Frontiers in Marine Science

TYPE Original Research
PUBLISHED 16 October 2024
DOI 10.3389/fmars.2024.1498869

Insights into the plankton community seasonal variations in a finer scale of the Bohai Sea: biodiversity, trophic linkage, and biotic-abiotic interplay

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Plankton play an indispensable role in the biogeochemical processes of marine ecosystem. However, unraveling the intricate interactions among biodiversity, trophic linkages, and biotic-abiotic interplay between phytoplankton-zooplankton remains a significant challenge. Here, we conducted field studies in the neritic area of the Bohai Sea during autumn 2023 and spring 2024 to explore seasonal variations of both phytoplankton and zooplankton through microscope. Our analysis revealed a sharp decline in trophic interactions across phytoplankton and zooplankton, with an abundance ratio in autumn 2023 being 5.5 times higher than in spring 2024. Additionally, dominant plankton species ($Y \geq 0.02$) exhibited obvious differences between the two seasons, with higher species diversity observed in autumn. Moreover, each dominant zooplankton species had distinct preferred food items in both seasons, with Rhizosolenia setigera being favored by Noctiluca scintillans and Acartia pacifica. Furthermore, a multivariate biota-environment analysis indicated that each dominant plankton species had unique correlation with specific environmental parameters, highlighting how plankton can fully exploit external environmental conditions to survive in seasonal variations. Ultimately, our findings emphasize significant seasonal dynamics and provide a solid foundation for assessing the potential impacts of environmental changes on plankton in coastal marine realm.

KEYWORDS

plankton, biodiversity, trophic linkage, biotic-abiotic interplay, seasonal variations, environmental change

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RECEIVED 19 September 2024
ACCEPTED 30 September 2024
PUBLISHED 16 October 2024

CITATION
Zhao Y, Wang C, Wang X, Wang W, Zhang T, He J, Shi W, Shi Y, Hu Z and Zhou X (2024) Insights into the plankton community seasonal variations in a finer scale of the Bohai Sea: biodiversity, trophic linkage, and biotic-abiotic interplay.
Front. Mar. Sci. 11:1498869.
doi: 10.3389/fmars.2024.1498869

Introduction

Compared to terrestrial ecosystems, oceans exhibit highly complicated environmental conditions over temporal scales, making them particularly vulnerable to both variable currents and intense anthropogenic disturbances, especially in the temperate sea for which experience four distinct seasons (Zhang et al., 2024). These fluctuating environmental conditions can significantly influence the structure of plankton communities and the associated biotic-abiotic interactions (Chapin III et al., 1997; Murphy et al., 2020; Anderson et al., 2021; Benedetti et al., 2021; Heneghan et al., 2023; Chust et al., 2024). For instance, the prolonged summer periods in the Arctic Ocean, driven by the global warming, have already shifted plankton communities toward ecosystems dominated by smaller species (e.g., Daufresne et al., 2009; Verberk et al., 2021; Wang et al., 2024a). Therein, the plankton community, encompassing phytoplankton and zooplankton, is deeply constrained by alien environment, especially for distinct seasonal marine areas.

In the marine realm, plankton form the foundation of the food web, showcasing immense species diversity and unique genetic variations that provide essential ecological functions and services (De Vargas et al., 2015; Cordier et al., 2022; Omstedt, 2024). As highlighted previously, phytoplankton play a crucial role by taking up CO_2 and releasing O_2 through photosynthesis, supporting heterotrophic organisms, while zooplankton serve as the basis for higher trophic levels, such as fish, through predator-prey relationships (Blanchard et al., 2017; Eddy et al., 2021; Baricevic et al., 2024). Plankton are irreplaceable in nutrient cycling and energy flow processes within marine ecosystems (Yi et al., 2024). Albeit a myriad of prevailing studies emphasizing ecological importance of plankton biodiversity and biogeography in disentangling marine biogeochemical cycles, substantial researches tends to focus separately on the ecological roles of phytoplankton and zooplankton (e.g., Oziel et al., 2020; Wang et al., 2020; Darnis et al., 2022; Segaran et al., 2023; Tagliabue et al., 2023). To date, there is a lack of comprehensive representations of trophic linkages between phytoplankton and zooplankton based on data-driven statistical analyses from field surveys.

Regarding biotic-abiotic interplay, a prevailing viewpoint suggested that physiological constraints dictate the range of suitable environmental conditions for each plankton species (Chust et al., 2024). Over recent decades, escalating global climate change has imposed significant impacts on marine ecosystems, challenging holopelagic species to develop relevant adaptive strategies (Stabeno et al., 2012; Yasumiishi et al., 2020; Carvalho et al., 2021; Atkinson et al., 2024). For example, warming and acidification can directly affect metabolic processes, leading to changes in plankton physiology and behavior, such as growth, body size, reproduction, and survival (McFeeters and Frost, 2011; Weydmann et al., 2012; Cripps et al., 2015; Garzke et al., 2015; Murphy et al., 2020; Wang et al., 2023a, 2023b). In this sense, albeit continuous attempts to explore the environment-plankton interaction for uncovering the ecological importance of various outer parameters (temperature, salinity, pH, dissolved oxygen, nutrient, etc.) on the plankton physiological condition (Serreze et al., 2009; Screen and Simmonds, 2010; Mandal et al., 2024; Noh et al., 2024), our understanding of their environmental affinities in seasonal temperate coastal seas remains insufficient.

Hence, focusing on the diversity of eukaryotic plankton species, trophic linkages, and biotic-abiotic interactions in a finer scale of the neritic seas across different seasons could enhance our understanding of plankton responses to complex seasonal environmental changes. The Bohai Sea, also known as Bohai Gulf, is the innermost gulf of the Yellow Sea along the coast of Northeast and North China, characterized by distinct seasonal variations, making it an ideal location for studying plankton responses to seasonal environmental shifts. Here, we hypothesize that plankton, including both phytoplankton and zooplankton, will exhibit significant seasonal community structure variations driven by differing environmental factors. Through synthesizing observational seasonal plankton data and employing available methodologies, the objective of this study is to: 1) disclose variations in biodiversity; 2) uncover trophic linkages between phytoplankton and zooplankton; and 3) assess biotic-abiotic interplay. Ultimately, our findings will provide a crucial baseline for evaluating the dynamics and functional roles of both phytoplankton and zooplankton in future biogeochemical cycles in coastal seas.

