



Unveiling the evolution of phytoplankton communities: Decades-long insights into the southern Yellow Sea, China (1959–2023)

Shujin Guo^{a,b,d}, Xiaoxia Sun^{a,b,d,e,*}, Jian Zhang^c, Qingzhen Yao^f, Chuanjie Wei^{d,g}, Feng Wang^{a,e}

^a Jiaozhou Bay National Marine Ecosystem Research Station, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, PR China

^b Laboratory for Marine Ecology and Environmental Science, Qingdao Marine Science and Technology Center, Qingdao 266237, PR China

^c National Marine Data and Information Service, Tianjin 300171, PR China

^d Center for Ocean Mega-Science, Chinese Academy of Sciences, Qingdao 266071, PR China

^e University of Chinese Academy of Sciences, Beijing 100049, PR China

^f Frontiers Science Center for Deep Ocean Multispheres and Earth System, and Key Laboratory of Marine Chemistry Theory and Technology, Ministry of Education, Ocean University of China, Qingdao 266100, PR China

^g Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, PR China

ARTICLE INFO

Keywords:

Phytoplankton
Long-term variation
Environmental changes
Diatoms
Dinoflagellates
Southern Yellow Sea

ABSTRACT

We obtained historical and observational data on phytoplankton communities from 1959 to 2023 to explore the responses of the phytoplankton community structure to long-term environmental changes in the southern Yellow Sea (SYS), China. The results revealed a decrease in the proportions of diatom cell abundance within the phytoplankton community by 8 %, accompanied by a corresponding increase in that of dinoflagellates. Dominant phytoplankton species were mainly chain-forming diatoms before 2000, and large dinoflagellate species from the genera *Tripos* and *Noctiluca* increased their dominance after 2000. Warm-water phytoplankton species have increased in dominance over the study period. Correlation analysis revealed that the ocean warming and alterations in nutrient structure (N/P and Si/N ratios) were mostly responsible for the long-term evolution trend, and these changes may result in an increase in dinoflagellate harmful algal blooms, reduced efficiency of the biological carbon pump, and heightened hypoxia in the future, which should draw our attention.

1. Introduction

Phytoplankton plays an important role as the foundation of the marine food web in the ocean. It can perform photosynthesis and serve as a vital food source for a diverse array of marine organisms. When nutrients are sufficient and other environmental conditions are suitable, it can form harmful algal blooms (HABs) and threaten marine life and ecological health. Additionally, phytoplankton is deeply involved in biogeochemical cycles and contributes significantly to nutrient cycling and carbon cycle in the marine environment (Beaugrand and Reid, 2003). Therefore, it plays a crucial role in maintaining the structure and function of aquatic ecosystems (Lehtinen et al., 2017). Influenced by intensive land-ocean interactions, coastal seas exhibit intricate characteristics and are more susceptible to human activities compared to open oceans (Strokal et al., 2014). Climate change and human activities have significantly altered marine environments in the coastal sea, with

ongoing global warming leading to elevated seawater temperatures and the anthropogenic discharge of nutrients into coastal areas experiencing a rapid increase in recent decades (Wählström et al., 2020). As a kind of rapidly reproducing and environmentally sensitive organism, how phytoplankton responds to these environmental changes would have a significant impact on the aquatic ecosystem stability and functionality in the coastal sea.

To gain a comprehensive understanding of the impact of environmental changes on phytoplankton communities, it is necessary to analyze long-term ecological monitoring data. Numerous studies have illustrated that climate change, nutrient enrichment, and other environmental changes can significantly influence phytoplankton communities. For instance, Jiang et al. (2014) conducted a study analyzing historical data on phytoplankton communities from 1959 to 2009 in the Changjiang (Yangtze River) estuary, China, and they observed a striking decrease in the diatom-dinoflagellate ratio and an escalation of HABs

* Corresponding author at: 7 Nanhai Road, Shinan District, Qingdao 266071, PR China.

E-mail address: xsun@qdio.ac.cn (X. Sun).

over the studied period. Godhe et al. (2015) studied phytoplankton and environmental data in the coastal southeast Arabian Sea from 1990 to 2010, and they discovered a shift in the phytoplankton community towards higher genus richness and diatom abundance. Wang et al. (2020) examined the response of the phytoplankton community to changes in environmental factors in Deep Bay and Mirs Bay in southern China from 1994 to 2016, and they found that the high level of nutrients resulting from urbanization provided a nutrient base for phytoplankton blooms. These studies mentioned above emphasize the significance of long-term ecological study and highlight the diverse ways in which environmental change can influence phytoplankton communities in coastal areas. Understanding these dynamics is crucial for the assessment and management of coastal marine ecosystems in the future.

The southern Yellow Sea (SYS) is a semi-closed marginal sea of the Northwest Pacific Ocean, situated between the mainland of China and the Korea Peninsula. It provides important ecosystem services for adjacent provinces and regions due to its unique ecological, environmental, and biological resources (Song et al., 2021). Characterized by its relatively shallow depth, the SYS exhibits a remarkable capacity to respond rapidly to atmospheric climate changes. Global warming has induced a noteworthy rise in sea temperature within the SYS, with the warming trend being four-to-six times higher than the global average (Xu and Xu, 2022). Besides the rising temperature, nutrient over-enrichment is another paramount environmental issue in this area (Chen et al., 2023). The coastal regions on both sides of the SYS are densely populated, with high levels of socio-economic development. The intensive land-ocean interactions in the region result in the direct or indirect input of substantial nutrients loads from rivers, particularly the Changjiang (Yangtze) River and Yellow River (Liu et al., 2021). Lin et al. (2005) found that the concentration of dissolved inorganic nitrogen had increased, and the concentrations of dissolved inorganic phosphate and dissolved silicate exhibited an overall decreasing trend from 1976 to 2000. Wei et al. (2015) also revealed an increase in dissolved inorganic nitrogen concentrations during the 1990s compared to the 1950s. The combined impacts of climate change and human activities have notably affected the ecosystem of the SYS, leading to evolutionary changes in the environmental conditions (Xu and Xu, 2022). How these long-term changes in environmental factors affect the phytoplankton community is a question worth exploring, which could provide useful information for the conservation and sustainable management of the marine ecosystems in this region.

Numerous phytoplankton studies have been conducted in the SYS since the 1950s (Qian and Chen, 1986; Yu and Li, 1993; Wang, 2003; Fu et al., 2012; Yang et al., 2016; Luan et al., 2020), primarily employing plankton nets with a 76 μm mesh size. Early phytoplankton samples were predominantly collected using this type of net due to Chinese marine monitoring specifications, while water sampling has been employed since 2009 (Tian and Sun, 2011; Liu et al., 2015; Lü et al., 2016; Jiang et al., 2019; Guo et al., 2020a, b). These studies have provided valuable information for the phytoplankton community structure and its ecological characteristics such as species composition, cell abundance, spatial distribution and so on. However, most of these studies are short-term phytoplankton investigations, and there have been few studies on phytoplankton community structure over long time periods in the SYS (Wang et al., 2022), which is not conducive to our understanding of the long-term changes in the ecosystem of the SYS. In this study, we focus on phytoplankton data obtained through net- and water-collection, considering the influence of environmental factors in the SYS over a period spanning from 1959 to the present. Our primary objective is to investigate the long-term changes in phytoplankton communities in response to environmental shifts in the SYS. To accomplish this, we analyze variations in phytoplankton abundance, composition, species diversity, and the succession of red tide species. Additionally, we examine the relationship between phytoplankton data and environmental parameters. By offering a comprehensive perspective on the historical and current status of phytoplankton communities in the

SYS, this study aims to provide useful insights for predicting future responses to environmental changes and effectively managing the ongoing anthropogenic pressures in the SYS.

2. Materials and methods

2.1. Study area

The research area under investigation is situated between approximately 120°E to 124°E and 33°N to 36°N latitude, encompassing a significant portion of the SYS (Fig. 1).

2.2. Samples collection, analysis and data sources

The data used in the present study are derived from previously published studies and our own observations conducted during 21 cruises from 1959 to 2023 in the SYS. The field data for the phytoplankton survey in this study are elaborated in Table 1. The phytoplankton survey data incorporated in this research originate from the following sources: (1) Data of the Yellow Sea from the comprehensive national marine survey in 1959 (specifically, May, August and November 1959) (Office of Integrated Oceanographic Survey of China, 1961); (2) Survey data of the SYS in the spring of 2001 from the 973 project “Ecosystem dynamics and sustainable utilization of biological resources in the East China Sea and Yellow Sea”; (3) Survey data of the SYS in the spring of 2009, spring and fall of 2011, and fall of 2012 from the open voyages of National Natural Science Foundation of China; (4) Survey data of the SYS in the summer of 2016, spring and summer of 2017 from the special project of the Chinese Academy of Sciences “Occurrence mechanism and prevention/control strategies of coastal ecological disasters”; (5) Survey data of the SYS in the spring, summer, and fall of 2018 from the open voyages of the Pilot National Laboratory for Marine Science and Technology (Qingdao), (6) Survey data of the SYS in the spring of 2023 from the project “Monitoring and enhancement of carbon sink in the coastal sea”. The sources of other data from published studies are also listed in Table 1.

Consistent sample collection and analysis methods were applied throughout each voyage. For net-collected phytoplankton, a standard shallow-water Net-III (length = 140 cm, diameter = 37 cm, mesh size = 76 μm) was employed. At each station, the net was lowered vertically to 2 m above the seabed at a controlled rate of 0.5 m/s and then drawn to the surface at 0.1 m/s. The collected phytoplankton samples were placed into 1 L opaque polyethylene (PE) bottles and preserved using 2 % buffered formaldehyde. For water-collected phytoplankton, seawater samples were collected from the surface using 12-L Niskin bottles. 1 L samples were fixed with 1 % buffered formaldehyde in situ and stored in PE bottles. Regarding dissolved inorganic nutrients samples, water samples were initially filtered through 0.7 μm pore size Whatman GF/F membranes (precombusted at 450 °C for 5 h). The filtrate was then collected in acid-cleaned 60-mL high-density polyethylene bottles and stored at -20 °C for subsequent analysis. Samples for chlorophyll *a* (Chl *a*) underwent filtration through cellulose acetate fiber filters (0.45 μm pore size; Whatman), and 250–500 mL seawater sample was processed according to the turbidity. Chl *a* samples were stored in the dark at -20 °C for further analysis in the laboratory.

In the laboratory, the net-phytoplankton samples underwent thorough mixing, and then 1 mL of the sub-sample was introduced into a Kolk-witz counting chamber (HYDRO-BIOS, Germany). Identification and quantification of cells were carried out using an Olympus microscope at $\times 200$ or $\times 400$ magnification. For water-phytoplankton samples, the samples were meticulously mixed, and a 25 mL sub-sample was introduced into a Utermöhl chamber, then allowed to settle undisturbed for 24 h. The enumeration of phytoplankton taxa was conducted using an inverted Olympus microscope at magnifications of $\times 200$ or $\times 400$ (Paxinos and Mitchell, 2000). The Chl *a* substance retained on filters underwent analysis using a Turner Design Fluorometer. Prior to

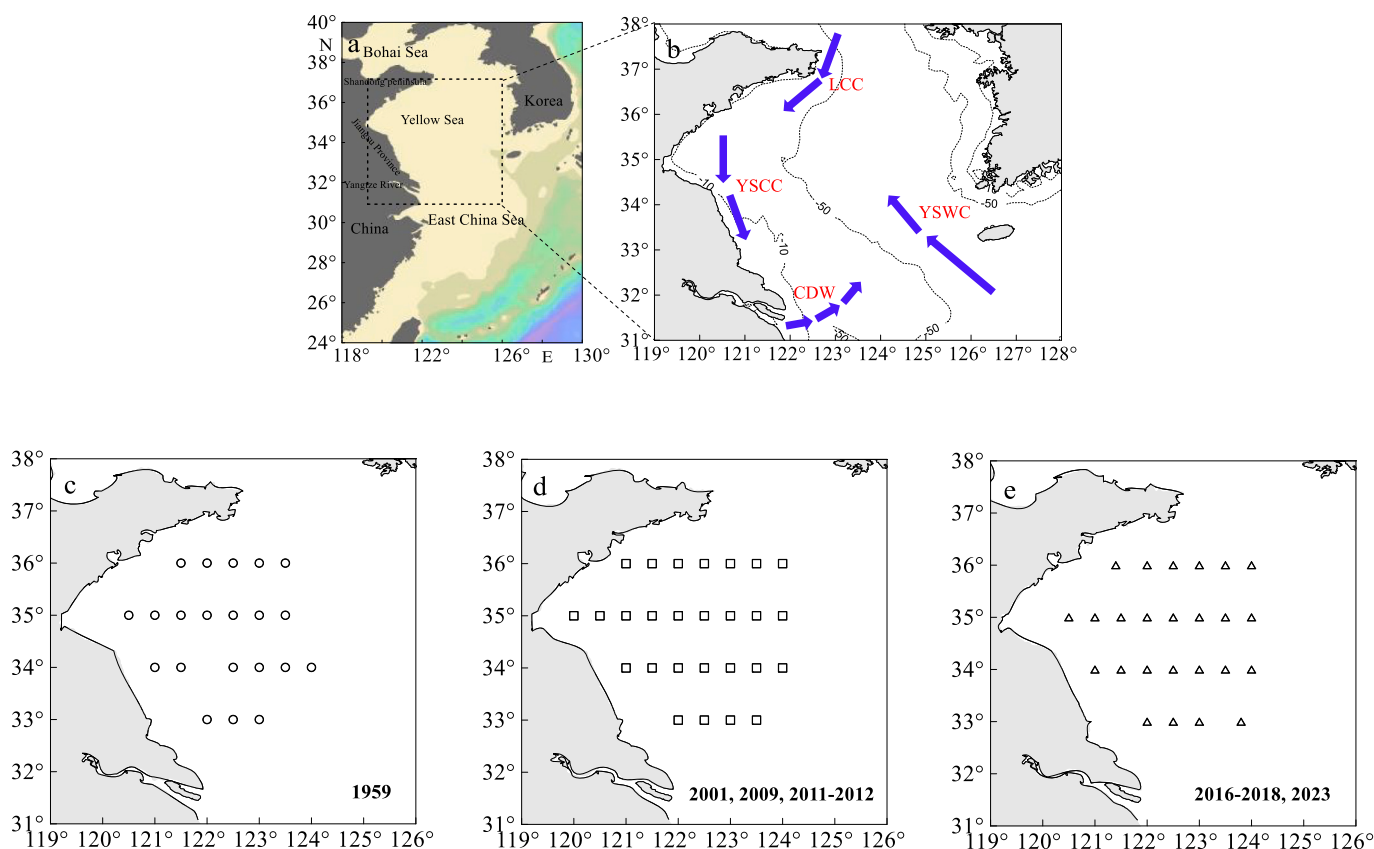


Fig. 1. Maps of the study area and sampling stations. a) Map of the Chinese seas, including the entire SYS (the dashed rectangle indicates the study area); b) Illustrates ocean currents in the SYS (Note: LCC, Lubei Coastal Current; YSCC: Yellow Sea Coastal Current; CDW, Changjiang Diluted Water; YSWC, Yellow Sea Warm Current); c-e) Depict the locations of survey stations during different time periods, c: Sampling stations from the comprehensive national marine survey in 1959 (Office of Integrated Oceanographic Survey of China, 1961); d: Sampling stations of cruises conducted between 2001 and 2012; e: Sampling stations of cruises conducted between 2016 and 2023 (detailed information for these cruises is described below).

