			Amino acid			reference
		V_{max}	ρ_{max}	K_s	V_{max}	ρ_{max}	K_s	V_{max}	ρ_{max}	K_s	V_{max}	ρ_{max}	K_s	
Skeletonema Costatum	Field	0.057	0.21	78.4	0.32	0.14	1.41	0.021	0.091	5.12	0.007	0.031	2.25	Li et al. (2010)
	Field		0.21			0.12		0.05						Lomas and Glibert (1999)
	Culture			0.4 ~ 0.5			0.8 ~ 0.36							Eppley et al. (1969)
	Culture	0.1	0.16	0.4										Lomas and Glibert (2000)
	Culture		0.09	0.33		0.38	5.91		0.74	27.1				Huang et al. (2020b)
Prorocentrum Donghaiense	Field				0.7	0.47	3.9	0.017	0.11	5.27	0.025	0.19	1.76	Li et al. (2010)
	Culture		1.77	1.08		0.08	1.44		0.88	0.64				Huang et al. (2020b)
	Culture	0.034		1.3 ± 0.1	0.067		5.3 ± 1.1	0.045		0.13 ± 0.01	0.032		9.9 ± 0.9	Hu et al. (2014)
	culture				0.075		7.1 ± 0.4	0.04		0.12 ± 0.01	0.031		12.5 ± 0.1	Hu et al. (2014)
Karenia Mikimotoi	Field	0.018	0.34	43.6	0.5	1.22	4.88	0.02	0.578	1.35	0.011	0.28	1.68	Li et al. (2010)
	culture		0.71	0.76		4.66	4.22		0.68	0.3				Huang et al. (2020b)
	Field	0.05		0.20 ± 0.14	0.055		0.35 ± 0.06	0.02			0.03			Bronk et al. (2002)
Aureococcus anophagefferens	culture		0.13	0.06		0.76	0.9		0.16	0.17				Ou et al. (2018)
	culture	0.019		0.15	0.099			0.057		0.04				Lomas et al. (1996)

*Units of K_s, V_{max} and ρ_{max} are μmol N l^{-1}, h^{-1} and μmol N l^{-1} h^{-1}, respectively.

Fig. 2. Temperature and salinity ranges during blooms of different HAB species in ECCS (dots represent outliers).
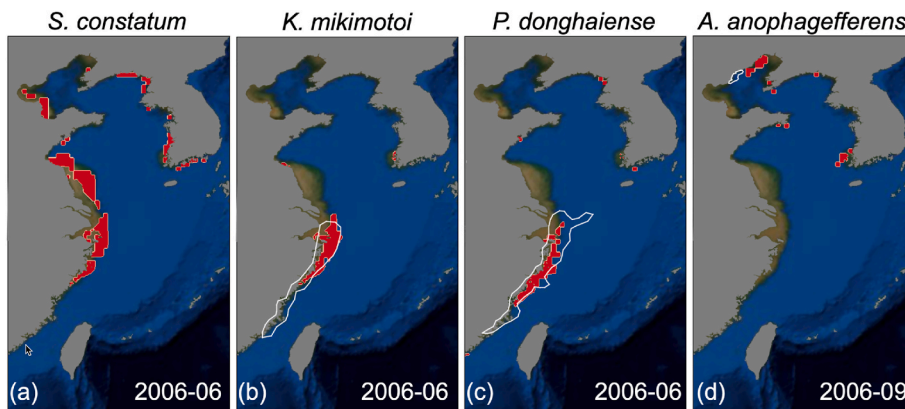
Fig. 3. Spatial suitability of habitat for (a) *S. costatum*, (b) *K.mikimotoi* and (c) *P. donghaiense* in June 2006 and (d) *A.anophagefferens* in September 2006. Red patches represent the physical habitats calculated by our algorithm. White polygons in (b–d) represent the area in where the occurrences of *K.mikimotoi*, *P. donghaiense* and *A. anophagefferens* blooms have been reported frequently (Data sources of the polygons are from Chen et al. (2021b); Lu et al. (2022); Yao et al., (2019).