Materials and methods

Field sampling and analysis

Plankton samples, including both phytoplankton and zooplankton, were collected in an inner bay of the Bohai Sea (Figure 1) aboard the fishing boat "Jintangyu02066" on November 14, 2023 (autumn), and April 17, 2024 (spring), respectively. The offshore distances of all stations range from 2.34 Km (station 7) to 15.39 Km (station 4). The seafloor of all stations located at neritic area of the Bohai Sea were shallower than 5.0 m. Phytoplankton samples were gathered using a standard net III (diameter 37.0 cm, mesh size 76 μm), trawled from a depth of 0.5 m off the bottom to the surface at each site, and preserved in acid Lugol's solution (1.5% final concentration). Zooplankton samples were collected using a standard net II (diameter 31.6 cm, mesh size 160 μm), also trawled from bottom to surface. After each tow, zooplankton specimens were fixed in a formaldehyde solution (2% final concentration) for subsequent analyses. Collectively, a total of 48 samples were collected and preserved in darkness at 4°C. In the laboratory, both phytoplankton and zooplankton samples were identified to the lowest taxonomic level using a binocular dissecting microscope (Olympus SZX16), referencing Guo (2004); Sun et al. (2015); Wang and Song (2017), and Zhang et al. (2019).

Seawater temperature (°C) and salinity were measured using a WTW Cond 3210 SET 1 portable water quality analyzer (Xylem, Munich, Germany). Chlorophyll *a* (Chl *a*) concentration was determined by filtering 1 L of seawater through a Whatman GF/F glass fiber filter and stored at -20°C. Plankton retained on the filter was extracted in 90% (vv^{-1}) acetone, and fluorescence was measured following the JGOFS protocol (Knap et al., 1996) using a Turner

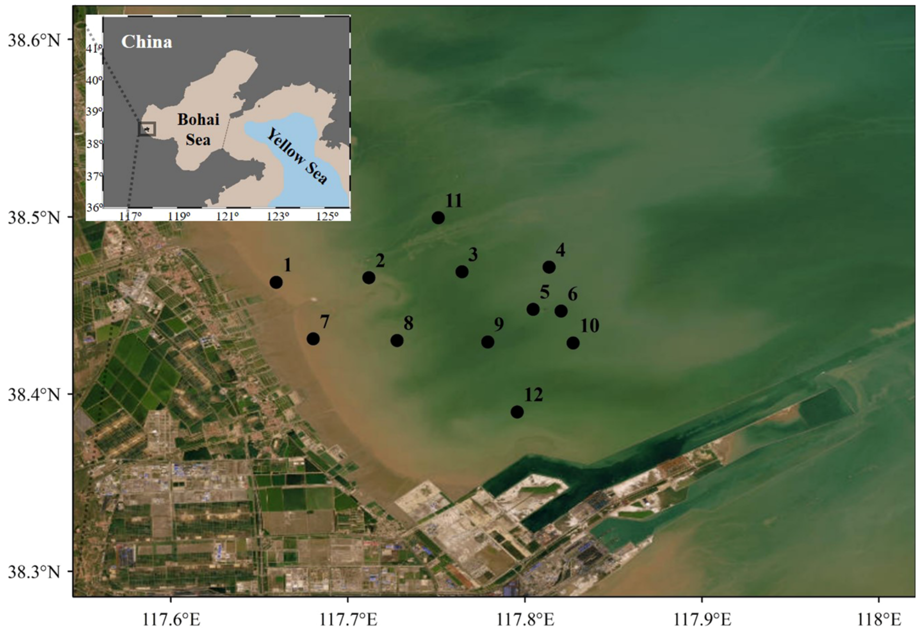

FIGURE 1
Survey stations in the neritic area of the Bohai Sea at both autumn 2023 and spring 2024.

Trilogy fluorometer Model 10 (Turner Designs, US). A PHSJ-3F pH analyzer was used for the pH measurement. For dissolved oxygen (DO), samples were collected in an iodine flask, treated with alkaline potassium iodide and manganese sulfate, and titrated with a standard sodium thiosulfate solution. Additionally, 100 mL water samples for nutrient analysis (ammonium-NH^{4+}, nitrate-NO$_3^-$, nitrite-NO$_2^-$ and phosphate-PO$_4^{3-}$) were filtered through a Whatman GF/F glass fiber membrane (0.7 μm), fixed with chloroform, and stored at -20°C. Nutrient concentrations were analyzed using a SEAL QuAAtro nutrient analyzer (Germany) (Ma et al., 2019, 2023). Zinc ions (Zn^{2+}) were measured by inductively coupled plasma mass spectrometry, with concentrations determined using an atomic absorption spectrophotometer (SpectrAA FS220, Australia).

Data processing

The dominance index (Y) of species in plankton (including phytoplankton or zooplankton) was calculated using the following formula (Xu and Chen, 1989):

$$Y = (n_i/N) \times f_i$$

where n_i is the number of individuals of species i in all samples, f_i is the occurrence frequency of species i in all samples and N is the total number of all taxa. Species with $Y \geq 0.02$ represented as the dominant species in plankton assemblage. Furthermore, all stations located at neritic area of the Bohai Sea with seafloor shallower than 5.0 m, thus we treat all environmental variables obtained from surface layer (1 m) can represent whole water column in our results for environment-plankton analysis. Moreover, the average value of each parameter was represented as mean ± SD in the following text.