analysis, Chl *a* was extracted by incubating the filters in 90 % acetone for 24 h at $-20\text{ }^{\circ}\text{C}$ (Trees et al., 2022). Temperature and salinity were measured in situ using a CTD (SBE 917 Plus). For nutrient analysis, nitrate (NO_3^- -N), nitrite (NO_2^- -N), ammonium (NH_4^+ -N), phosphate (PO_4^{3-} -P), and silicate (SiO_3^{2-} -Si) concentrations were analyzed using a Bran-Lubbe Quattro-SFA autoanalyzer according to Aydin-Onen et al. (2012). The limits of quantification were 0.02, 0.02, 0.03, 0.04, and $0.01\text{ }\mu\text{mol/L}$ for NO_3^- -N, NO_2^- -N, NH_4^+ -N, PO_4^{3-} -P and SiO_3^{2-} -Si, respectively. The sum of NO_3^- -N, NO_2^- -N and NH_4^+ -N concentrations was defined as dissolved inorganic nitrogen (DIN).

To unveil the long-term variation trends of physicochemical parameters in the SYS, historical data were collected and combined with our observational data to reflect the long-term variation trends of environmental parameters. Given that the majority of historical surveys (predating 2000) in the SYS were primarily concentrated along the 35°N transect managed by the State Oceanic Administration (SOA) of China, spanning a radial range of $120.0^{\circ}\text{E} - 124.5^{\circ}\text{E}$ (Wang, 2020), efforts were made to ensure the comparability and temporal coherence of the data. Consequently, data of temperature, salinity, and nutrients pertaining to the summer (August/July) along 35°N transect in the SYS were meticulously curated from historical investigations as well as our own observational data. This comprehensive approach aimed to unveil the long-term trends in environmental variations in the study area. The temperature and salinity data encompassed in this study were sourced from various surveys: those conducted between 1960 and 1998 were obtained from the SOA of China; those from 2010 to 2011 and 2014 to 2015 were obtained from National Marine Data Information Service (NMDIS) of China; the other data spanning from 2012 to 2018 were acquired through our own observations (refer to Table S1). For the

nutrients data, the data for the years 1960, 1992, and 2010 were obtained from the National Marine Data Information Service (NMDIS) of China; the data from 1977 to 1987, 1998, 2011, and 2015 were derived from the SOA, and the data from 2012 to 2013 and 2016 to 2017 were from our own observations (refer to Table S2). Since China only started monitoring NH_4^+ -N from 1985, data for DIN only became available from 1985, and data for PO_4^{3-} -P and SiO_3^{2-} -Si have been available since 1960.

To unveil the long-term variations in phytoplankton HABs occurrences, this study collected and compiled a comprehensive dataset covering HABs events in the SYS from 1972 to 2022. Information was sourced from various references, including the book “Investigation and Assessment of Red Tides (1933-2017) in China” by Liang (2012), the annual reports such as the “Bulletins of Marine Disasters in China (2009-2022)”, “Bulletins of Marine Environment Status in China (2009-2022)”, “Bulletins of Marine Environment Status from the Provinces of Shandong and Jiangsu (2009-2022)” issued by the SOA of China, and Li et al. (2021).

2.3. Data analysis

To assess phytoplankton community diversity, the Shannon-Wiener diversity index (H') (Strong, 2016) and Pielou's evenness index (J) (Lehtinen et al., 2017) were employed. They were calculated using the following formulas:

$$H' = - \sum_{i=1}^S P_i \log_2 P_i$$

Table 1
Field data for SYS cruises and historical data sources.

Sampling method	Period	No. of stations	Longitude and latitude	References
Net-collected	1959 (Spring, summer and Fall)	21	120°-124°E, 33°-36°N	Office of Integrated Oceanographic Survey of China, 1961
	1980 (Summer)	9	120°-122°E, 34°-35°N	Qin et al., 2011
	1986 (Spring)	—	120°-125°E, 32°-37°N	Luan et al., 2020
	2001 (Spring)	27	120°-124°E, 33°-36°N	Present study
	2002 (Summer)	9	120°-122°E, 34°-35°N;	Qin et al., 2011
	2002 (Winter)	48	121°-125°E, 32°-37°N	Wang, 2003
	2005 (Spring)	—	120°-125°E, 32°-37°N	Luan et al., 2020
	2008 (Summer)	9	120°-122°E, 34°-35°N	Qin et al., 2011
	2009 (Spring)	27	120°-124°E, 33°-36°N	Present study
	2011 (Spring, Fall)	27	120°-124°E, 33°-36°N	Present study
	2012 (Fall)	27	120°-124°E, 33°-36°N	Present study
	2015 (Spring)	—	120°-125°E, 32°-37°N	Luan et al., 2020
	2016 (Summer)	25	120.5°-124°E, 33°-36°N	Present study
	2017 (Spring, Summer)	25	120.5°-124°E, 33°-36°N	Present study
	2018 (Summer, Fall)	25	120.5°-124°E, 33°-36°N	Present study
	2023 (Spring)	25	120.5°-124°E, 33°-36°N	Present study
	Water-collected	2009 (Spring)	30	121°-124.5°E, 33°-37°N
2011 (Spring, summer, fall)		28	121°-125.5°E, 31.5°-36°N	Jiang et al., 2019
2014 (Spring)		22	121°-124°E, 32°-36°N	Zhang et al., 2016
2016 (Summer)		25	120.5°-124°E, 33°-36°N	Present study
2017 (Spring and summer)		25	120.5°-124°E, 33°-36°N	Present study
2018 (Spring, summer, and fall)		25	120.5°-124°E, 33°-36°N	Present study
2023 (Spring)		25	120.5°-124°E, 33°-36°N	Present study

Note: “—” indicates that the station numbers cannot be obtained.

$$J = \frac{H'}{\log_2 S}$$

where P_i represents the proportion of the cell abundance of species i in the total cell abundance within a sample, and S denotes the species richness in that sample. The Dominance index (Y) was calculated to identify the dominant phytoplankton species during each cruise, with the formula provided below:

$$Y = \frac{n_i}{N} \times f_i$$

where n_i represents the sum of cell abundances for species i across all

samples; N is the sum of cell abundances for all species; and f_i is the frequency of occurrence for species i across all samples.

The increasing or decreasing trends in phytoplankton and environmental parameters data were analyzed using the non-parametric Mann-Kendall (MK) test in SPSS 26.0 software. The MK test is widely employed for detecting both ascending and descending trends (Yue et al., 2002). In this study, statistical significance was acknowledged when $p < 0.05$. Notably, the non-parametric MK test offers the advantage of not requiring adherence to any specific distribution pattern, and it accommodates the presence of missing data points. In other data analyses, instances of missing yearly data were disregarded, and the statistical evaluations were conducted exclusively on the available dataset. To explore the relationship between phytoplankton data and environmental factors, Pearson's rank correlations between phytoplankton data and environmental variables from water samples of all sampling cruises were calculated using the “ggcorrplot” package and visualized with the “ggplot2” packages in R software (version 3.6.2) (McKenna et al., 2016). Statistical significance was defined as $p < 0.05$.

3. Results

3.1. Long-term variations in environmental parameters

From 1960 to 2018, the sea surface temperature (SST) in the SYS exhibited a range of 21.51 to 27.49 °C during the summer along the 35°N section. The SST displayed discernible temporal variations, with an initial increase from 1960 to 1987. Subsequently, a decline occurred until 1998, followed by a subsequent rise that persisted until 2018. Notably, temperatures exhibited a consistent upward trajectory throughout the study period (MK-test, $p < 0.05$), indicating a warming rate of 0.61 °C per decade (Fig. 2a). The sea surface salinity (SSS) ranged from 29.98 to 31.56. Although the SSS exhibited a slightly declining trend over the study duration (Fig. 2b), statistical analysis indicated that this trend was not statistically significant (MK-test, $p > 0.05$).

The long-term variations in nutrient concentrations and ratios within the surface layer in the SYS are illustrated in Fig. 3. The concentration of DIN at the surface layer ranged from 1.23 to 3.76 μmol/L, indicating an ascending trend from 1985 to 2017 (Fig. 3a). Meanwhile, the concentration of $\text{PO}_4^{3-}\text{-P}$ fluctuated within a range of 0.06 to 0.27 μmol/L (Fig. 3b). In general, the $\text{PO}_4^{3-}\text{-P}$ and $\text{SiO}_3^{2-}\text{-Si}$ concentrations exhibited a declining trend from 1960 to 2017. Upon analyzing the long-term trends of nutrient ratios, it becomes evident that the nitrogen-to-phosphorus (N/P) ratio has experienced a fluctuating but overall increasing trend since 1985 (Fig. 3d). This ratio consistently remained above 16:1, especially after the year 2000. Conversely, the silicon-to-nitrogen (Si/N) ratio demonstrated a fluctuating yet decreasing trend (Fig. 3e), while consistently maintaining a value higher than 1:1.

3.2. Long-term variations in phytoplankton community structure

3.2.1. Species number and composition

In total, 424 phytoplankton species, comprising 264 diatoms, 127 dinoflagellates, 15 haptophytes, and 18 other taxonomic species, were identified with net and water-collected samples in the study area. Diatoms and dinoflagellates were the most dominant phytoplankton groups. For net-phytoplankton samples, the species richness exhibited a high fluctuating pattern in the SYS (Fig. 4a). The percentage of diatom species within the overall phytoplankton community showed a gradual decline from 1959 to 2023 (MK-test, $p < 0.05$) (Fig. 4c), while that of dinoflagellate exhibited an increase (MK-test, $p < 0.05$) (Fig. 4e). For water-phytoplankton samples, the species richness of phytoplankton increased from 2009 to 2011, and then displayed a slight fluctuation trend from 2011 to 2023 (Fig. 4b). Both diatoms and dinoflagellates demonstrated non-significant increasing/decreasing trends in the proportion of species richness (Fig. 4d, f).

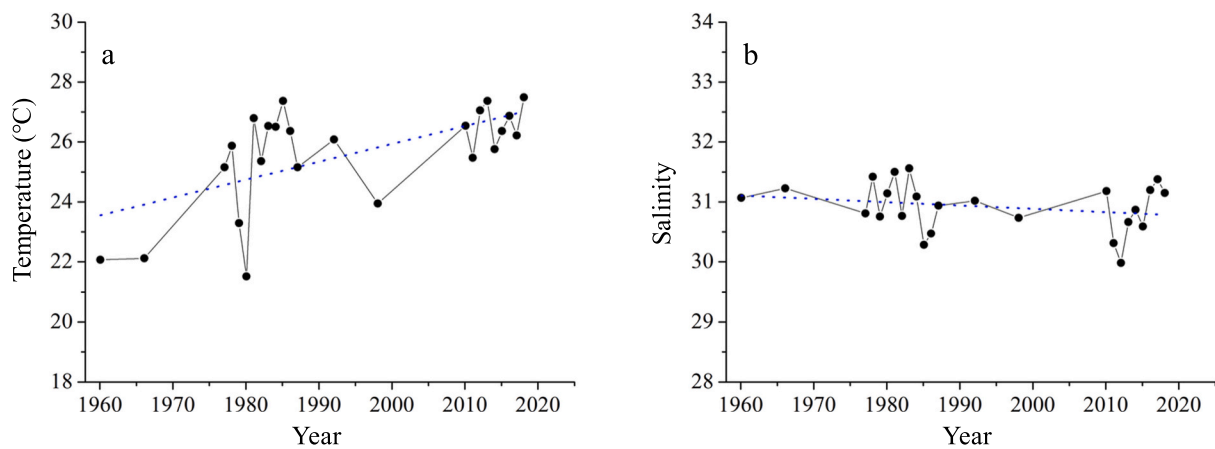


Fig. 2. Long-term variations in temperature (a, °C) and salinity (b) in the surface layer along the 35°N transect in the SYS during summer from 1960 to 2018 (data sources are shown in Table S1). The blue dotted lines represent the variation trend lines determined by linear regression. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