the physical habitat for each grid from multi physical parameters are as follows:

$$
\begin{cases}
score_{cij} = 1 & if \ Min(Env_{ij}) \leq Para_{cj} \leq Max(Env_{ij}) \\
score_{cij} = 0 & if \ Para_{cj} \leq Min(Env_{ij}) \ or \ Para_{cj} \geq Max(Env_{ij})
\end{cases}
$$

$$
\begin{cases}
habitat_{ci} = True & if \ \sum_{i=1}^{n} score_{cij} = n \\
habitat_{ci} = False & if \ \sum_{i=1}^{n} score_{cij} < n
\end{cases}
$$

Where $habitat_{ci}$ represents if the physical condition in grid c is suitable for bloom of species i; n is the number of parameters in the criterion; The value of $score_{cij}$ represents if the value of the physical condition j in the grid c ($Para_{cj}$) fall into the range of the envelope for species i (Env_{ij}).

The spatial variation of water temperature, water salinity and sea surface light intensity derived from the Copernicus Global Ocean Physics Reanalysis dataset (https://resources.marine.copernicus.eu). In this study, we use the average value in the upper 5 m depth to define the water temperature and salinity values in each grid. In order to obtain the average light intensity in the water column (depth = 5 m), we use the chlorophyll-a (Chl-a) concentration (extracted from the Copernicus Global Ocean Biochemistry Hindcast dataset (https://resources.marine.copernicus.eu)) and suspended sediment concentration (derived from satillate-derived dataset (http://mds.nmdis.org.cn/)) to calibrate the sea surface light intensity (Los et al., 2008).

$$I_d = I_{top} \times e^{(-et_d \times H_d)}$$

$$et_d = eat_d + est_d + eb_d$$

$$eat_d = ea \times Chl_d$$

$$est_d = es \times SPM_d$$

Where I_d represents the light intensity (W m^{-2}) at the water layer d; I_{top} is the light intensity at the water surface; et is the total extinction coefficient (m^{-1}) which is comprised of extinction coefficient of algae (eat), extinction coefficient of suspended sediment (est) and background extinction coefficient (eb). Chl and SPM represent the concentrations of Chl-a (g m^{-3}) and suspended sediment (g m^{-3}), respectively. ea and es are constant extinction coefficients of algae and suspended sediment (m^2 g^{-1}), respectively. H is the water depth (m). Here, the values of ea, es and eb are 0.21, 0.03 and 0.04, respectively (Blauw et al., 2009).

3. Results

3.1. Light

Through in-situ and laboratory culture experiments, the optimum light intensity of different HAB species under appropriate temperatures has been determined (Table 1). The light saturation of diatoms like *S. costatum* and *Chaetoceros* is 266 μE m^{-2} s^{-1}, which exceeds that of most dinoflagellates and flagellates. The light saturation of *K. mikimotoi* in the ECCS ranges from 58 to 82 μE m^{-2} s^{-1}, similar to that of *P. donghaiense* (58–80 μE m^{-2} s^{-1}). *A. anophagefferens* has lower light saturation than the dinoflagellates (50 μE m^{-2} s^{-1}).

3.2. Temperature

The results of laboratory culture experiments indicated that nearly all HAB species have optimum temperatures in the range of 20–25 °C (Table 2). While the observations during bloom events showed that the temperatures of *K. mikimotoi* blooms were higher and concentrated in a narrow range (22.4–25 °C) compared with those of the other species (Fig. 2a). *P. donghaiense* could develop a bloom event in a relatively

lower temperature envelope (16.6–25.2 °C) than *K. mikimotoi*. *N. scintillans* blooms were found in a wide temperature range (12–30 °C). The minimum temperature of *S. costatum* and *A. anophagefferens* blooms were below 15 °C which was lower than that of *K. mikimotoi* and *N. scintillans* indicating an advantage under low temperatures.

3.3. Salinity

S. costatum and *N. scintillans* blooms have wide range of salinity adaptation from 18 to 32 and from 22 to 35, respectively. *P. donghaiense* and *K. mikimotoi* blooms show similar salinity adaptation, most of which occurred where salinity exceeds 25. *A. anophagefferens* blooms in ECCS primarily occurred in waters with salinity around 30. (Fig. 2b).

3.4. Physical criteria

The spatial distributions of physical habitat for physical conditions in June and September 2006 were compared with the reported location of blooms of these species in the ECCS (Fig. 3). Intensive blooms of *K. mikimotoi* and *P. donghaiense* mainly distributed in the western nearshore of the ECS, which matched well with the outcomes of our physical criteria (Fig. 3b and c). Suitability for physical habitat of *A. anophagefferens* in the BS was detected in September 2006, though the potential risk distribution produced by our model is more northwest than the reported occurrence location.