Distributional data, including sampling maps, phytoplankton, zooplankton, and environmental variables, were visualized using ODV (Ocean Data View, Version 4.7), Surfer (Version 13.0), Grapher (Version 12.0), and OriginPro 2021 (Version 9.6). In addition, the Biota-Environment analysis was conducted based on Spearman's correlation between log-transformed abiotic parameters and square root-transformed abundance data (t-test), utilizing both PRIMER (Version 5.0) and OriginPro 2021 (Version 9.6). Furthermore, the slope of the phytoplankton-zooplankton (Δ_K) was carried out to quantize their ecological interaction.

Results

Seasonal environmental features, plankton abundance and trophic interaction

Most environmental parameters, except for NO$_2^-$ and PO$_4^{3-}$, exhibited distinct seasonal variations in the neritic area of the Bohai Sea (Figure 2). In spring 2024, average values for temperature (16.6 ± 1.0°C), pH (8.1 ± 0.1) and NO$_3^-$ (0.2 ± 0.1 mg/L) were higher by 7.3°C, 0.2, and 0.1 mg/L, respectively, compared to autumn 2023. Additionally, Chl *a* concentrations were significantly higher at stations 1–5 in spring 2024 than in autumn 2023, while they were nearly equal at other stations (Figure 2). Furthermore, salinity (average 28.4 ± 0.2), DO (average 10.2 ± 0.2 mg/L), NH^{4+} (average 0.1 ± 0.0 mg/L), and Zn^{2+} (average 17.8 ± 7.3 μg/L) were lower in most stations during spring 2024 compared to autumn 2023, where values were 27.9 ± 0.2, 8.0 ± 0.2 mg/L, 0.0 ± 0.0 mg/L, and 9.6 ± 4.5 μg/L, respectively (Figure 2).

Total phytoplankton abundance at each station ranged from 6.6 to 40.2 × 10^6 cells/m^3 (average 18.4 ± 9.8 × 10^6 cells/m^3) in autumn 2023,

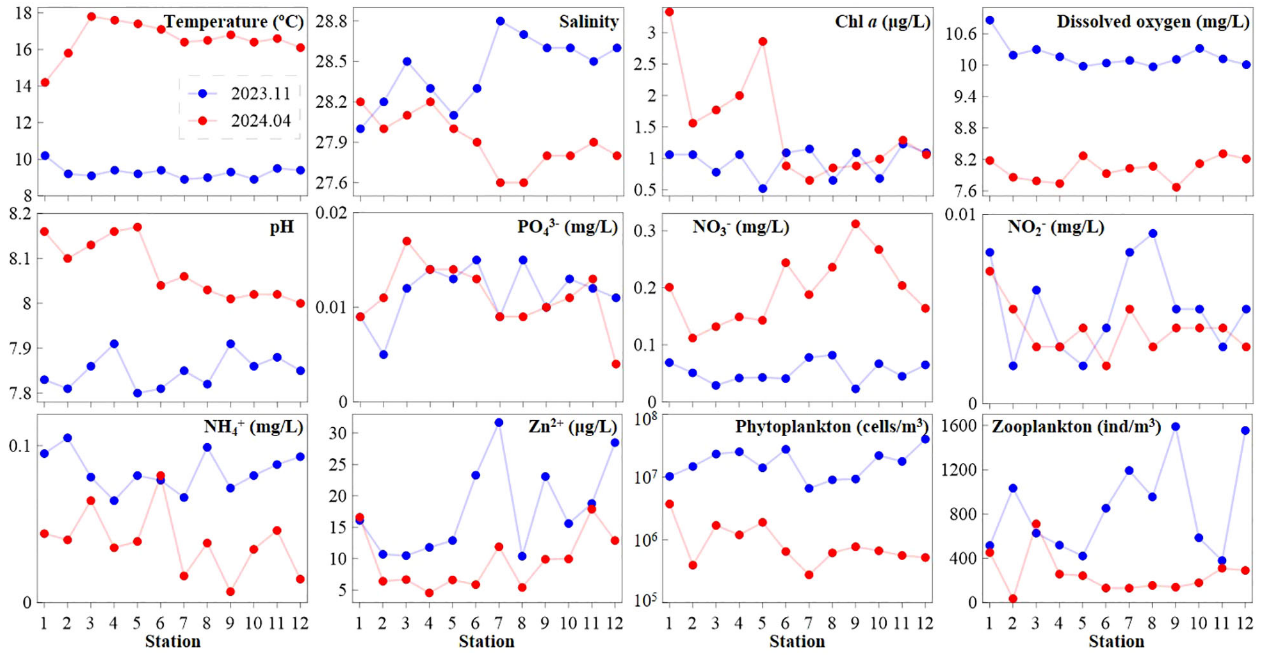

FIGURE 2
Seasonal variations in environmental variables and plankton (including phytoplankton and zooplankton) total abundance.

compared to 0.3–3.0 × 10^6 cells/m^3 (average 1.0 ± 0.8 × 10^6 cells/m^3) in spring 2024, indicating an average value 18.4 times higher in autumn. Similarly, zooplankton showed higher abundance in autumn 2023, with average value (852.1 ± 421.1 ind/m^3) being 3.4 folds higher than that in spring 2024 (253.4 ± 180.5 ind/m^3) (Figure 2). The trend of increased plankton abundance in autumn 2023 coincided with variations in salinity, dissolved oxygen, NH_4^+, and Zn^{2+} (Figure 2). In terms of trophic interactions, average abundance ratio of phytoplankton: zooplankton was 2.2× 10^4: 1 and 0.4× 10^4: 1 in autumn 2023 and spring 2024, respectively (Figure 3). Additionally, the phytoplankton-zooplankton slope in autumn 2023 (Δ_K = -9.96) was steeper than in spring 2024 (Δ_K = -8.27) (Figure 3).