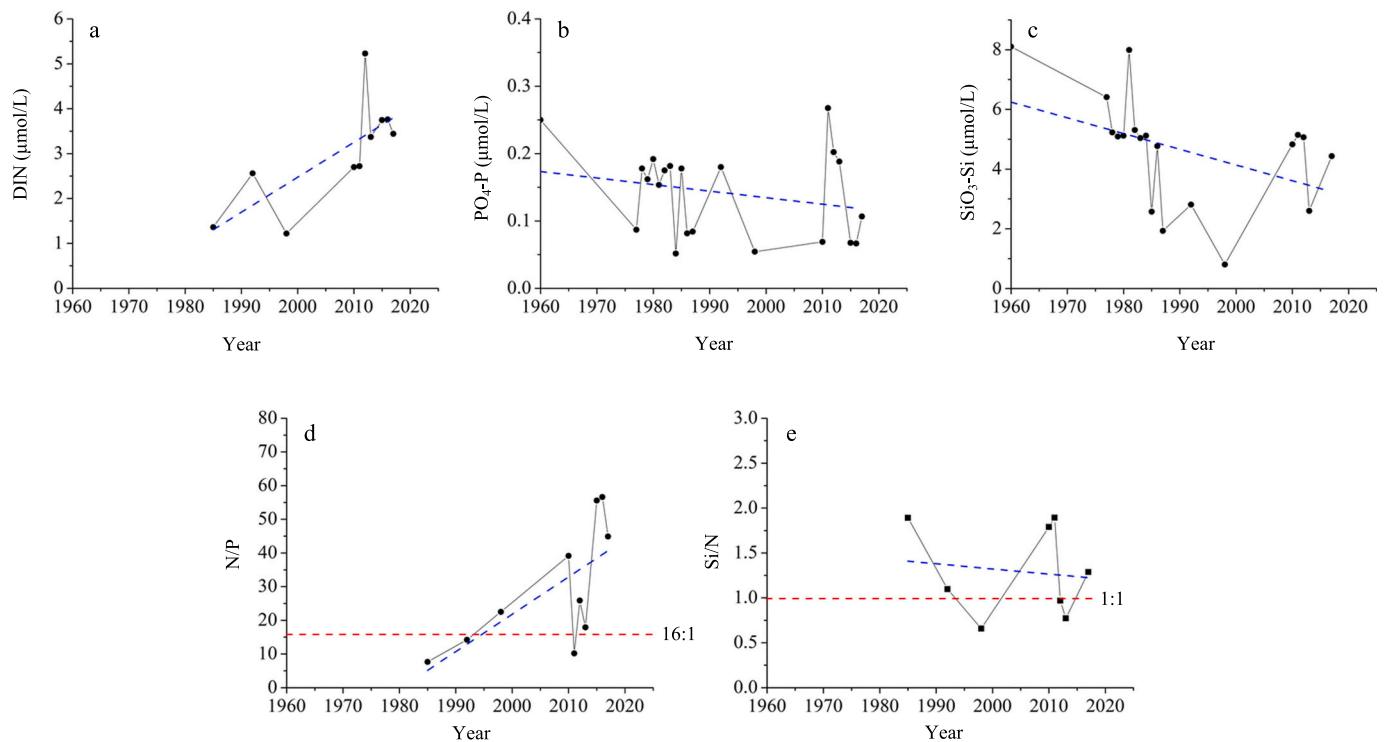


Fig. 3. Long-term variations in nutrient concentrations ($\mu\text{mol/L}$) and ratios within the surface layer along the 35°N transect in the SYS during the summers from 1966 to 2017 (data source are shown in Table S2). The blue dotted lines represent the variation trend lines determined by linear regression, and the red dotted lines represent the Redfield ratios of $\text{N/P} = 16:1$ and $\text{Si/N} = 1:1$ (Ptacnik et al., 2010). N refers to DIN here. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2.2. Phytoplankton biomass (Chl *a* and cell abundance)

Long-term variations in mean surface Chl *a* and the maximum surface Chl *a* value in the SYS are presented in Fig. 5. The mean surface Chl *a* concentration ranged from 0.27 to 3.20 $\mu\text{g/L}$, with an average value of 0.96 $\mu\text{g/L}$. The lowest value appeared in fall 1996, and the highest value appeared in summer 2015 (Fig. 5a). Generally, the surface mean Chl *a* concentration showed an overall increasing trend from 1996 to 2023 (MK-test, $p < 0.05$) (Fig. 5a). The surface maximum Chl *a* concentration exhibited a similar variation trend to that of the surface mean Chl *a* concentration (Fig. 5b).

Long-term variations in the cell abundance of phytoplankton are depicted in Fig. 6. For net-phytoplankton, cell abundance increased

from 1959 to 2023, despite high variation during this period (MK-test, $p < 0.05$) (Fig. 6a). The variation of diatom cell abundance was similar to that of total phytoplankton abundance (Fig. 6c), and that of dinoflagellate showed a gradually increasing trend (MK-test, $p < 0.05$) (Fig. 6e). For water-phytoplankton, cell abundance increased from 2011 to 2023 (MK-test, $p < 0.05$) (Fig. 6b), and both diatom and dinoflagellate cell abundance showed a similar variation trend (Fig. 6d, f). From 1959 to 2023, the proportions of diatom cell abundance within the whole phytoplankton community decreased by 8 % (Fig. 7a), while that of dinoflagellates increased with a comparable magnitude (Fig. 7c).

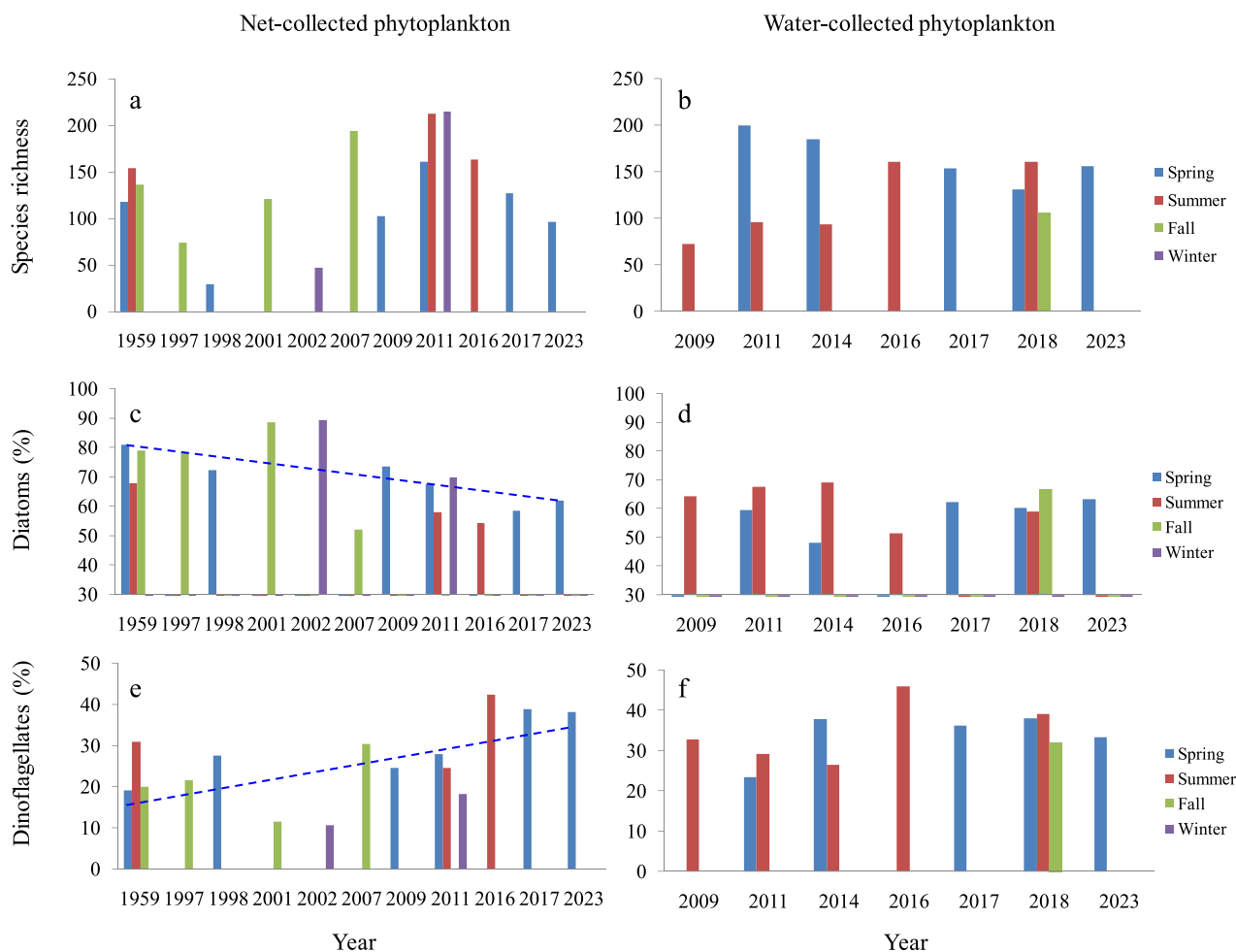


Fig. 4. Long-term variations in the total phytoplankton species number and proportions of diatoms and dinoflagellates species number in the total phytoplankton community for net- and water-collected samples in the SYS (data source are shown in Table S3).

3.2.3. Variation in dominant phytoplankton species

For net-phytoplankton, the dominant species mainly consisted of chain-forming diatoms before 2000, such as the genera *Chaetoceros*, *Thalassiosira*, *Paralia*, *Rhizosolenia*, and *Pseudo-nitzschia* (Table 2). After 2000, large dinoflagellates species appeared among the dominant species in the SYS, such as the *Triplos* spp. and *Noctiluca scintillans*. For water-phytoplankton, dominant species were mainly composed of diatom species from 2009 to 2023, and several small dinoflagellate species also appeared among the dominant species (e.g. *Prorocentrum cordatum* and *Scrippsiella trochoidea*) (Table 2). Generally, the dominant species shifted from a diatom-dominated community to a diatom-dinoflagellate co-dominated community in the SYS. In terms of ecological habits, the dominant species were mostly eurythermal and temperate species before 2000 (Table 2). After 2000, subtropical-tropical phytoplankton species appeared as dominant species more frequently in both net- and water-collected samples.

3.2.4. Community diversity

For net-phytoplankton, the Shannon-Wiener diversity index (H') of the phytoplankton community ranged from 1.91 to 2.76 (mean = 2.18 ± 0.22), and it showed a gradually decreasing trend (MK-test, $p < 0.05$) (Fig. 8a). For water-phytoplankton, H' ranged from 1.98 to 3.10 (mean = 2.43 ± 0.30), and no significant increasing/decreasing trend was observed from 2009 to 2023 (Fig. 8b). For net-phytoplankton, Pielou's evenness (J) indices ranged from 0.52 to 0.79 (mean = 0.63 ± 0.07), and it showed a gradually decreasing trend over the study period (MK-test, $p < 0.05$) (Fig. 8c). For water-phytoplankton, J ranged from 0.58 to 0.77

(mean = 0.65 ± 0.05), and no significant increasing/decreasing trend was observed (Fig. 8d).

3.3. Long-term trends in HABs

The frequency and types of HABs in the SYS are shown in Fig. 9. The main causative species of HABs have notably changed over the past several decades. Before 2000, HABs were mainly caused by diatoms, with only two HAB events caused by dinoflagellates. The dominant HAB species were mainly *Skeletonema* spp. and *N. scintillans* (Table S7). After 2000, the number of HABs caused by dinoflagellates increased remarkably, accounting for more than half of the total HAB events in the SYS. Several dinoflagellate species have become the new causative species of HABs, such as *Karenia* spp., *Gonyaulax* spp., *Heterosigma* spp. and *Akashiwo* spp. (Table S7).

3.4. Correlation analysis

The correlation between phytoplankton data and environmental parameters is depicted in Fig. 10. The phytoplankton cell abundance exhibited a negative correlation with salinity, while displaying positive correlations with silicate concentration and the Si/N ratio (Fig. 10a). Diatom cell abundance showed significant positive correlations with silicate concentration and the Si/N ratio, along with a significant negative correlation with salinity and the N/P ratio. For dinoflagellates, cell abundance exhibited a significant negative correlation with nitrite, nitrate, DIN, and phosphate concentration. The percentage of diatoms in

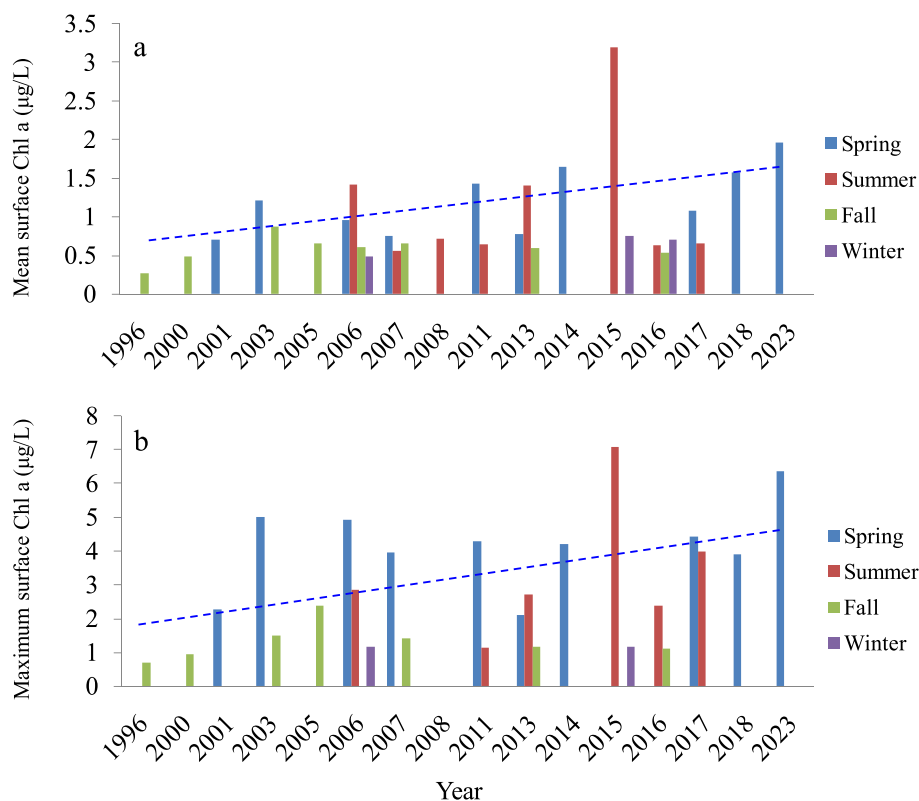


Fig. 5. Long-term changes in mean surface Chl *a* (a, µg/L) and maximum surface Chl *a* (b, µg/L) in the SYS (data source is shown in Table S4).

the total cell abundance (diatom%) displayed a significant positive correlation with phosphate concentration and a negative correlation with the N/P ratio. Conversely, the percentage of dinoflagellates (%) demonstrated a significant positive correlation with the N/P ratio and a negative correlation with the Si/N ratio. As the N/P ratio increases, the relative abundance of diatoms in the total phytoplankton cell abundance gradually diminishes, and the lower values of diatom proportion coincide with regions characterized by elevated N/P ratios and diminished Si/N ratios (Fig. 10b). Conversely, the proportion of dinoflagellates in total phytoplankton cell abundance shows an increase with the elevation of the N/P ratio.