3.5. Nutrients

Generally, the DIP concentration was higher during diatom blooms than during dinoflagellate and Pelagophyceae blooms, irrespective of the pre-/post-bloom or bloom periods (Fig. 4a). Most of the DIP concentrations during the pre/post period of diatom, dinoflagellate and Pelagophyceae blooms were in the range of 0.4–1.4 μmol l^{-1}, 0.4–1.0 μmol l^{-1} and 0–0.4 μmol l^{-1}, respectively. During the bloom periods, the DIP concentrations in diatom, dinoflagellate and Pelagophyceae blooms were generally around 0.4 μmol l^{-1}, 0.2 μmol l^{-1} and 0.2 μmol l^{-1}, respectively.

The DIN concentrations during bloom periods are not strictly lower than during the pre-/post-bloom periods for diatom blooms (Fig. 4b). Most of the observed DIN concentrations during diatom blooms were above 10 μmol l^{-1}. Compared to the corresponding periods of diatom blooms, the DIN concentrations during the pre-/post periods or bloom periods of dinoflagellates were lower and even can reach extremely low levels (<2 μmol l^{-1}) (Fig. 4b). Interestingly, although the DIN concentrations during pre-/post-bloom periods of Pelagophyceae were lower than during blooms of diatoms and dinoflagellates, the DIN concentration during bloom periods of Pelagophyceae were equal to or even higher than in pre-/post-bloom periods (Fig. 4b).

According to the V$_{max}$ values listed in Table 3, *S. costatum* has higher V$_{max}$ for DIN (NO$_3^-$ and NH$_4^+$) but lower V$_{max}$ for dissolved organic N (DON) (urea and amino acid) compared to others, suggesting a higher preference of *S. costatum* for DIN. The K$_s$ values of *A. anophagefferens* are lower than those of other species, especially for urea (Table 3). Therefore, it is likely that the DIN requirement level for the dominant ECCS HAB species is in the order of diatoms > dinoflagellates > Pelagophyceae.

The DSi concentration during the pre/post bloom period of diatoms was highest, and the average DSi concentration during diatom blooms almost equaled that during pre-/post-bloom and bloom periods of dinoflagellate and Pelagophyceae (Fig. 4c).

4. Discussion

4.1. Physical criteria

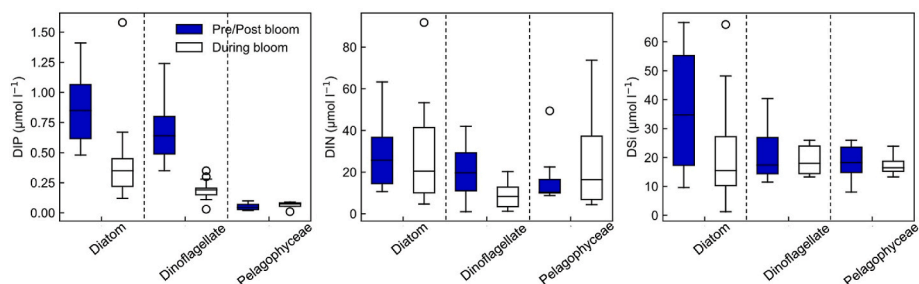Good fidelity between the physical habitat selected by the physical

Fig. 4. DIP, DIN and DSi concentrations in pre-bloom, bloom and post-bloom periods of diatoms, dinoflagellates and Pelagophyceae in ECCS.

criteria and the region of intense blooms indicates a high possibility to predict the HAB dominated by specific species in the ECSS (Fig. 3). Meanwhile, the role of physical conditions on determining the spatial distribution was highlighted.