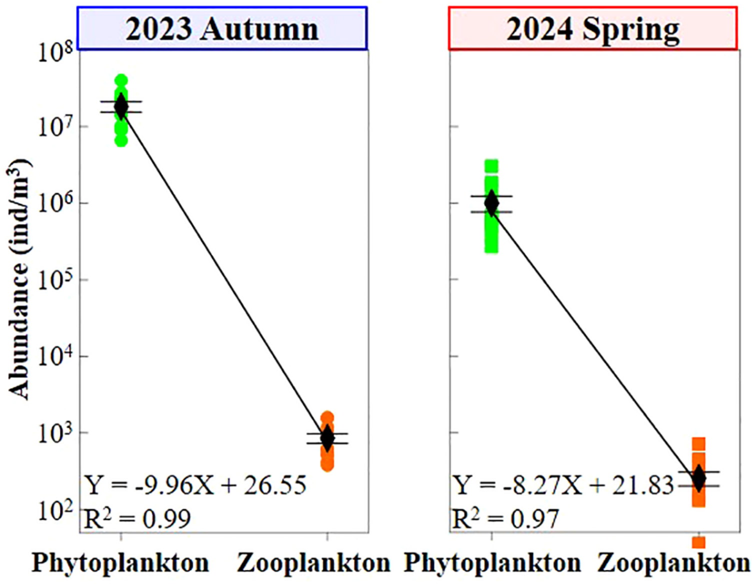

FIGURE 3
Variations in both abundance ratio and trophic linkage between phytoplankton and zooplankton at different seasons.

Notable seasonal variations for dominant plankton composition

Overall, a total of 64 phytoplankton species (32 genera) from 3 phyla, and 26 zooplankton species (20 genera) from 7 phyla were recorded in the neritic area of the Bohai Sea during autumn 2023 and spring 2024 (Tables 1, 2). Among them, phytoplankton species richness was higher in autumn 2023 (57 species) compared to spring 2024 (33 species) (Table 1), while zooplankton showed little variation between the two seasons (Table 2). Besides, in autumn 2023, there were 49 species in the phylum Bacillariophyta (86.0%), 1 species in Chrysophyta (1.8%), and 7 species in Pyrrophyta (12.2%), whereas spring 2024 featured only Bacillariophyta species (Table 2). Based on the dominance index ($Y \geq 0.02$), phytoplankton species and 7 zooplankton species were identified in both seasons (Figure 4; Tables 1, 2), with 9 phytoplankton species noted in autumn 2023 and 4 phytoplankton species in spring 2024 (Table 1). For zooplankton, 6 species were dominant species in autumn 2023 and 5 in spring 2024, respectively (Table 2).

Dominant species of both phytoplankton and zooplankton exhibited clear seasonal variation (Figure 4; Tables 1, 2). Among the targeted co-occurring phytoplankton, only *Chaetoceros curvisetus* and *Pseudo-nitzschia pungens* were dominant in both seasons. In autumn 2023, dominant species included *Eucampia zodiacus* ($Y = 0.18$), *C. lorenzianus* ($Y = 0.07$), *Coscinodiscus subtilis* ($Y = 0.04$) and *C. asteromphalus* ($Y = 0.02$), while *Rhizosolenia setigera* ($Y = 0.40$) and *Skeletonema costatum* ($Y = 0.17$) were dominant species at spring 2024 (Figure 4; Table 1). For zooplankton, four species (*Acartia pacifica*, *Calanus sinicus*, *Aidanosagitta crassa*, and *Noctiluca scintillans*) were identified in both seasons (Table 2). Copepodite ($Y = 0.04$) and Nauplius ($Y = 0.03$) were the dominant species in autumn 2023, whereas Polychaete larva ($Y = 0.04$) was the dominant taxon in spring 2024 (Figure 4; Table 1).

Additionally, the abundance proportions (AP) of all dominant phytoplankton were ≥ 87.8% (average 91.6 ± 1.9%) in autumn 2023 and ≥ 56.2% (average 83.6 ± 10.5%) in spring 2024, respectively. Similarly, dominant zooplankton species exhibited AP values of ≥ 87.9% (average 94.0 ± 3.6%) and ≥ 42.8% (average 88.3 ± 14.7%) during these seasons (Figure 4). In autumn 2023, the top three dominant phytoplankton species were *C. castracanei* (AP = 34.3%), *E. zodiacus* (AP = 17.8%) and *Ceratium macroceros* (AP = 9.1%). In contrast, those species shift to *R. setigena* (AP = 40.3%), *C. curvisetus* (AP = 22.7%) and *S. costatum* (AP = 16.7%) in spring 2024 (Figure 4A). Similarly, the dominant zooplankton species in

TABLE 1 List of phytoplankton composition, maximum abundance (A_{max}), occurrence frequency (OF) and its dominance index (Y) in study area at both autumn 2023 and spring 2024.

Phylum	Genus	Species	2023 Autumn			2024 Spring		
			A_{max} (ind/m^3)	OF (%)	Y	A_{max} (ind/m^3)	OF (%)	Y
Bacillariophyta	*Actinocyclus*	*Actinocyclus octonarius*	166563	91.7	<0.01	2700	8.3	<0.01
	Bacteriastrum	*Bacteriastrum* sp.	10588	8.3	<0.01			
	Cerataulina	*Cerataulina pelagica*	12031	8.3	<0.01			
	Chaetoceros	*Chaetoceros affinis*				38800	41.7	<0.01
		C. borealis	10588	8.3	<0.01			
		C. castracanei	**15329722**	**100**	**0.34**			
		C. compressus	**2843611**	**100**	**0.05**			
		C. curvisetus	**2497222**	**100**	**0.04**	**1124500**	**91.7**	**0.21**
		C. densus	204531	41.7	<0.01	114700	41.7	<0.01
		C. diadema	232926	58.3	<0.01	78000	8.3	<0.01
		C. lorenzianus	**2360278**	**100**	**0.07**	8100	8.3	<0.01
		C. tortissimus				12100	16.7	<0.01
	Coscinodiscus	*Coscinodiscus apiculatus*				9300	8.3	<0.01
		C. argus	64063	25	<0.01	2800	8.3	<0.01
		C. asteromphalus	**1208333**	**100**	**0.02**	28700	50	<0.01
		C. debilis				28700	8.3	<0.01
		C. deformatus	19219	25	<0.01			
		C. gigas	64063	50	<0.01	16100	16.7	<0.01
		C. granii	89688	91.7	<0.01	15700	41.7	<0.01
		C. jonesianus	5100	8.3	<0.01			