4. Discussion

4.1. The increase in warm-water phytoplankton species

Due to their abbreviated generation times, phytoplankton can exhibit significant sensitivity to climate change (Neukermans et al., 2018). Warm-water phytoplankton species tend to be more adaptable than their cold-water counterparts, potentially benefiting from ocean warming and elevated growth rates (Huertas et al., 2011). Therefore, the rising sea temperatures accompanying climate change could have pronounced effects on phytoplankton ecological habitats. In this study, the dominant phytoplankton species in the SYS exhibited a prevalence of mainly eurythermal and temperate species before 2000 (Table 2). However, after 2000, there was a discernible shift towards subtropical-tropical phytoplankton species, exemplified by *Guinardia flaccida*, *Bidduphia regia*, *Rhizosolenia imbricate* and *Chaetoceros pseudo-curvisetus*. This alteration signifies an increased dominance of warm-water phytoplankton species within the study area. The SST in the SYS exhibited a noteworthy increasing trend over the past decades in this study (Table 2a), which was consistent with other studies (Park et al., 2015; Li et al., 2017), providing clear evidence of a warming trend in the SYS. The elevated temperatures may facilitate the expansion of the

biogeographic ranges of warm-water phytoplankton species, consequently influencing their geographical distribution patterns. Warm-water species originally confined to lower latitudes seas may extend their range northward, thereby occupying ecological niches within the SYS.

The increase in dominance of warm-water species in this study underscores a notable shift in phytoplankton phenology attributed to regional warming in the SYS. Similar trends have been observed in other coastal seas, including the Mediterranean Sea (Raitsos et al., 2010), Baltic Sea (Wasmund et al., 2008), and coastal seas around Australia (Ajani et al., 2020), where an increasing dominance of warm-water phytoplankton species has been reported. Chen et al. (2023) studied phytoplankton community in the Jiaozhou Bay, China, and they found that cold-water species of phytoplankton decreased during 2020–2021 compared with 2004–2005 (Chen et al., 2023). Beyond phytoplankton, an increase in warm-water copepod species and warm-water fish has also been observed in the SYS in recent decades (Liang et al., 2018; Shi et al., 2020). The results from this study and other studies suggest a transformative shift of marine ecosystems towards a warmer dynamic regime in this region.

4.2. Shift from diatom-dominated to diatom-dinoflagellate co-dominated phytoplankton community structure

In this study, there was a significant decrease in the proportions of diatom cell abundance within the phytoplankton community in the SYS (Fig. 7a), accompanied by a notable increase in that of dinoflagellates (Fig. 7c). The variation of dominant species composition also suggests that the phytoplankton community structure has evolved from a diatom-dominated state (before 2000) to a diatom-dinoflagellate co-dominated state (after 2000) (Table 2). The decline in diatoms proportions and the concurrent increase in dinoflagellates proportions have also been documented in other coastal seas worldwide. For instance, Widdicombe et al. (2010) observed that diatoms decreased while dinoflagellates

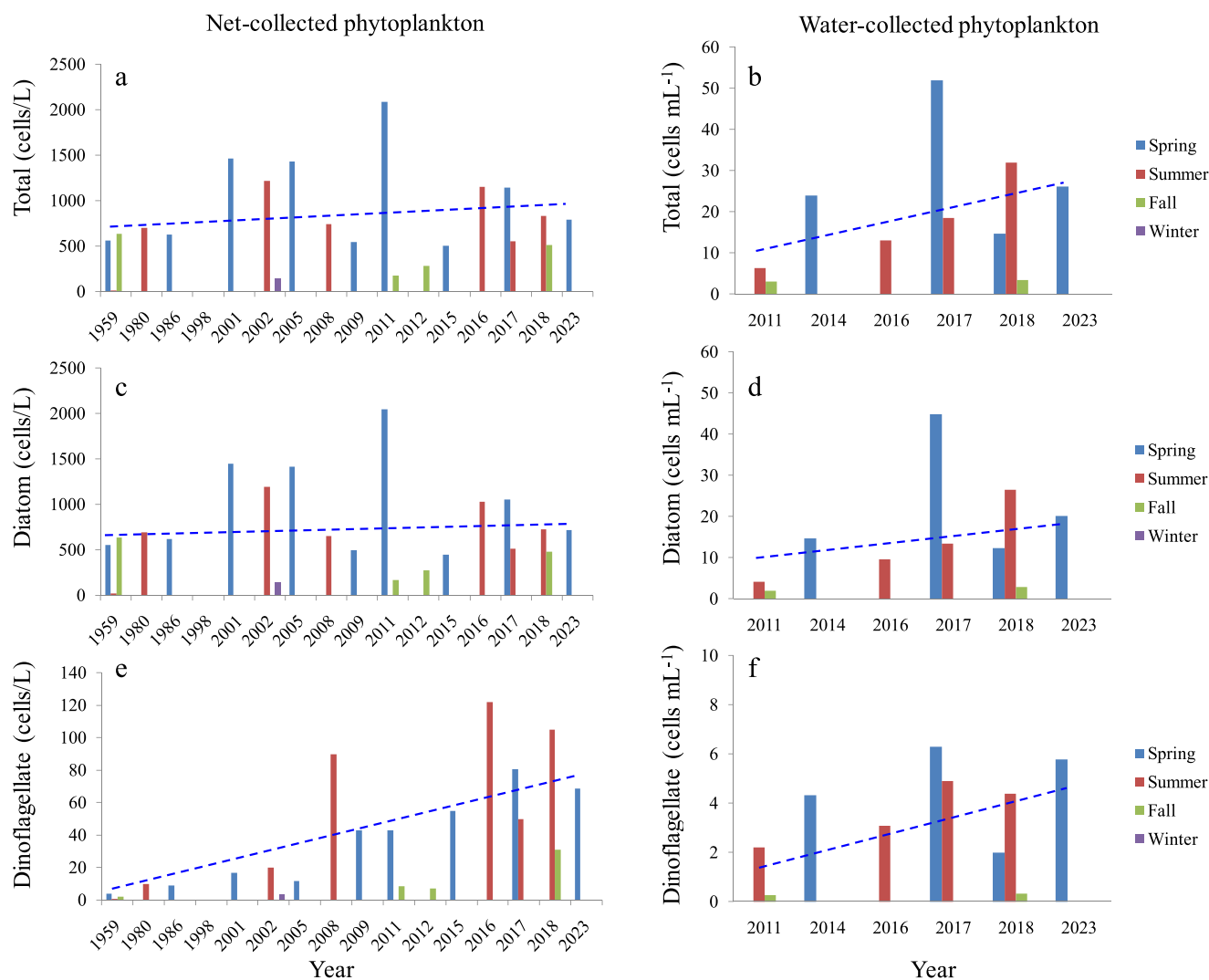


Fig. 6. Long-term changes in net- (cells/L) and water-collected (cells/mL) phytoplankton abundance in the SYS (data source is shown in Table S5).

increased in cell abundance in the Western English Channel from 1992 to 2007. Wasmund et al. (2011) investigated the long-term variation in phytoplankton communities in the central Baltic Sea from 1979 to 2005, noting a shift towards higher dinoflagellate abundance and dominance during this period. Yang et al. (2020) reported substantial increases in dinoflagellate relative abundance in Daya Bay from 1991 to 2017, and the frequency of dinoflagellate blooms rising rapidly since the 2000s. Therefore, this evolution trend of phytoplankton communities is not only a problem faced by the SYS, but also a problem in several other coastal seas.

Prior research has demonstrated that alterations in nutrient concentrations and composition can exert profound effects on phytoplankton community, and diatoms and dinoflagellates exhibit divergent adaptive strategies in response to nutrient conditions (Fu et al., 2012). In this study, DIN concentration exhibited an increasing trend, whereas $\text{PO}_4^{3-}\text{-P}$ and $\text{SiO}_3^{2-}\text{-Si}$ concentrations displayed an overall declining trend in the SYS (Fig. 3a-c). The trends in N/P and Si/N ratios (Fig. 3d, e) suggested a transition in the SYS from a N-limited state to a P-limited and potential Si-limited state according to the Redfield ratio (Ptacnik et al., 2010). The shift in inorganic nutrient supplies and their ratios would play a pivotal role in shaping the phytoplankton community structure. Diatoms, as a wholly autotrophic phytoplankton group, always exhibit rapid growth and gain dominance under conditions with sufficient nutrients (Guo et al., 2014; Zhou et al., 2017). The significant

positive correlation between diatom cell abundance and nutrient concentrations in this study (Fig. 10a) also verified this view. However, the growth of diatoms cells is easily inhibited under nutrients limited condition, particularly under phosphorus limitation (Xiao et al., 2018). Mesocosm experiments conducted in the North Sea and northern Yellow Sea demonstrated that diatoms struggle to compete at low phosphate concentrations (Egge, 1998; Liang et al., 2019). The significant negative correlation between the relative abundance of diatoms and N/P ratios (Fig. 10a) in this study further supports this observation. In contrast to diatoms, many dinoflagellate species possess the ability to utilize dissolved organic phosphate (DOP) with alkaline phosphatase enzymes under phosphorus limitation (Lin et al., 2012). Furthermore, many dinoflagellates species exhibit mixotrophic/heterotrophic modes, such as direct engulfment of prey, peduncle feeding, and pallium feeding (Jeong et al., 2010; Sherr and Sherr, 2007). Field studies have revealed that phosphorus limitation commonly stimulates dinoflagellates to ingest particulate nutrients (Stoecker, 1999), potentially contributing to their survival advantage over diatoms in phosphorus-limited condition. Therefore, the observed decline in diatom proportions and the concurrent rise in dinoflagellate proportions can be attributed to variations in nutrient ratios in the SYS. This aligns with the findings of Xiao et al. (2018) in the coastal East China Sea, where they predicted a 19% decrease in diatoms and a 60% increase in dinoflagellates by the year 2100 in response to increasing N/P ratios and decreasing Si/N ratios.

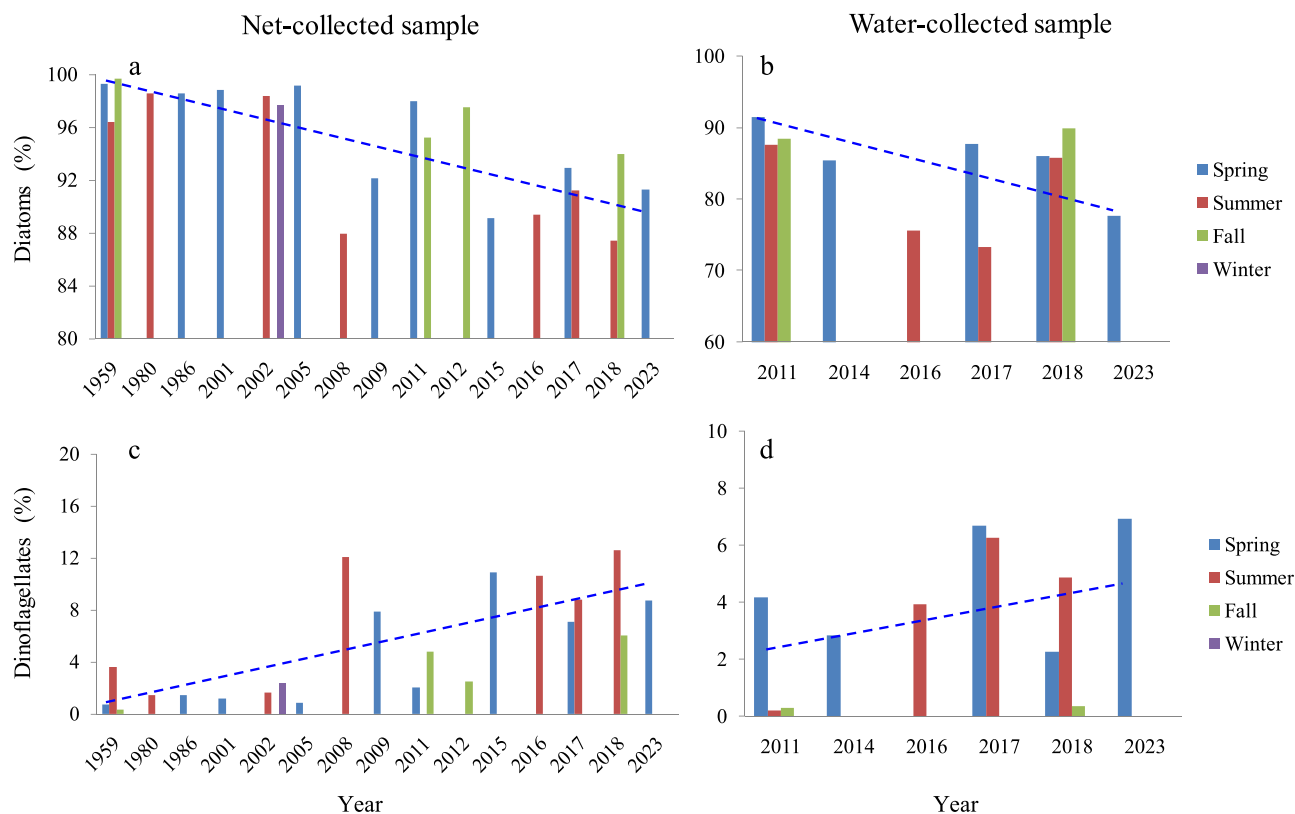


Fig. 7. Long-term changes in the proportion of diatoms and dinoflagellates in total phytoplankton cell abundance for net- (a, c) and water-collected (b, d) phytoplankton in the SYS (data source is shown in Table S5).