The optimum temperature and salinity range of *S. costatum* was wide (Fig. 2b). This explains why *S. costatum* blooms occur in most coastal areas, even in the river-plume in the CJE. Comparatively, *P. donghaiense* and *K. mikimotoi* have relatively higher salinity envelopes (Deng et al., 2009; Ding and Zhang, 2018a; Si, 2016; Wang and Huang, 2003; You, 2006) (Fig. 2b). And the sensitivity of *P. donghaiense* and *K. mikimotoi* to temperature variation was high (Dai et al., 2014) (Fig. 2a). These characteristics indicate that stable temperature and salinity conditions were prerequisite for the bloom formation and maintenance of *P. donghaiense* and *K. mikimotoi* (Ding and Zhang, 2018b; Yao et al., 2007). The Taiwan Warm Current, a branch of the Kuroshio Current (Fig. 1), is characterized by relatively high temperature and salinity that favor dinoflagellates (Fig. 2) (Yang et al., 2018a), which explained the potential risk of *P. donghaiense* and *K. mikimotoi* blooms occur in the area under the influence of Taiwan Warm Current (Jiang et al., 2015).

Our model located the potential risk of *A. anophagefferens* bloom in the North part of the ECCS may relevant to its more competitive capability under low temperatures (LaRoche et al., 1997; Nuzzi and Waters, 2004; Xiao et al., 2018) (Fig. 2a). Most *A. anophagefferens* blooms decayed when the water temperature exceeded 25 °C (Moniruzzaman et al., 2018; Nuzzi and Waters, 2004). In addition, *A. anophagefferens* prefers high salinity (>24) (LaRoche et al., 1997). High water diversion for agriculture and urban use and decreasing precipitation in the Haihe, Liaohe and Yellow River basins lead to a significant decline of freshwater discharged to the BS since the 1960s (Fig. 5b) (Dai et al., 2009; Li et al., 2014b). Reduction of freshwater input increased the salinity in the BS (Lin et al., 2001) and provided suitable and stable salinity conditions for Pelagophyceae (Fig. 2b).

4.2. Chemical criteria

Applying the chemical criteria comprised by all kinds of bio-available nutrients, cannot be approached yet. Nevertheless, historical data of the BS and YS suggested that since the 1960s, the DIN concentration increased continuously (Fig. 6), while the DIP concentrations declined even to below 0.4 μmol l^{-1} during summer and spring in recent
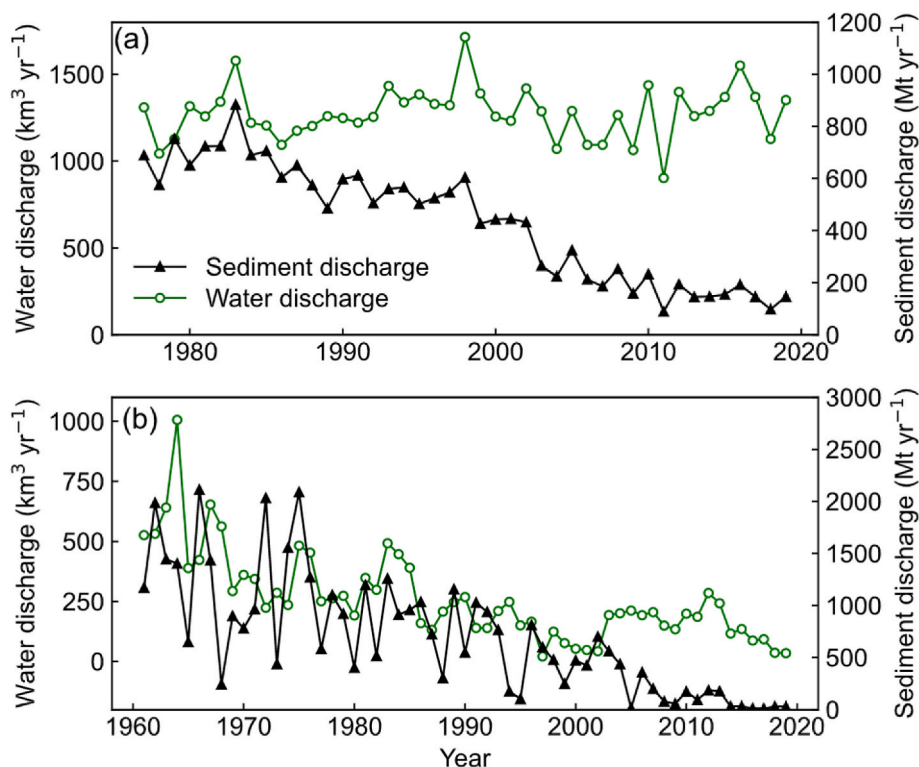