(Continued)

TABLE 1 Continued

Phylum	Genus	Species	2023 Autumn			2024 Spring		
			A_{max} (ind/m^3)	OF (%)	*Y*	A_{max} (ind/m^3)	OF (%)	*Y*
		C. oculus-iridis	64063	75	<0.01	4000	25	<0.01
		C. radiatus	8375	8.3	<0.01	57300	41.7	<0.01
		C. subtilis	**2875833**	**100**	**0.04**	4000	8.3	<0.01
		C. wailesii	15882	16.7	<0.01	86000	50	<0.01
		Coscinodiscus sp1				8500	16.7	<0.01
	Cyclotella	*Cyclotella* sp.	217500	75	<0.01			
	Ditylum	*Ditylum brightwellii*	48333	83.3	<0.01	13000	58.3	<0.01
	Eucampia	***Eucampia zodiacus***	**7405234**	**100**	**0.18**	37300	41.7	<0.01
	Guinardia	*Guinardia flaccida*	659844	91.7	0.01			
		G. striata	402778	91.7	<0.01	18700	41.7	<0.01
	Lauderia	*Lauderia annulata*	66300	91.7	<0.01			
	Leptocylindrus	*Leptocylindrus danicus*	469000	100	<0.02	19500	33.3	<0.01
	Meuniera	*Meuniera membranacea*	185278	33.3	<0.01			
	Nitzschia	*Nitzschia acicularis*				13000	8.3	<0.01
		N. closterium				6200	33.3	<0.01
		N. longissima	10455	16.7	<0.01	8100	25	<0.01
		N. lorenziana	7000	8.3	<0.01	15500	16.7	<0.01
	Odontella	*Odontella sinensis*	24394	8.3	<0.01			
	Paralia	*Paralia sulcata*	139425	16.7	<0.01	430000	16.7	<0.01
	Pieurosigma	*Pieurosigma pelagicum*	24167	16.7	<0.01			
	Pinnularia	*Pinnularia* sp.	4956	8.3	<0.01			
	Planktoniella	*Planktoniella blanda*				5400	8.3	<0.01
	Pleurosigma	*Pleurosigma acutum*	7000	16.7	<0.01			
		Pleurosigma sp.	4225	8.3	<0.01			
	Proboscia	*Proboscia alata*	36094	25	<0.01			
	Pseudo-nitzschia	***Pseudo-nitzschia pungens***	**2601944**	**100**	**0.07**	**86000**	**91.7**	**0.03**
	Rhizosolenia	*Rhizosolenia alata*	161111	100	<0.01			
		R. setigera	241667	100	<0.01	**1347300**	**100**	**0.40**
		R. styliformis	14000	16.7	<0.01			
	Schroederella	*Schroederella delicatula*	739922	100	0.01	143300	58.3	0.01
	Skeletonema	***Skeletonema costatum***	372879	58.3	<0.01	**630700**	**100**	**0.17**
	Stephanopyxis	*Stephanopyxis palmeriana*	14000	8.3	<0.01			
	Synedra	*Synedra* sp.	5294	8.3	<0.01			
	Thalassionema	*Thalassionema frauenfeldii*	94091	33.3	<0.01			
		T. longissima	15882	16.7	<0.01	86000	8.3	<0.01
	Thalassiosira	*Thalassiosira eccentrica*	38438	50	<0.01			

(Continued)

TABLE 1 Continued

Phylum	Genus	Species	2023 Autumn			2024 Spring		
			A_{max} (ind/m^3)	OF (%)	*Y*	A_{max} (ind/m^3)	OF (%)	*Y*
		T. rotula	288750	75	<0.01			
Chrysophyta	*Dictyocha*	*Dictyocha fibula*	161111	91.7	<0.01			
Pyrrophyta	*Ceratium*	*Ceratium furca*	89688	75	<0.01			
		C. fusus	56389	66.7	<0.01			
		C. macroceros	**3705000**	**100**	**0.09**			
		C. tripos	83636	83.3	<0.01			
	Glenodinium	*Glenodinium* sp.	69697	16.7	<0.01			
	Prorocentrum	*Prorocentrum micans*	4225	8.3	<0.01			

phytoplankton in bold black were dominant species with Y ≥ 0.02.

TABLE 2 List of zooplankton species composition, maximum abundance (A_{max}), occurrence frequency (OF) and its dominance index (*Y*) in study area at both autumn 2023 and spring 2024.