It should be noted that several studies present different results on the long-term variation trend in phytoplankton community in the coastal sea. [Hinder et al. \(2012\)](#) monitored diatom and dinoflagellate abundance in the northeast Atlantic and North Sea from 1960 to 2009, discovering a decline in dinoflagellate abundance, accompanied by an increase in diatom abundance. [Godhe et al. \(2015\)](#) analyzed the long-term trends in the phytoplankton community in the coastal southeastern Arabian Sea between 1990 and 2010, founding an increase in diatom abundances. [Totti et al. \(2019\)](#) explored the interannual variability of phytoplankton from 1988 to 2016 in the coastal Adriatic Sea, observing a decrease in dinoflagellate abundance and an increase in the frequency of diatom blooms. These divergent trends in diatom/dinoflagellate proportion variations underscore the non-uniformity of responses across different coastal seas. Such variations may be linked to the distinctive environmental conditions characterizing each specific region.

4.3. Reduction in phytoplankton diversity

The Shannon-Wiener diversity index (H) is one of the most widely employed metrics for quantifying species diversity. Its significance lies in its close association with the trophic state of water bodies, serving as an indicator of potential ecosystem modifications resulting from the impacts of climate change and human activities. The changes in phytoplankton diversity have far-reaching implications for fundamental ecosystem functions and processes, including biomass production, water quality maintenance, as well as the entire marine ecosystem structure. These changes, in turn, can have consequences for the ocean's capacity for food production and climate regulation ([Vallina et al., 2014](#)). In the present study, the H for the net-phytoplankton community exhibited a range from 1.91 to 2.76 in the SYS ([Fig. 8a](#)). This range was notably lower than those reported in the Mediterranean Sea (2.4–3, [Ignatiades et al., 2009](#)) and the southeastern Arabian Sea (2.30–4.59, [Minu et al.,](#)

[2014](#)), but comparable to values documented in other coastal seas, such as the Bohai Sea (1.67–2.47, [Wang et al., 2019](#)) and the East China Sea (0.64–3.10, [Noman et al., 2019](#)). Compared with 1959, there was a substantial decrease by 27 % in the H in 2023 in the SYS (from 2.76 to 2.01) ([Fig. 8a](#)). Simultaneously, Pielou's evenness (J) indices experienced a decline of almost 23 % (from 0.79 to 0.61) during the same period ([Fig. 8c](#)). These observations indicate an evolving trend towards a more unstable and unbalanced marine ecosystem in the SYS.

Climate change and anthropogenic impacts are likely to drive biodiversity loss, leading to a decrease in ecosystem stability, thereby influencing both the functioning and structure of marine ecosystems ([Henson et al., 2021](#)). The warming of the oceans and alterations in nutrient supply are anticipated to compel a reorganization of phytoplankton communities. The decline observed in the phytoplankton diversity index in this study was quite consistent with that of [Henson et al. \(2021\)](#), in which they predicted that the Shannon-wiener diversity index and Pielou's evenness indices would decrease at temperate latitudes in the North Pacific by the end of century. This diminishing trend in phytoplankton diversity suggests a shift of phytoplankton community towards a dominance of a fewer specific phytoplankton taxa, rather than a more 'balanced' state. This transformation may pose significant challenges to the productivity of the entire marine food web, with potentially greater consequences at higher trophic levels compared to the impact on phytoplankton.

4.4. Potential impacts on the ecosystem of the SYS

In this study, the rise in the prevalence of dinoflagellate HABs, as illustrated in [Fig. 9](#) and [Table S7](#), constitutes a significant evolutionary aspect of HABs in the SYS over the past few decades. The dinoflagellate cysts, potentially serving as a "seed bank" for dinoflagellate HABs, have also exhibited noteworthy increases in the SYS ([Kim et al., 2018](#); [Dai et al., 2020](#)), providing support in sedimentary records for this trend.

Table 2

Long-term changes in dominant species composition of net- and water-collected phytoplankton in the SYS (data source are shown in Table S1). Bold font represents dinoflagellate species.

	Time	Main dominant species	Reference
Net-sample	Spring, 1959	<i>Rhizosolenia sinensis</i> ^b , <i>Ditylum brightwellii</i> ^c , <i>Navicula</i> spp., <i>Chaetoceros</i> spp., <i>Thalassiosira</i> spp.	This study
	Summer, 1959	<i>Paralia sulcata</i> ^b , <i>Hemiaulus</i> spp., <i>Rhizosolenia</i> spp., <i>Nitzschia</i> spp., <i>Coscinodiscus</i> spp.	This study
	Fall, 1958	<i>Hemiaulus</i> spp., <i>Thalassiosira</i> spp., <i>Rhizosolenia</i> spp., <i>Paralia sulcata</i> ^b , <i>Nitzschia</i> spp.	This study
	Summer, 1980	<i>Skeletonema costatum</i> ^b , <i>Dactyliosolen mediterraneus</i> ^c	Qin et al., 2011
	Spring, 2001	<i>Chaetoceros</i> spp., <i>Thalassiosira</i> spp., <i>Rhizosolenia</i> spp.	This study
	Summer, 2002	<i>Guinardia flaccida</i> ^a , <i>Pseudo-nitzschia pungens</i> ^b , <i>Chaetoceros densus</i> ^b , <i>Rhizosolenia styliformis</i> ^b , <i>Bacillaria paradoxa</i> ^b	Qin et al., 2011
	Winter, 2002	<i>Coscinodiscus</i> spp., <i>Chaetoceros</i> spp., <i>Achnanthes longipos</i> ^c , <i>Biddulphia regia</i> ^a , <i>Corethron hystrix</i> ^b	Wang, 2003
	Summer, 2008	<i>Thalassiothrix frauenfeldii</i> ^b , <i>Eucampia zoodiacus</i> ^c , <i>Chaetoceros compressus</i> ^b , <i>Chaetoceros affinis</i> ^b , <i>Tripus fusus</i> ^c	Qin et al., 2011
	Spring, 2009	<i>Skeletonema</i> sp. ^b , <i>Noctiluca scintillans</i> ^b , <i>Chaetoceros lorenzianus</i> ^b , <i>Paralia sulcata</i> ^b , <i>Coscinodiscus radiatus</i> ^b	This study
	Spring, 2011	<i>Ditylum brightwellii</i> ^c , <i>Navicula</i> spp., <i>Chaetoceros</i> spp., <i>Rhizosolenia</i> spp., <i>Thalassiosira</i> spp.	This study
	Fall, 2011	<i>Chaetoceros</i> spp., <i>Tripus</i> spp., <i>Coscinodiscus</i> spp.	This study
	Winter, 2011	<i>Paralia sulcata</i> ^b , <i>Bacillaria paradoxa</i> ^b , <i>Navicula corymbosa</i> ^a , <i>Phaeocystis</i> sp. ^b	Gao et al., 2013
	Summer, 2012	<i>Chaetoceros</i> spp., <i>Tripus brevis</i> ^a , <i>Noctiluca scintillans</i> ^b , <i>Coscinodiscus</i> spp.	This study
	Fall, 2012	<i>Pseudo-nitzschia</i> spp., <i>Chaetoceros pseudo-curvisetus</i> ^a , <i>Rhizosolenia imbricata</i> ^a , <i>Tripus</i> spp.	This study
	Summer, 2013	<i>Rhizosolenia</i> spp., <i>Pseudo-nitzschia</i> spp., <i>Chaetoceros</i> spp., <i>Tripus</i> spp., <i>Coscinodiscus</i> spp.	This study
	Spring, 2017	<i>Thalassiosira</i> spp., <i>Chaetoceros femur</i> ^a , <i>Tripus</i> spp., <i>Paralia sulcata</i> ^b , <i>Coscinodiscus</i> spp.	This study
	Summer, 2017	<i>Chaetoceros debilis</i> ^c , <i>Chaetoceros pseudo-curvisetus</i> ^a , <i>Chaetoceros curvisetus</i> ^c , <i>Chaetoceros costatus</i> ^a , <i>Chaetoceros affinis</i> ^b	This study
	Fall, 2018	<i>Detonula pumila</i> ^a , <i>Skeletonema</i> spp. ^b , <i>Pseudo-nitzschia pungens</i> ^b , <i>Tripus fusus</i> ^c	This study
	Spring, 2023	<i>Chaetoceros</i> spp., <i>Tripus horridum</i> ^b , <i>Eucampia zoodiacus</i> ^c , <i>Pseudo-nitzschia delicatissima</i> ^c , <i>Coscinodiscus janischii</i> ^a	This study
	Spring, 2009	<i>Prorocentrum dentatum</i> ^c , <i>Pseudo-nitzschia delicatissima</i> ^a , <i>Paralia sulcata</i> ^b , <i>Nitzschia</i> sp., <i>Karenia</i> sp.	Tian and Sun, 2011
Water-sample	Spring, 2011	<i>Thalassiosira pacifica</i> ^c , <i>Chaetoceros cinctus</i> ^b , <i>Paralia sulcata</i> ^b , <i>Ditylum brightwellii</i> ^c , <i>Prorocentrum cordatum</i> ^b	Jiang et al., 2019
	Summer, 2011	<i>Paralia sulcata</i> ^b , <i>Distephanus speculum</i> var. <i>oconarium</i> ^b , <i>Heterocapsa</i> cf. <i>circularisquama</i> ^b , <i>Scrippsiella trochoidea</i> ^a , <i>Chaetoceros costatus</i> ^a	Jiang et al., 2019
	Fall, 2011	<i>Coccolithophores</i> spp., <i>Rhaphoneis amphiceros</i> ^c , <i>Paralia sulcata</i> ^b , <i>Scrippsiella trochoidea</i> ^a , <i>Thalassionema nitzschioides</i> ^c	Jiang et al., 2019
	Winter, 2011	<i>Paralia sulcata</i> ^b , <i>Rhaphoneis amphiceros</i> ^c , <i>Cryptophytes</i> spp., <i>Scrippsiella trochoidea</i> ^a , <i>Thalassionema nitzschioides</i> ^c	Jiang et al., 2019
	Spring, 2014	<i>Guinardia delicatula</i> ^c , <i>Ditylum brightwellii</i> ^c , <i>Paralia sulcata</i> ^b , <i>Chaetoceros</i> spp., <i>Prorocentrum cordatum</i> ^b	Zhang et al., 2016
	Summer, 2016	<i>Tripus fusus</i> ^c , <i>Dictyocha fibula</i> ^b , <i>Tripus horridum</i> ^b , <i>Paralia sulcata</i> ^b , <i>Prorocentrum cordatum</i> ^b	This study
	Spring, 2017	<i>Paralia sulcata</i> ^b , <i>Thalassiosira nordenskioldii</i> ^c , <i>Thalassiosira pacifica</i> ^c , <i>Pseudo-nitzschia delicatissima</i> ^c , <i>Prorocentrum cordatum</i> ^b	This study
	Summer, 2018	<i>Nitzschia</i> spp., <i>Guinardia flaccida</i> ^a , <i>Leptocylindrus danicus</i> ^c , <i>Hemiaulus sinensis</i> ^c , <i>Pseudo-nitzschia delicatissima</i> ^c	This study
	Fall, 2018	<i>Paralia sulcata</i> ^b , <i>Chaetoceros curvisetus</i> ^c , <i>Pseudo-nitzschia delicatissima</i> ^c , <i>Donkinia recta</i> ^c , <i>Coscinodiscus</i> spp.	This study
	Spring, 2023	<i>Eucampia zoodiacus</i> ^c , <i>Thalassionema nitzschioides</i> ^c , <i>Chaetoceros curvisetus</i> ^c , <i>Pseudo-nitzschia delicatissima</i> ^c , <i>Scrippsiella trochoidea</i> ^a	This study

^a Subtropical-tropical species.

^b Eurythermal species.

^c Temperate species.

Therefore, dinoflagellates HABs have been increasing in their dominance in various HAB types in the SYS. HABs can produce algal toxins, which are responsible for >60,000 intoxication incidents per year worldwide (Heil and Muni-Morgan, 2021). Besides this, HABs can also be responsible for the loss of commercial value to coastal communities through closing of fisheries and decreased tourism (Wells et al., 2020). The SYS plays a pivotal role in providing a multitude of highly valuable ecosystem services, encompassing primary and secondary productivity, and the support of economically significant fisheries and aquaculture activities (Song et al., 2021). The alterations observed in diatoms and dinoflagellates HABs in the SYS can have significant implications for these crucial services, which needs to be carefully monitored in the future.