Fig. 5. Long-term changes of water and sediment discharge from the main rivers exported to the ECCS. (a) The sum of water and sediment discharge from the Huai, Yangtze, Qiantangjiang and Pearl Rivers; (b) The sum of water and sediment discharge from the Liao, Hai and Yellow Rivers (Data source: Dai et al. (2009); and (Ministry-of-Water-Resources-of-the-People's-Republic-of-China, 2020)).
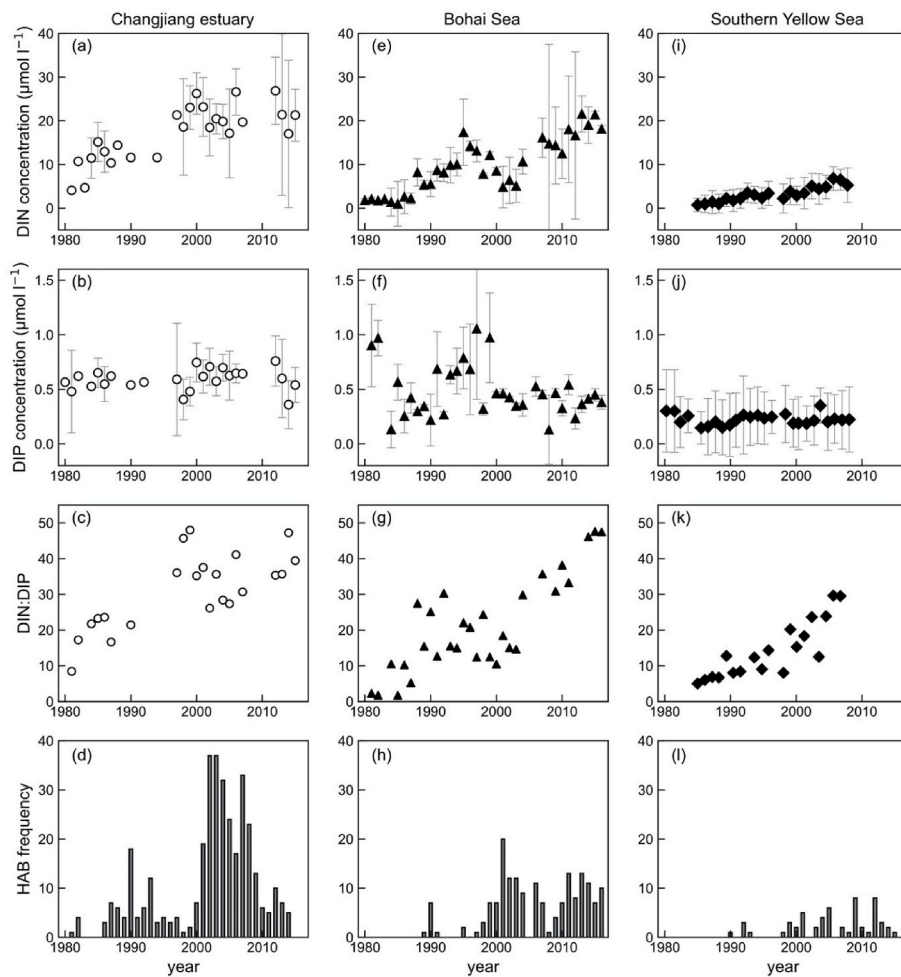
Fig. 6. Long-term changes of DIN and DIP concentrations, DIN:DIP ratios and annual frequency of HAB in the Changjiang estuary (left column), Bohai Sea (middle) and southern Yellow Sea (right column). Nutrient concentrations in the Changjiang estuary are obtained from Li et al. (2015); Mu et al. (2020); Wang et al. (2016); Zhang (2020), those in the Bohai Sea are obtained from Zhang (2020), and those in the southern Yellow Sea are obtained from Wei et al. (2015)). Data on HAB frequency are obtained from Liang (2012); Wang et al. (2021); Xiao et al. (2019).