Phylum	Genus	Species	2023 Autumn			2024 Spring		
			A_{max} (ind/m^3)	OF (%)	*Y*	A_{max} (ind/m^3)	OF (%)	*Y*
Arthropoda	*Acartia*	*Acartia hongi*	12.7	8.3	<0.01	25	58.3	0.01
		A. pacifica	**266.7**	**66.7**	**0.06**	**185.7**	**100**	**0.19**
	Calanopia	*Calanopia thompsoni*				7.1	16.7	<0.01
	Calanus	***Calanus sinicus***	**83.6**	**75**	**0.03**	**442.9**	**100**	**0.34**
	Centropages	*Centropages tenuiremis*	12.7	8.3	<0.01	16.7	83.3	<0.02
	Ditrichocorycaeus	*Ditrichocorycaeus affinis*	107.7	41.7	<0.01	3.6	25	<0.01
	Labidocera	*Labidocera euchaeta*	11.1	8.3	<0.01	16.7	58.3	<0.01
		L. rotunda	23.8	33.3	<0.01			
	Oithona	*Oithona similis*	88.9	41.7	<0.01	4.2	33.3	<0.01
	Paracalanus	*Paracalanus parvus*	7.7	8.3	<0.01	7.1	41.7	<0.01
	Pseudodiaptomus	*Pseudodiaptomus arabicus*				1.9	16.7	<0.01
	–	**Nauplius**	**110.3**	**75**	**0.03**	8.3	58.3	<0.01
	–	**Copepodite**	**96.3**	**83.3**	**0.04**	16.7	8.3	<0.01
	Acetes	*Acetes chinensis*				1.7	8.3	<0.01
	Brachyura	*Brachyura zoea* larva				50	75	0.03
	Cirripedia	*Cirripedia nauplius*	6.4	8.3	<0.01			
	Leucon	*Leucon* sp.	36.8	8.3	<0.01			
	Macruran	*Macruran* larva				3.3	33.3	<0.01
	Neomysis	*Neomysis orientalis*	9.52	25	<0.01			
	Pseudevadne	*Pseudevadne tergestina*	14.3	8.3	<0.01			
Annelida	–	**Polychaete larva**	21.2	16.7	<0.01	**33.3**	**100**	**0.04**
Chaetognatha	*Aidanosagitta*	***Aidanosagitta crassa***	**427.7**	**100**	**0.17**	**37**	**91.7**	**0.03**
Chordata	–	Fish egg				3.6	8.3	<0.01

(Continued)

TABLE 2 Continued

Phylum	Genus	Species	2023 Autumn			2024 Spring		
			A_{max} (ind/m^3)	OF (%)	Y	A_{max} (ind/m^3)	OF (%)	Y
Ciliophora	*Favella*	*Favella panamensis*	76.9	16.7	<0.01			
Cnidaria	*Rathkea*	*Rathkea octopunctata*				144.8	33.3	0.01
Protozoa	*Noctiluca*	***Noctiluca scintillans***	**1142.9**	**100**	**0.54**	**203.6**	**83.3**	**0.18**

zooplankton in bold black were dominant species with Y ≥ 0.02; – means uncertain genus classification.

autumn 2023 were *Noctiluca scintillans* (AP = 54.4%) and *A. crassa* (AP = 16.6%), which changed to *C. sinicus* (AP = 34.3%) and *N. scintillans* (AP = 22.2%) in spring 2024 (Figure 4B. Overall, compared to phytoplankton, zooplankton exhibited less variation in dominant species across seasons, indicating a stronger community stability (Figure 4; Tables 1, 2).

Seasonal dynamics in both interspecific and trophic level relationships

Dominant phytoplankton and zooplankton species showed varying correlations in both interspecific and trophic level relationships during autumn 2023 and spring 2024 (Figure 5). In

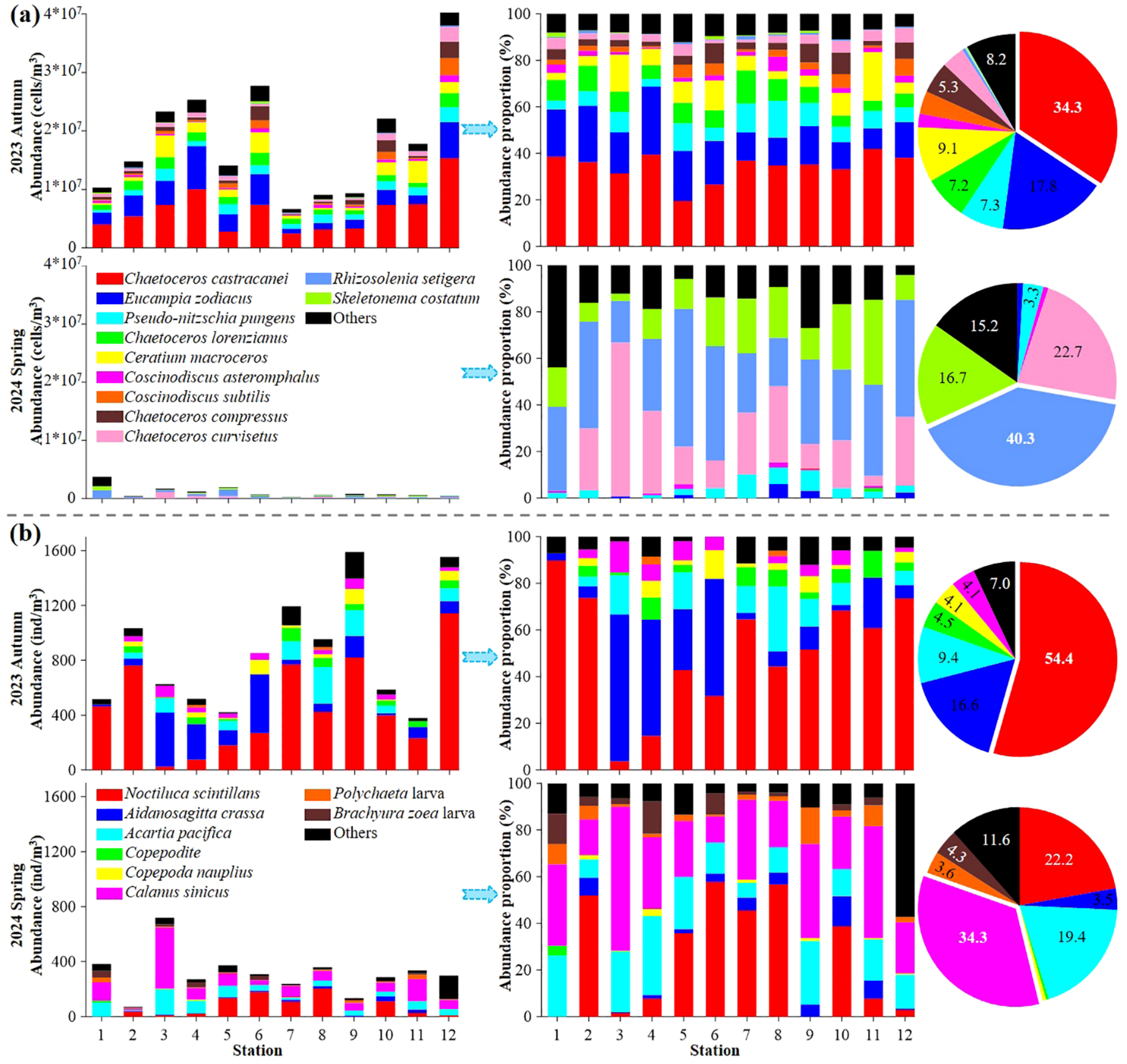

FIGURE 4
Seasonal variations in both abundance and abundance proportion of dominant phytoplankton **(A)** and zooplankton **(B)** species. Each color indicated one dominant phytoplankton or zooplankton species.