Shifts in the phytoplankton community structure can also have profound impacts on the biological carbon pump (BCP) efficiency in the ocean. The BCP plays a pivotal role in the transfer of CO₂ from the atmosphere to the oceans and subsequently to the sea bottom. The efficiency of the BCP is significantly influenced by phytoplankton community structure (Basu and Mackey, 2018). Cai et al. (2015) found a strong correlation between particulate organic carbon (POC) export flux and the fraction of diatoms in the coastal South China Sea. Le Moigne et al. (2015) found that POC export efficiency was higher in blooming

diatom dominated areas than that in mixed communities dominated areas. Different phytoplankton groups exhibit variations in the size and composition of their cell walls and coverings, which influence their sinking velocities. Notably, diatoms are highly effective in transporting carbon to depth by forming rapidly sinking aggregates (Tréguer et al., 2018). Moreover, diatom cells are inherently heavy among phytoplankton groups due to their frustules, which are composed of biogenic silica and acts as ballast (Durkin et al., 2013). Consequently, diatoms are highly efficient in transporting carbon to depths within the ocean. Dinoflagellates, however, usually sink slower than diatoms in the water column due to the absence of the ‘ballast effect’ of silica walls and their weaker ability to form large-size aggregates (Guo et al., 2016). Therefore, the relative abundance of diatoms and dinoflagellates, or the prevalence of either group, becomes a determining factor in the proportion and quality of organic carbon settling to the sea floor and the degree of disintegration in the upper water column (Siegel et al., 2023). A diatom-dominated community tends to contribute to a conspicuous flux of organic matter, while a dinoflagellate-dominated community is more likely to disintegrate in the upper mixed layer, fueling the microbial food-web in the productive layer due to their slower sinking velocities (Guo et al., 2016; Spilling et al., 2018). Therefore, the increasing dominance in dinoflagellate and the decreasing dominance in

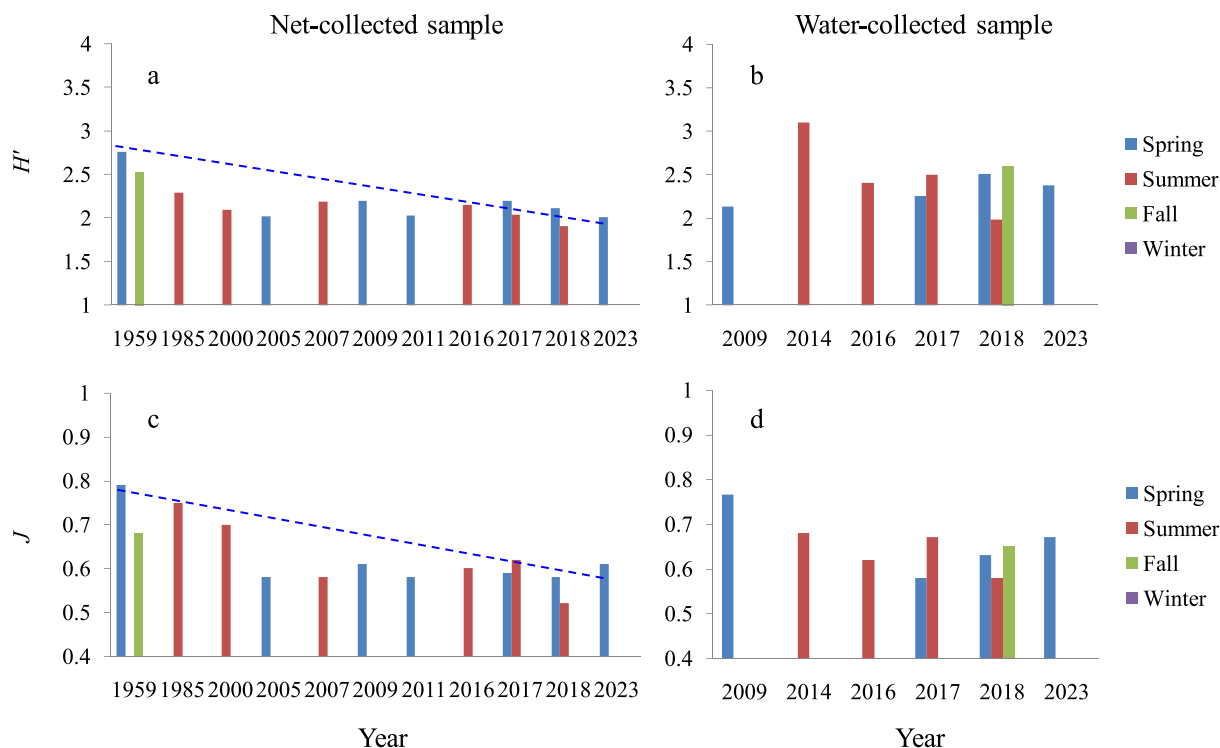


Fig. 8. Long-term changes in Shannon-Wiener diversity index (H') (a, b) and Pielou's evenness (J) (c, d) of net- and water-collected phytoplankton in the SYS (data source is shown in Table S6).

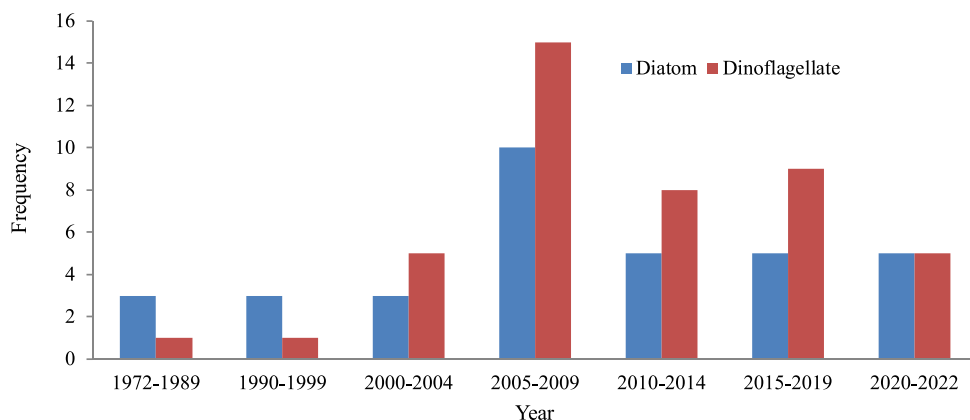


Fig. 9. Long-term variation in frequency of harmful algal blooms (HABs) caused by diatoms and dinoflagellates in the SYS.

diatoms in the SYS (Fig. 7) may lead to a lower BCP efficiency in the future (Fig. 11).

The rise in dinoflagellate dominance within the phytoplankton community would result in slower sinking velocities and longer residence times of phytoplankton organic carbon in the water column, which would favor more apparent oxygen utilization (AOU) within the water column, leading to an enhancement of oxygen depletion and a decrease in dissolved oxygen (DO) concentrations. Wei et al. (2021) found that hypoxia is primarily attributed to the intensified water column oxygen consumption by slowly sinking particulate organic carbon in the central Bohai Sea, which is associated with the shift in phytoplankton community structure towards an increase in dinoflagellate proportion. In the SYS, the DO concentration has also shown a declining trend over the past several decades (Li et al., 2015; Guo et al., 2020a, b), and this aligns with the increasing proportion of dinoflagellates in this area (Fig. 7). Therefore, the effect of the rise in dinoflagellates on the reduction in DO concentrations in the SYS warrants further attention in

future investigations. Understanding these dynamics is crucial for comprehending the potential consequences of shifts in phytoplankton community structure on oxygen levels within the water column, which has broader implications for the overall health and functioning of the marine ecosystems in the SYS.

5. Conclusions

Contemporary marine ecosystems face various global change phenomena, encompassing climate change and shifts in nutrient conditions. To get a comprehensive understanding and, ultimately, the ability to predict how these factors influence the structure and functioning of marine ecosystems require a long-term perspective. In this study, we combined observational and historical data to confirm that long-term changes in the phytoplankton community structure in the SYS were closely related to environmental variations caused by climatic warming and human activities. The evolving trend of phytoplankton community

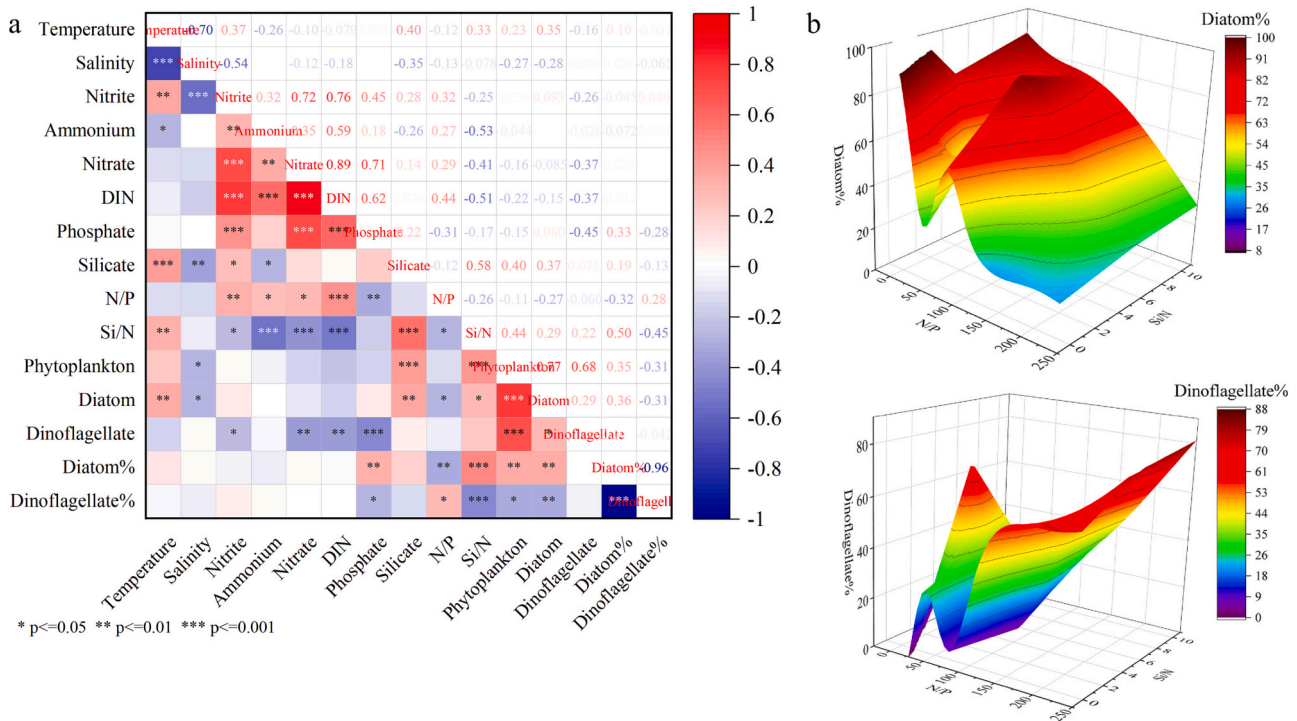


Fig. 10. The relationship between phytoplankton data and environmental data. a: Pearson's rank analysis of environmental parameters and phytoplankton community structure; b: The response of diatoms (%) and dinoflagellates (%) in total phytoplankton cell abundance to N/P and Si/N ratios. Data from water samples of all sampling cruises.

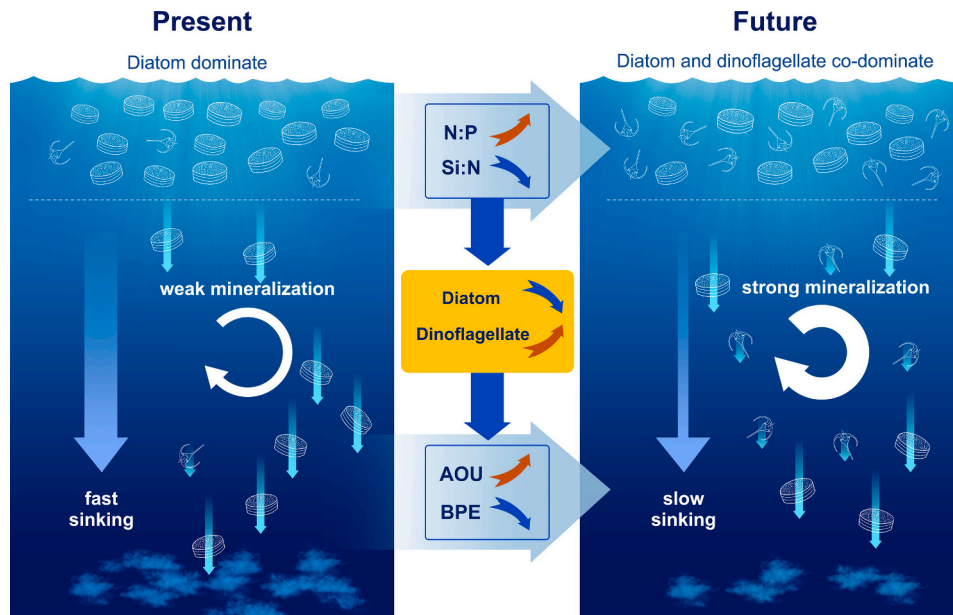


Fig. 11. Conceptual diagram of the impact of phytoplankton community structure changes on the SYS ecosystem. AOU: apparent oxygen utilization; BPE: biological carbon pump efficiency.

structure over the past several decades was characterized by an increase in warm-water phytoplankton species, a decrease in the proportion of diatoms cell abundance and an increase in that of dinoflagellates. The warming of seawater and changes in nutrients structure (N/P ratio and Si/N ratio) are the fundamental reasons for this shift. The consequences of shifts in phytoplankton communities and their impacts on higher trophic organisms such as zooplankton, fish, and benthos communities are unknown, which should capture our attention in the future. Furthermore, other ecological effects resulting from this change, such as

the increase in dinoflagellates HABs, alterations in the efficiency of the biological carbon pump, and impacts on the extent of hypoxia, are also worthy of our attention. This study will be useful for both local and international environmental managers, given the widespread impact of climate changes and human activities on coastal seas worldwide.