years (Lin et al., 2005; Wang et al., 2019b; Yang et al., 2018b). In the nearshore areas of the ECS, the DIN concentration increased from 5 μmol l^{-1} in 1959 to 25 μmol l^{-1} in 2010, but the DIP concentration remained stable at levels around 0.6 μmol l^{-1} (Li et al., 2014a). Generally, the coastal waters of the ECCS altered from N-limited to P-limited systems during the past half century (Fig. 6). The simulated total N and P (TN:TP) molar ratio of the nutrient sources to the coastal waters of the ECCS exceeded 25 since the 1980s (Wang et al., 2021). However, in some nearshore regions and estuaries, the DIN:DIP ratios exceeding 100 can occur temporarily in recent years (Wang et al., 2009; Yao et al., 2019). Besides, high deposition rates in reservoirs also impact the transportation of particulate materials like biogenic Si and bioavailable particulate P (Ran et al., 2013; Tang et al., 2018), which may enhance the imbalance of N, Si and P in the coastal area.

As a potential limitation, DIP concentrations are nearly always lower during bloom periods than during pre-bloom and post-bloom periods (Fig. 4a), which highlight the competitiveness of species that can endure low DIP concentration and/or use dissolved organic P (DOP) effectively (Qu et al., 2020; Wang et al., 2011). The assimilation rate of *P. donghaiense* was 8 times higher than that of *S. costatum* indicating more efficient DIP utilization (Qu et al., 2020). In addition, diatoms can only use one or two specific forms of DOP with an extremely low efficiency, while *P. donghaiense* and *K. mikimotoi* show favorable growth when using multiple DOP species as the sole P source (Huang et al., 2005; Wang et al., 2011).

A. anophagefferens (Pelagophyceae) is insensitive to DIP concentration (Gobler et al., 2011), and shows a strong competitive advantage under low DIP conditions compared with diatoms and dinoflagellates

(Fig. 4a). Qin et al. (2014) indicated that the alkaline phosphatase (AP) activity of *A. anophagefferens* was 73 times higher than that of diatoms (Qin et al., 2014). In addition, field observations in the BS showed that the AP activity during an *A. anophagefferens* bloom was 5.7 times higher than that during a dinoflagellate bloom (Liu et al., 2016b). According to the long-term observations of nutrient changes in the lower reach of the Yellow River, the DOP concentration has increased during the past decade while the DIP concentration has decreased, and the contribution of DOP to total dissolved P (TDP) has risen from less than 50%–95% (Wu et al., 2021). Since the Yellow River is the primary P source in the BS (Wang et al., 2019b), the composition of TDP in the BS has also changed and is dominated by DOP in recent years (Zhang et al., 2020). This may be an important reason for the *A.anophagefferen*s blooms and a typical feature of the BS instead of a general phenomenon in other parts of the ECCS (Liu et al., 2016a; Zhang et al., 2021).

The influence of residence time and efficiency of water exchange can be illustrated by comparing river-dominated estuaries and coastal lagoons (Glibert et al., 2010). Glibert et al. (2010) indicated that lagoonal blooms were often dominated by picoplankton, such as *A. anophagefferens*, rather than large-size phytoplankton which usually bloom in river-dominated estuaries. The comparison of the BS and CJE can thus provide an example of the impact of water residence time on HABs in the ECCS (Fig. 7). The water residence time of the BS ranges from 1.1 to 5.2 years (Liu et al., 2017), which is much longer than the ca. 6 days above the pycnocline in the Changjiang Diluted Water plume area (Gu et al., 2012). Even for the whole ECS, the water residence time of 5.7–11 months is much less than that of the BS (Liu et al., 2019). Owing to the long residence time, the accumulated effects of imbalanced
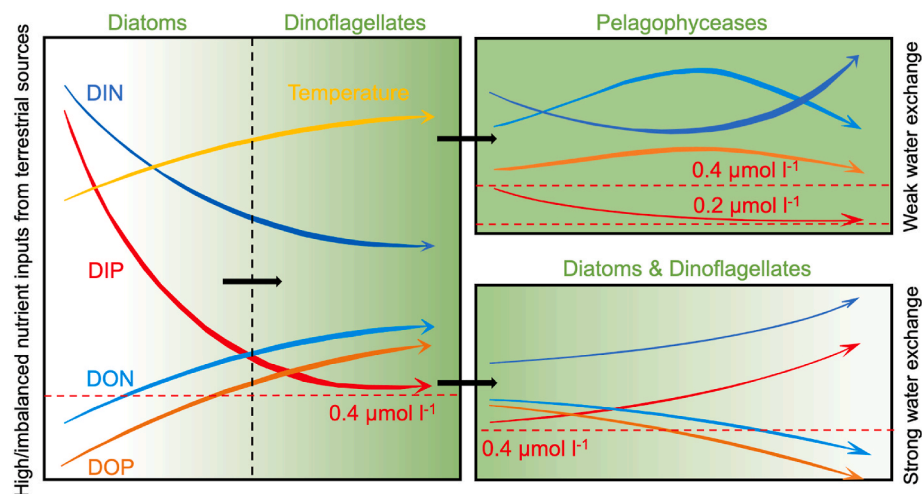
Fig. 7. A sketch illustrating the nutrients variations along with the HAB succession in the Bohai Sea and the Changjiang estuary.