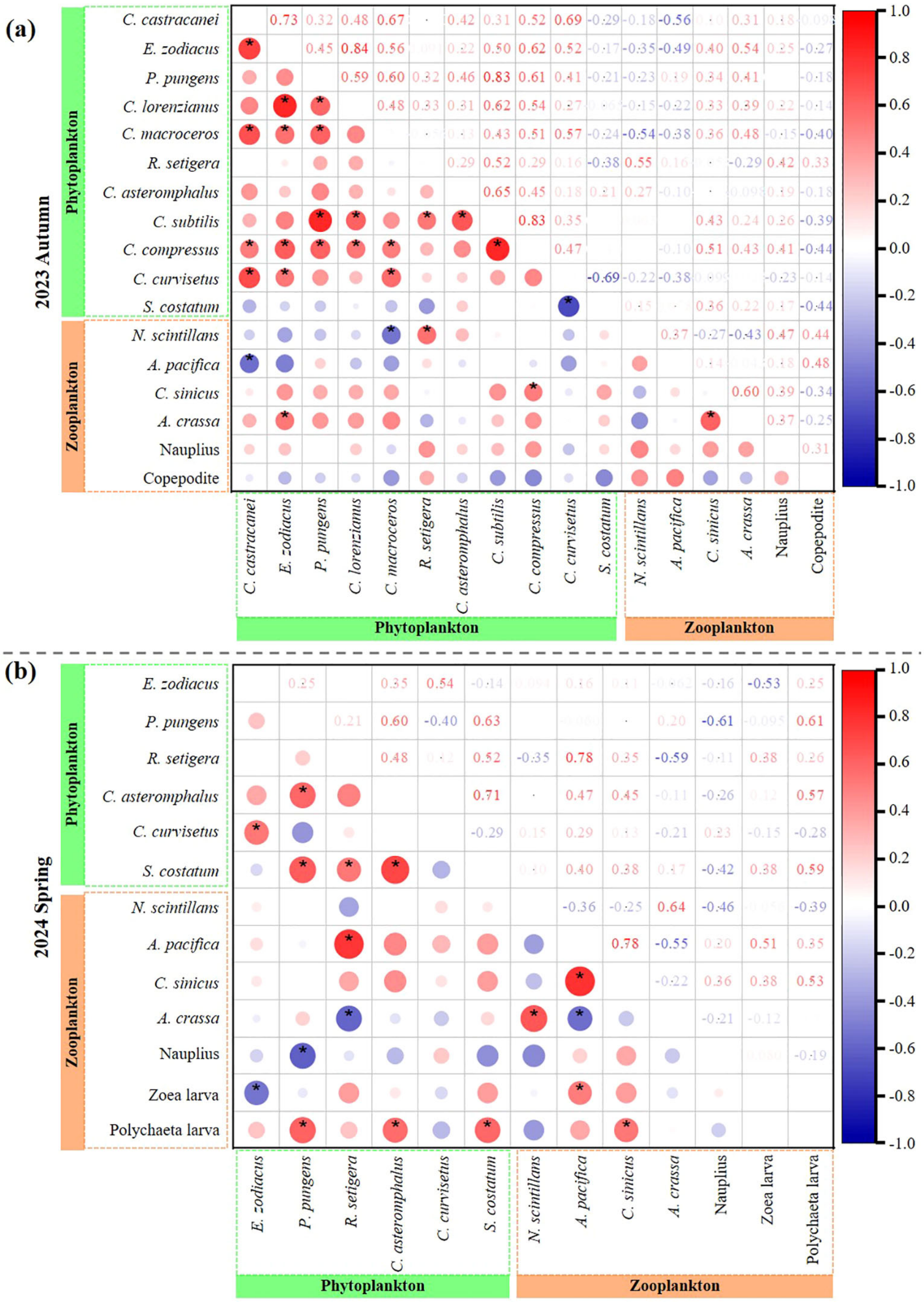

FIGURE 5
Spearman's rank correlation between dominant phytoplankton and zooplankton species in autumn 2023 **(A)** and spring 2024 **(B)**. *: $p < 0.05$, t-test.

terms of interspecific relationships, most dominant phytoplankton species displayed significant positive correlations, indicating mutually beneficial coexistence, except for *S. costatum*-*C. curvisetus*, which exhibited a significant negative correlation, indicating competitive interactions in autumn 2023 (Figure 5A). In spring 2024, significant positive correlations were observed among *C. asteromphalus*-*P. pungens*, *C. curvisetus*-*E. zoodiacus*, *S. costatum*- *P. pungens*/*R. setigena*/*C. asteromphalus*, suggesting mutually beneficial coexistence (Figure 5B). Targeted zooplankton, only *A. crassa*-*C. sinicus* showed a significant positive correlation, indicating mutual coexistence in autumn 2023 (Figure 5A). However, in spring 2024, the interspecific relationships among *C. sinicus*/*Brachyura* zoea larva-*A. pacifica*, *A. crassa*-*N. scintillans*, Polychaeta larva-*C. sinicus* were mutually beneficial, all exhibiting significant positive correlations. Conversely, the relationship between *A. crassa*-*A. pacifica* was competitive, showing a significant negative correlation (Figure 5B).