CRedit authorship contribution statement

Shujin Guo: Writing – original draft, Methodology, Investigation,

Formal analysis, Conceptualization. **Xiaoxia Sun**: Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization. **Jian Zhang**: Resources, Data curation. **Qingzhen Yao**: Investigation, Formal analysis. **Chuanjie Wei**: Formal analysis. **Feng Wang**: Visualization.

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.

Data availability

Data supporting these findings are available from the corresponding author upon reasonable request.

Acknowledgement

The authors thank all the crews in R/V “Kexue 3” for their support in the sample collection. This work was supported by the International Partnership Program of Chinese Academy of Sciences (133137KYSB20200002), the National Natural Science Foundation of China (No. 32371619, U2006206), the International Partnership Program of Chinese Academy of Sciences (121311KYSB20190029), and the Laoshan Laboratory (No. LSKJ202204005).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2024.116179>.

References

- Ajani, P.A., Davies, C.H., Eriksen, R.S., Richardson, A.J., 2020. Global warming impacts micro-phytoplankton at a long-term Pacific Ocean coastal station. *Front. Mar. Sci.* 7, 878. <https://doi.org/10.3389/fmars.2020.576011>.
- Aydin-Onen, S., Kocak, F., Kucuksezgin, F., 2012. Evaluation of spatial and temporal variation of inorganic nutrient species in the eastern Aegean Sea waters. *Mar. Pollut. Bull.* 64 (12), 2849–2856. <https://doi.org/10.1016/j.marpolbul.2012.08.032>.
- Basu, S., Mackey, K.R.M., 2018. Phytoplankton as key mediators of the biological carbon pump: their responses to a changing climate. *Sustainability* 10, 869. <https://doi.org/10.3390/su10030869>.
- Beaugrand, G., Reid, P.C., 2003. Long-term changes in phytoplankton, zooplankton and salmon related to climate. *Glob. Chang. Biol.* 9, 801–817. <https://doi.org/10.1046/j.1365-2486.2003.00632.x>.
- Cai, P.H., Zhao, D.C., Wang, L., Huang, B.Q., Dai, M.H., 2015. Role of particle stock and phytoplankton community structure in regulating particulate organic carbon export in a large marginal sea. *J. Geophys. Res.* 120, 2063–2095. <https://doi.org/10.1002/2014JC010432>.
- Chen, W.Q., Wang, X.J., Yang, S.M., 2023. Response of phytoplankton community structure to environmental changes in the coastal areas of northern China. *Mar. Pollut. Bull.* 195, 115300. <https://doi.org/10.1016/j.marpolbul.2023.115300>.
- Dai, L., Yu, R.C., Geng, H.X., Zhao, Y., Zhang, Q.C., Kong, F.Z., Chen, Z.F., Zhao, J.Y., Zhou, M.J., 2020. Resting cysts of *Alexandrium catenella* and *A. pacificum* (Dinophyceae) in the Bohai and Yellow Seas, China: abundance, distribution and implications for toxic algal blooms. *Harmful Algae* 93, 101794. <https://doi.org/10.1016/j.hal.2020.101794>.
- Durkin, C.A., Bender, S.J., Chan, K.Y.K., Gaessner, K., Grünbaum, D., Armbrust, E.V., 2013. Silicic acid supplied to coastal diatom communities influences cellular silicification and the potential export of carbon. *Limnol. Oceanogr.* 58 (5), 1707–1726. <https://doi.org/10.4319/lo.2013.58.5.1707>.
- EGGE, J.K., 1998. Are diatoms poor competitors at low phosphate concentrations? *J. Mar. Syst.* 16, 191–198. [https://doi.org/10.1016/S0924-7963\(97\)00113-9](https://doi.org/10.1016/S0924-7963(97)00113-9).
- Fu, M.Z., Wang, Z.L., Pu, X.M., Xu, Z.J., Zhu, M.Y., 2012. Changes of nutrient concentrations and N:P:Si ratios and their possible impacts on the Huanghai Sea ecosystem. *Acta Oceanol. Sin.* 31(4), 101–112. doi:<https://doi.org/10.1007/s13131-012-0224-x>.
- Gao, Y., Jiang, Z.B., Liu, J.J., Chen, Q.Z., Zeng, J.N., Huang, W., 2013. Seasonal variations of net-phytoplankton community structure in the southern Yellow Sea. *J. Ocean Univ. China* 12 (4), 557–567. <https://doi.org/10.1007/s11802-013-2258-x>.
- Godhe, A., Narayanaswamy, C., Klais, R., Venkatesha Moorthy, K.S., Ramesh, R., Rai, A., Venkataswamy Reddy, H.R., 2015. Long-term patterns of net phytoplankton and hydrography in coastal SE Arabian Sea: what can be inferred from genus level data? *Estuar. Coast. Shelf Sci.* 162 (5), 69–75. <https://doi.org/10.1016/j.ecss.2015.03.006>.
- Guo, S.J., Feng, Y.Y., Wang, L., Dai, M.H., Liu, Z.L., Bai, Y., Sun, J., 2014. Seasonal variation in the phytoplankton community of a continental-shelf sea: the East China Sea. *Mar. Ecol. Prog. Ser.* 516, 103–126. <https://doi.org/10.3354/meps10952>.
- Guo, S.J., Sun, J., Zhao, Q.B., Feng, Y.Y., Huang, D.J., Liu, S.M., 2016. Sinking rates of phytoplankton in the Changjiang (Yangtze River) estuary: a comparative study between *Prorocentrum dentatum* and *Skeletonema dorinii* bloom. *J. Mar. Syst.* 154, 5–14. <https://doi.org/10.1016/j.jmarsys.2015.07.003>.
- Guo, S.J., Yao, Q.J., Wei, C.J., Sun, X.X., 2020a. Phytoplankton community structure in the southern Yellow Sea and East China Sea and its relationship with environmental factors. *Advances in Marine Science* 38 (3), 476–492 (in Chinese with English abstract).
- Guo, J.Q., Yuan, H.M., Song, J.M., Li, X.G., Duan, L.Q., 2020b. Hypoxia, acidification and nutrient accumulation in the Yellow Sea Cold Water of the South Yellow Sea. *Sci. Total Environ.* 745, 141050. <https://doi.org/10.1016/j.scitotenv.2020.141050>.
- Heil, C.A., Muni-Morgan, A.L., 2021. Florida’s harmful algal bloom (HAB) problem: escalating risks to human, environmental and economic health with climate change. *Front. Ecol. Evol.* 9, 646080. <https://doi.org/10.3389/fevo.2021.646080>.
- Henson, S.A., Cael, B.B., Allen, S.R., Dutkiewicz, S., 2021. Future phytoplankton diversity in a changing climate. *Nat. Commun.* 12, 5372. <https://doi.org/10.1038/s41467-021-25699-w>.
- Hinder, S.L., Hays, G.C., Edwards, M., Roberts, E.C., Walne, A.W., Gravenor, M.B., 2012. Changes in marine dinoflagellate and diatom abundance under climate change. *Nat. Clim. Chang.* 2, 271–275. <https://doi.org/10.1038/nclimate1388>.
- Huertas, I.E., Rouco, M., López-Rodas, V., Costas, E., 2011. Warming will affect phytoplankton differently: evidence through a mechanistic approach. *Proc. R. Soc. B* 278 (1724), 3534–3543. <https://doi.org/10.1098/rspb.2011.0160>.
- Ignatiades, L., Gotsis-skretas, O., Pagou, K., Krasakopoulou, E., 2009. Diversification of phytoplankton community structure and related parameters along a large-scale longitudinal east-west transect of the Mediterranean Sea. *J. Plankton Res.* 31 (4), 411–428. <https://doi.org/10.1093/plankt/fbn124>.
- Jeong, H.J., Yoo, Y.D., Kim, J.S., Seong, K.A., Kang, N.S., Kim, T.H., 2010. Growth, feeding and ecological roles of the mixotrophic and heterotrophic dinoflagellates in marine planktonic food webs. *Ocean Science Journal* 45 (2), 65–91. <https://doi.org/10.1007/s12601-010-0007-2>.
- Jiang, Z.B., Liu, J.J., Chen, J.F., Chen, Q.Z., Yan, X.J., Xuan, J.L., Zeng, J.N., 2014. Responses of summer phytoplankton community to drastic environmental changes in the Changjiang (Yangtze River) Estuary during the past 50 years. *Water Res.* 54, 1–11. <https://doi.org/10.1016/j.watres.2014.01.032>.
- Jiang, Z.B., Chen, J.F., Gao, Y.X., Zhai, H.C., Jin, H.Y., Zhou, F., Shou, L., Yan, X.J., Chen, Q.Z., 2019. Regulation of spatial changes in phytoplankton community by water column stability and nutrients in the southern Yellow Sea. *J. Geophys. Res.* 124, 2610–2627. <https://doi.org/10.1029/2018JG004785>.
- Kim, S.Y., Roh, Y.H., Shin, H.H., Huh, S., Kang, S.H., Lim, D., 2018. Decadal-scale variations of sedimentary dinoflagellate cyst records from the Yellow Sea over the last 400 years. *Estuar. Coast. Shelf Sci.* 200, 91–98. <https://doi.org/10.1016/j.ecss.2017.10.006>.
- Le Moigne, F.A.C., Poulton, A.J., Henson, S.A., Daniels, C., Fragoso, G.M., Mitchell, E., Richier, S., Russell, B.C., Smith, H.E.K., Tarling, G.A., Young, J.R., Zubkov, M., 2015. Carbon export efficiency and phytoplankton community composition in the Atlantic sector of the Arctic Ocean. *J. Geophys. Res.* 120, 3896–3912. <https://doi.org/10.1002/2015JC010700>.
- Lehtinen, S., Tamminen, T., Ptacnik, R., Andersen, T., 2017. Phytoplankton species richness, evenness, and production in relation to nutrient availability and imbalance. *Limnol. Oceanogr.* 62 (4), 1393–1408. <https://doi.org/10.1002/lno.10506>.
- Li, H.M., Zhang, C.S., Han, X.R., Shi, X.Y., 2015. Changes in concentrations of oxygen, dissolved nitrogen, phosphate, and silicate in the southern Yellow Sea, 1980–2012: sources and seaward gradients. *Estuar. Coast. Shelf Sci.* 163, 44–55. <https://doi.org/10.1016/j.ecss.2014.12.013>.
- Li, A., Yu, F., Si, G.C., Wei, C.J., 2017. Long-term variation in the salinity of the Southern Yellow Sea Cold Water Mass, 1976–2006. *J. Oceanogr.* 73, 321–331. <https://doi.org/10.1007/s10872-016-0405-x>.
- Li, X.Y., Yu, R.C., Geng, H.X., Li, Y.F., 2021. Increasing dominance of dinoflagellate red tides in the coastal waters of Yellow Sea, China. *Mar. Pollut. Bull.* 168, 112439. <https://doi.org/10.1016/j.marpolbul.2021.112439>.
- Liang, Y.B., 2012. Investigation and Assessment of Red Tide in China (1933–2009). Ocean Press, Beijing.
- Liang, C., Xian, W.W., Pauly, D., 2018. Impacts of ocean warming on China’s fisheries catches: an application of ‘mean temperature of the catch’ concept. *Front. Mar. Sci.* 5, 26. <https://doi.org/10.3389/fmars.2018.00026>.
- Liang, Y., Zhang, G.T., Wan, A.Y., Zhao, Z.X., Wang, S.W., L, Q., 2019. Nutrient-limitation induced diatom-dinoflagellate shift of spring phytoplankton community in an offshore shellfish farming area. *Mar. Pollut. Bull.* 141, 1–8. <https://doi.org/10.1016/j.marpolbul.2019.02.009>.
- Lin, C., Ning, X., Sun, J., Lin, Y., Xu, B., 2005. Environmental changes and the responses of the ecosystems of the Yellow Sea during 1976–2000. *J. Mar. Syst.* 55, 223–234. <https://doi.org/10.1016/j.jmarsys.2004.08.001>.
- Lin, X., Zhang, H., Cui, Y.D., Lin, S.J., 2012. High sequence variability, diverse subcellular localizations, and ecological implications of alkaline phosphatase in dinoflagellates and other eukaryotic phytoplankton. *Front. Microbiol.* 3, 235. <https://doi.org/10.3389/fmicb.2012.00235>.
- Liu, H.J., Huang, Y.J., Zhai, W.D., Guo, S.J., Jin, H.L., Sun, J., 2015. Phytoplankton communities and its controlling factors in summer and autumn in the southern Yellow Sea, China. *Acta Oceanol. Sin.* 34 (2), 114–123. <https://doi.org/10.1007/s13131-015-0620-0>.
- Liu, Z.Q., Gan, J.P., Hu, J.Y., Wu, H., Cai, Z.Y., Deng, Y.F., 2021. Progress on circulation dynamics in the East China Sea and southern Yellow Sea: origination, pathways, and