nutrient input from terrestrial sources via rivers and consumption by primary production cause extremely low DIP concentrations and high N:P ratios in the BS, with DIN/DIP values > 30 particularly after 2010 (Fig. 4) (Wang et al., 2019b; Xin et al., 2019). Moreover, organic nutrients formed during the decay of algae are not flushed to the open ocean, leading to the accumulation of DON and DOP, which promotes growth of *A. anaophagefference* (Wang et al., 2009). Therefore, the occurrence of *A. anaophagefference* blooms in the BS since 2010 can be recognized as an ecological adaptation to the specific conditions in this semi-closed ecosystem (Fig. 7).

As we discussed above, nutrients concentrations and compositions act significantly on HABs succession. Therefore, how to earn precise nutrients variations spatially and temporally under the influence of land-based pollution input, exchange with open ocean and internal biogeochemical cycle is a challenge, but also a prerequisite for elaborating the succession of HABs. According to the data in Fig. 4a and discussion above, we came up with a hypothetical succession scheme (Fig. 7), which need to be proved by future's studies. Meanwhile, our study indicated that using biogeochemical models with high resolution to reproduce the nutrients dynamics driven by numerous deeply coupled physical/biochemical processes is feasible for future's HAB research.

4.3. Climate change

Climate change influences HAB succession through altering the environmental conditions, such as temperature, light and precipitation (Gobler et al., 2017; Ho et al., 2019; Hutchins and Fu, 2017). During the past 45 years (1970–2015), the average rate of warming in Chinese coastal seas has been 0.17 °C per decade (Xiao et al., 2019). Xiao et al. (2019) suggested that seawater warming caused an increase in HABs frequency and a shift towards earlier occurrence of HABs within the year. Warming prolongs the HAB-preference period within the year. Moreover, temperature also controls phytoplankton composition. Increasing water temperatures negatively affect diatoms, while the high temperatures favor many dinoflagellates (Paerl and Scott, 2010; Xiao et al., 2018) (see also Table 2). In addition to the direct effect of increasing water temperature, elevated surface temperature promoted water-column stability and thermal stratification which, in turn, favor an increased presence of dinoflagellates because of their strong vertical migrators (Gobler et al., 2017). Therefore, through its impact on stratification, warming in the ECCS indirectly accelerates the shift from diatoms to dinoflagellates (Chen et al., 2021a; Liu et al., 2016c). However, since nutrient loading and warming have occurred simultaneously during past decades in the ECCS, it is hard to disentangle the individual impact of these two major factors.

5. Concluding remarks

Eutrophication and nutrient stoichiometric imbalance are severe in both CJE and BS, but the hydrodynamics are different. In the CJE, mixing through water exchange with the open ocean reduces the chance of further succession of HABs. In contrast, the lack of flushing, the long water residence time and the enhanced stratification through increasing water temperature in the BS, amplifies the nutrient imbalance and enhances the accumulation of organic nutrients, conditions favorable for the HAB species *A. anaophagefference*.

This analysis also uncovers a number of knowledge lacunae. i) Referring to nutrient imbalances, available data often lack observations of organic nutrient forms, which hampers the investigation of relationships between the changing organic nutrient concentrations and proportions and HAB evolution in the ECCS during the past decades. ii) Although in the literature there is consensus on the role of climate warming in the proliferation of HABs, disentangling the role of the combining global change processes of warming and nutrient pollution is a difficult task. Therefore, the use of models can help to disentangle all these simultaneous processes and the impacts on HAB development in environments like ECCS, as demonstrated for example by Glibert et al. (2014).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.csr.2023.104991.

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