- destinations of shelf currents. *Prog. Oceanogr.* 193, 102553 <https://doi.org/10.1016/j.pocean.2021.102553>.
- Lü, M.X., Luan, Q.S., Peng, L., Cui, Y., Wang, J., 2016. Assemblages of phytoplankton in the Yellow Sea in response to the physical processes during the summer of 2014. *Advances in Marine Science* 34 (1), 70–84 (in Chinese with English abstract).
- Luan, Q.S., Kang, Y.D., Wang, J., 2020. Long-term changes within the phytoplankton community in the Yellow Sea (1985–2015). *Journal of Fishery Sciences of China* 27 (1), 1–11 (in Chinese with English abstract).
- McKenna, S., Meyer, M., Gregg, C., Gerber, S., 2016. S-CorrPlot: an interactive scatterplot for exploring correlation. *J. Comput. Graph. Stat.* 25, 445–463. <https://doi.org/10.1080/10618600.2015.1021926>.
- Minu, P., Shaju, S.S., Muhamed, A.P., Meenakumari, B., 2014. Phytoplankton community characteristics in the coastal waters of the southeastern Arabian Sea. *Acta Oceanol. Sin.* 33 (12), 170–179. <https://doi.org/10.1007/s13131-014-0571-x>.
- Neukermans, G., Oziel, L., Babin, M., 2018. Increased intrusion of warming Atlantic water leads to rapid expansion of temperate phytoplankton in the Arctic. *Glob. Chang. Biol.* 24 (6), 2545–2553. <https://doi.org/10.1111/gcb.14075>.
- Noman, M.A., Sun, J., Gang, Q., Guo, C., Islam, M.S., Li, S., Yue, J., 2019. Factors regulating the phytoplankton and tintinnid microzooplankton communities in the East China Sea. *Cont. Shelf Res.* 181, 14–24. <https://doi.org/10.1016/j.csr.2019.05.007>.
- Office of Integrated Oceanographic Survey of China, 1961. Dataset of the national integrated oceanographic survey. Survey data of biological compositions in the Bohai, Huanghai and East China Seas, Beijing, vol. 2 (in Chinese).
- Park, K.A., Lee, E.Y., Chang, E., Hong, S., 2015. Spatial and temporal variability of sea surface temperature and warming trends in the Yellow Sea. *J. Mar. Syst.* 143, 24–38. <https://doi.org/10.1016/j.jmarsys.2014.10.013>.
- Paxinos, R., Mitchell, J.G., 2000. A rapid Utermöhl method for estimating algal numbers. *J. Plankton Res.* 22 (12), 2255–2262. <https://doi.org/10.1093/plankt/22.12.2255>.
- Ptácnik, R., Andersen, T., Tamminen, T., 2010. Performance of the Redfield ratio and a family of nutrient limitation indicators as thresholds for phytoplankton N vs. P limitation. *Ecosystems* 13, 1201–1214. <https://doi.org/10.1007/s10021-010-9380-z>.
- Qian, S.B., Chen, G.W., 1986. The comprehensive investigation in a long Yangtze River estuary to Jezu Island and its adjacent waters: phytoplankton ecology. *Journal of Ocean College of Shandong* 16 (2), 26–55 (in Chinese).
- Qin, Y.T., Ji, H.H., Song, C.Y., 2011. Phytoplankton ecological characteristics in green tide area of Southern Yellow Sea. *Mar. Environ. Sci.* 30 (3), 394–397 (in Chinese with English abstract).
- Raitsos, D.E., Beaugrand, G., Georgopoulos, D., Zenetos, A., Pancucci-Papadopoulou, A. M., Theocharis, A., Papatthanassiou, E., 2010. Global climate change amplifies the entry of tropical species into the Eastern Mediterranean Sea. *Limnol. Oceanogr.* 55 (4), 1478–1484. <https://doi.org/10.4319/lo.2010.55.4.1478>.
- Sherr, E.B., Sherr, B.F., 2007. Heterotrophic dinoflagellates: a significant component of microzooplankton biomass and major grazers of diatoms in the sea. *Mar. Ecol. Prog. Ser.* 352, 187–197. <https://doi.org/10.3354/meps07161>.
- Shi, Y.Q., Niu, M.X., Zuo, T., Wang, J., Luan, Q.S., Sun, J.Q., Yuan, W., Shan, X.J., Pakhomov, E.A., 2020. Inter-annual and seasonal variations in zooplankton community structure in the Yellow Sea with possible influence of climatic variability. *Prog. Oceanogr.* 185, 102349 <https://doi.org/10.1016/j.pocean.2020.102349>.
- Siegel, D.A., DeVries, T., Cetinić, I., Bisson, K.M., 2023. Quantifying the ocean's biological pump and its carbon cycle impacts on global scales. *Annu. Rev. Mar. Sci.* 15, 329–356. <https://doi.org/10.1146/annurev-marine-040722-115226>.
- Song, J.J., Zhang, Z.P., Chen, L., Wang, D., Liu, H.J., Wang, Q.X., Wang, M.Q., Yu, D.D., 2021. Changes in ecosystem services values in the south and north Yellow Sea between 2000 and 2010. *Ocean Coast. Manag.* 202, 105497 <https://doi.org/10.1016/j.ocecoaman.2020.105497>.
- Spilling, K., Olli, K., Lehtoranta, J., Kremp, A., Tedesco, L., Tamelander, T., Klais, R., Peltonen, H., Tamminen, T., 2018. Shifting diatom-dinoflagellate dominance during spring bloom in the Baltic Sea and its potential effects on biogeochemical cycling. *Front. Mar. Sci.* 5, 327. <https://doi.org/10.3389/fmars.2018.00327>.
- Stoecker, D.K., 1999. Mixotrophy among dinoflagellates. *J. Eukaryot. Microbiol.* 46, 397–401. <https://doi.org/10.1111/j.1550-7408.1999.tb04619.x>.
- Strokal, M., Yang, H., Zhang, Y.C., Kroeze, C., Li, L.L., Luan, S.J., Wang, H.Z., Yang, S.S., Zhang, Y.S., 2014. Increasing eutrophication in the coastal seas of China from 1970 to 2050. *Mar. Pollut. Bull.* 85, 123–140. <https://doi.org/10.1016/j.marpolbul.2014.06.011>.
- Strong, W.L., 2016. Biased richness and evenness relationships within Shannon-Wiener index values. *Ecol. Indic.* 67, 703–713. <https://doi.org/10.1016/j.ecolind.2016.03.043>.
- Tian, W., Sun, J., 2011. Later spring phytoplankton community in southern Yellow Sea in 2009. *Mar. Sci.* 35 (6), 19–24 (in Chinese with English abstract).
- Totti, C., Romagnoli, T., Accoroni, S., Coluccelli, A., Pellegrini, M., Campanelli, A., Grilli, F., Marini, M., 2019. Phytoplankton communities in the northwestern Adriatic Sea: Interdecadal variability over a 30-years period (1988–2016) and relationships with meteorological drivers. *J. Mar. Syst.* 193, 137–153. <https://doi.org/10.1016/j.jmarsys.2019.01.007>.
- Trees, C.C., Bidigare, R.R., Karl, D.M., Van Heukelem, L., Dore, J., 2022. Fluorometric chlorophyll *a*: Sampling, laboratory methods, and data analysis protocols, in: *Ocean Optics Protocols for Satellite Ocean Color Sensor Validation, NASA/TM-2002-210004/Rev3-Vol2*, edited by: Mueller J L and Fargion G S, NASA Goddard Space Flight Center, Greenbelt, Maryland, 269–283.
- Tréguer, P., Bowler, C., Moriceau, B., Dutkiewicz, S., Gehlen, M., Aumont, O., Bittner, L., Dugdale, R., Finkel, Z., Iudicone, D., Jahn, O., Guidi, L., Lasbleiz, M., Leblanc, K., Levy, M., Pondaven, P., 2018. Influence of diatom diversity on the ocean biological carbon pump. *Nat. Geosci.* 11, 27–37. <https://doi.org/10.1038/s41561-017-0028-x>.
- Vallina, S.M., Follows, M.J., Dutkiewicz, S., Montoya, J.M., Cermeño, P., Loreau, M., 2014. Global relationship between phytoplankton diversity and productivity in the ocean. *Nat. Commun.* 5, 4299. <https://doi.org/10.1038/ncomms5299>.
- Wählström, I., Höglund, A., Almroth-Rosell, E., MacKenzie, B.R., Gröger, M., Eilola, K., Plikshs, M., Andersson, H.C., 2020. Combined climate change and nutrient load impacts on future habitats and eutrophication indicators in a eutrophic coastal sea. *Limnol. Oceanogr.* 65 (9), 2170–2187. <https://doi.org/10.1002/lno.11446>.
- Wang, J., 2003. Study on phytoplankton in the Yellow Sea in autumn and winter. *Marine Fisheries Research* 24 (1), 15–23 (in Chinese with English abstract).
- Wang, J.J., 2020. Spatiotemporal Variations and Influence Factors of Nutrients in the Western South Yellow Sea. Doctor Dissertation. Ocean University of China.
- Wang, Y.B., Sun, Y.Y., Wang, C.X., Chen, W.W., Hu, X.K., 2019. Net-phytoplankton community structure and its environmental correlations in central Bohai Sea and the Bohai Strait. *Aquat. Ecosyst. Health Manag.* 22 (4), 481–493. <https://doi.org/10.1080/14634988.2019.1693223>.
- Wang, R., Wu, J.J., Yiu, K.F., Shen, P.P., Lam, P.K.S., 2020. Long-term variation in phytoplankton assemblages during urbanization: a comparative case study of Deep Bay and Mirs Bay, Hong Kong, China. *Sci. Total Environ.* 745, 140993 <https://doi.org/10.1016/j.scitotenv.2020.140993>.
- Wang, Y., Liu, Y.J., Guo, H., Zhang, H.B., Li, D.M., Yao, Z.W., Wang, X.C., Jia, C., 2022. Long-term nutrient variation trends and their potential impact on phytoplankton in the southern Yellow Sea. *China. Acta Oceanologica Sinica* 41 (6), 54–67. <https://doi.org/10.1007/s13131-022-2031-3>.
- Wasmund, N., Göbel, J., Bodungen, B.V., 2008. 100-years-changes in the phytoplankton community of Kiel bight (Baltic Sea). *J. Mar. Syst.* 73 (3), 300–322. <https://doi.org/10.1016/j.jmarsys.2006.09.009>.
- Wasmund, N., Tuimala, J., Suikkanen, S., Vandepitte, L., Kraberg, A., 2011. Long-term trends in phytoplankton composition in the western and central Baltic Sea. *J. Mar. Syst.* 87, 145–159. <https://doi.org/10.1016/j.jmarsys.2011.03.010>.
- Wei, Q.S., Yao, Q.Z., Wang, B.D., Wang, H.W., Yu, Z.G., 2015. Long-term variation of nutrients in the southern Yellow Sea. *Cont. Shelf Res.* 111, 184–196. <https://doi.org/10.1016/j.csr.2015.08.003>.
- Wei, H., Zhao, L., Zhang, H.Y., Lu, Y.Y., Yang, W., Song, G.S., 2021. Summer hypoxia in Bohai Sea caused by changes in phytoplankton community. *Anthr. Coasts* 4, 77–86. doi:<https://doi.org/10.1139/anc-2020-0017>.
- Wells, M.L., Karlson, B., Wulff, A., Kudela, R., Trick, C., Asnaghi, V., Berdalet, E., Cochlan, W., Davidson, K., De Rijcke, M., Dutkiewicz, S., Hallegraeff, G., Flynn, K., Legrand, C., Paerl, H., Silke, J., Suikkanen, S., Thompson, P., Trainer, V., 2020. Future HAB science: directions and challenges in a changing climate. *Harmful Algae* 91, 101632. <https://doi.org/10.1016/j.hal.2019.101632>.
- Widdicombe, C.E., Eloi, D., Harbour, D., Harris, R.P., Somerfield, P.J., 2010. Long-term phytoplankton community dynamics in the Western English Channel. *J. Plankton Res.* 32 (5), 643–655. <https://doi.org/10.1093/plankt/fbp127>.
- Xiao, W.P., Liu, X., Irwin, A.J., Edward, A.L., Wang, L., Chen, B.Z., Zeng, Y., Huang, B.Q., 2018. Warming and eutrophication combine to restructure diatoms and dinoflagellates. *Water Res.* 128, 206–216. <https://doi.org/10.1016/j.watres.2017.10.051>.
- Xu, Y.N., Xu, T.B., 2022. An evolving marine environment and its driving forces of algal blooms in the Southern Yellow Sea of China. *Mar. Environ. Res.* 178, 105635 <https://doi.org/10.1016/j.marenvres.2022.105635>.
- Yang, Y., Sun, X.X., Zheng, S., Zhao, Y.F., 2016. Distribution and long-term variation of net phytoplankton in south Yellow Sea in early summer. *Oceanologia et Limnologia Sinica* 47 (4), 755–763 (in Chinese with English abstract).
- Yang, X., Tan, Y.H., Li, K.Z., Zhang, H.C., Liu, J.X., Xiang, C.H., 2020. Long-term changes in summer phytoplankton communities and their influencing factors in Daya Bay, China (1991–2017). *Mar. Pollut. Bull.* 161, 111694 <https://doi.org/10.1016/j.marenvres.2022.105635>.
- Yu, J.L., Li, R.X., 1993. The study on the phytoplankton ecology in the Bohai and Yellow Seas. *Advances in Marine Science* 3, 52–59 (in Chinese with English abstract).
- Yue, S., Pilon, P., Cavadias, G., 2002. Power of the Mann-Kendall and Spearman's rho tests for detecting monotonic trends in hydrological series. *J. Hydrol.* 259, 254–271. [https://doi.org/10.1016/S0022-1694\(01\)00594-7](https://doi.org/10.1016/S0022-1694(01)00594-7).
- Zhang S, Leng X Y, Feng Y Y, Ding, C.L., Yang, Y., Wang, J., Wang, H.J., Sun, J., 2016. Ecological provinces of spring phytoplankton in the Yellow Sea: species composition. *Acta Oceanol. Sin.* 35(8), 114–125. doi:<https://doi.org/10.1007/s13131-016-0872-3>.
- Zhou, Y.P., Zhang, Y.M., Li, F.F., Tan, L.J., Wang, J.T., 2017. Nutrients structure changes impact the competition and succession between diatom and dinoflagellate in the East China Sea. *Sci. Total Environ.* 574, 499–508. <https://doi.org/10.1016/j.scitotenv.2016.09.092>.