As for trophic level relationships in phytoplankton (prey)-zooplankton (predator), Spearman's rank correlation indicated significant positive correlations for *R. setigera-N. scintillans*, *C. compressus-C. sinicus*, *E. zodiacus-A. crassa* in autumn 2023, while *C. macroceros-N. scintillans*, *C. castracanei-A. pacifica* exhibited negative correlations (Figure 5A). In spring 2024, significant positive correlations were observed between *R. setigena* and *A. pacifica*, as well as *P. pungens*/*C. asteromphalus*/*S. costatum* with Polychaeta larvae, while *R. setigena-A. crassa*, *P. pungens*-Nauplius, *E. zoodiacus-Brachyura* zoea larva exhibited negative correlations (Figure 5B). Specifically, these patterns suggest that each zooplankton species has unique preferred food items in both autumn 2023 and spring 2024, with *R. setigera* being a favored food source for both *N. scintillans* and *A. pacifica*.

Biotic-abiotic interplay and its seasonal variations

Plankton dominant species displayed varied responses to environmental parameters during autumn 2023 and spring 2024 (Figures 6, 7; Tables 3, 4). Regarding phytoplankton-abiotic interactions, only *E. zoodiacus*, *P. pungens* and *C. asteromphalus* exhibited similar trends with environmental variables, suggesting they may prefer overlapping niches and face strong competition (Figure 6; Tables 3). Additionally, *C. castracanei*, *R. setigena*, *C. compressus* and *S. costatum* thrived in high-temperature and high-pH conditions, contrasting with *E. zoodiacus*, *P. pungens*, *C. lorenzianus*, *C. asteromphalus*, *C. subtilis*, and *C. curvisetus* (Figure 6). Meanwhile, each species exhibited distinct trends in response to nutrient availability, reflecting their varying utilization efficiencies. Notably, all species, except *R. setigena* and *S. costatum*, showed an increasing trend with Zn^{2+} (Figure 6).

Regarding zooplankton-abiotic interplay, our results revealed that *N. scintillans*, Nauplius and Copepodite exhibited similar trends in response to the complex environmental variables of temperature, salinity, Chl *a*, dissolved oxygen (DO), and pH, indicating strong competition among these species (Figure 7). Except above-mentioned three species, *A. crassa*, *A. pacifica* and Polychaete larva also benefited from low temperature and high DO conditions. Notably, only *C. sinicus* and *Brachyura* zoea larva displayed an increasing trend with rising temperature (Figure 7; Tables 4). Furthermore, with the exception of *A. pacifica*, *A. crassa*, and Nauplius, other species displayed unique responses to nutrient variables (Figure 7; Table 4). Specifically, all species, except *C. sinicus*, demonstrated an increasing trend with Zn^{2+} (Figure 7).

To further quantify the physical-biological interplay in the neritic area of the Bohai Sea during autumn 2023 and spring 2024, we conducted principal component analysis (PCA) using abundance of phytoplankton, zooplankton and their dominant species to assess abiotic influences (Figure 8). The PCA revealed that two principal components effectively distinguished the environmental conditions across the two seasons, accounting for a substantial proportion of biotic variation $\geq$ 71.0% in autumn 2023 and $\geq$ 71.1% in spring 2024 (Figure 8). Furthermore, each dominant species (both phytoplankton and zooplankton) exhibited unique correlations with specific environmental parameters throughout the seasonal variations (Figure 8). For instance, *A. crassa* showed a significant positive correlation with PO_4^{3-}. However, at spring 2024, its significant positive correlation shifted to with both temperature and DO (Figure 8). This phenomenon demonstrates that plankton can effectively leverage external environmental factors to survive seasonal changes.

Discussion

This study provides a holistic paradigm and epitome of field-based significant divergences in both phytoplankton and zooplankton communities and its interplay with environmental factors during autumn 2023 and spring 2024 spanning a finer scale located at neritic area of the Bohai Sea. Unlike existing global models for plankton, which often rely on predefined parameters (Spalding et al., 2012; Anderson et al., 2021; Benedetti et al., 2021; Heneghan et al., 2023; Tagliabue et al., 2023; Atkinson et al., 2024), the seasonal dynamics of plankton traits observed through ship-borne field surveys are shaped by a dynamic feedback loop between microbes and their environment, influenced by unique physicochemical conditions, as hypothesized. However, it is important to note that our study area may not fully represent the diverse adaptive strategies of plankton seasonal variations across temperate coastal regions.

Remarkable seasonal divergences in plankton trophic interaction and composition

Marine eukaryotic plankton, including both phytoplankton and zooplankton, represents a vast diversity of organisms that serve as essential food sources for commercial fish through fundamental trophic level transfers (prey-predator interactions) (Cordier et al., 2022; Omstedt, 2024). Consequently, the bioindex reflecting the abundance ratio of phytoplankton to zooplankton is crucial for exploring and understanding plankton trophic interactions. Previous studies reported abundance ratios in pico-, nano-, and microplankton of approximately 10^6: 10^3: 1 in the Mediterranean Sea (Tanaka and Rassoulzadegan, 2002) and the Tropical North/West Pacific Ocean (Sohrin et al., 2010; Wang et al., 2023c), forming a pyramid shape from low to high trophic levels (Trebilco et al., 2013). Our findings regarding the phytoplankton-to-zooplankton ratio align with this pattern. Furthermore, the abundance ratio in autumn 2023 was 5.5 times higher than in spring 2024 (Figure 3), and the steeper phytoplankton-zooplankton slope collectively indicates that the plankton community in the former season experienced lower feeding pressure on zooplankton and stronger environmental resistance than in the latter season (De Vargas et al., 2015; Cordier et al., 2022).

Plankton species diversity plays a vital role in regulating ecosystem processes and resource utilization efficiency, thereby influencing marine ecosystem functioning and biogeochemical cycling (Chapin III et al., 1997). Similarly, a higher diversity of functionally similar species enhances the stability of resistance and

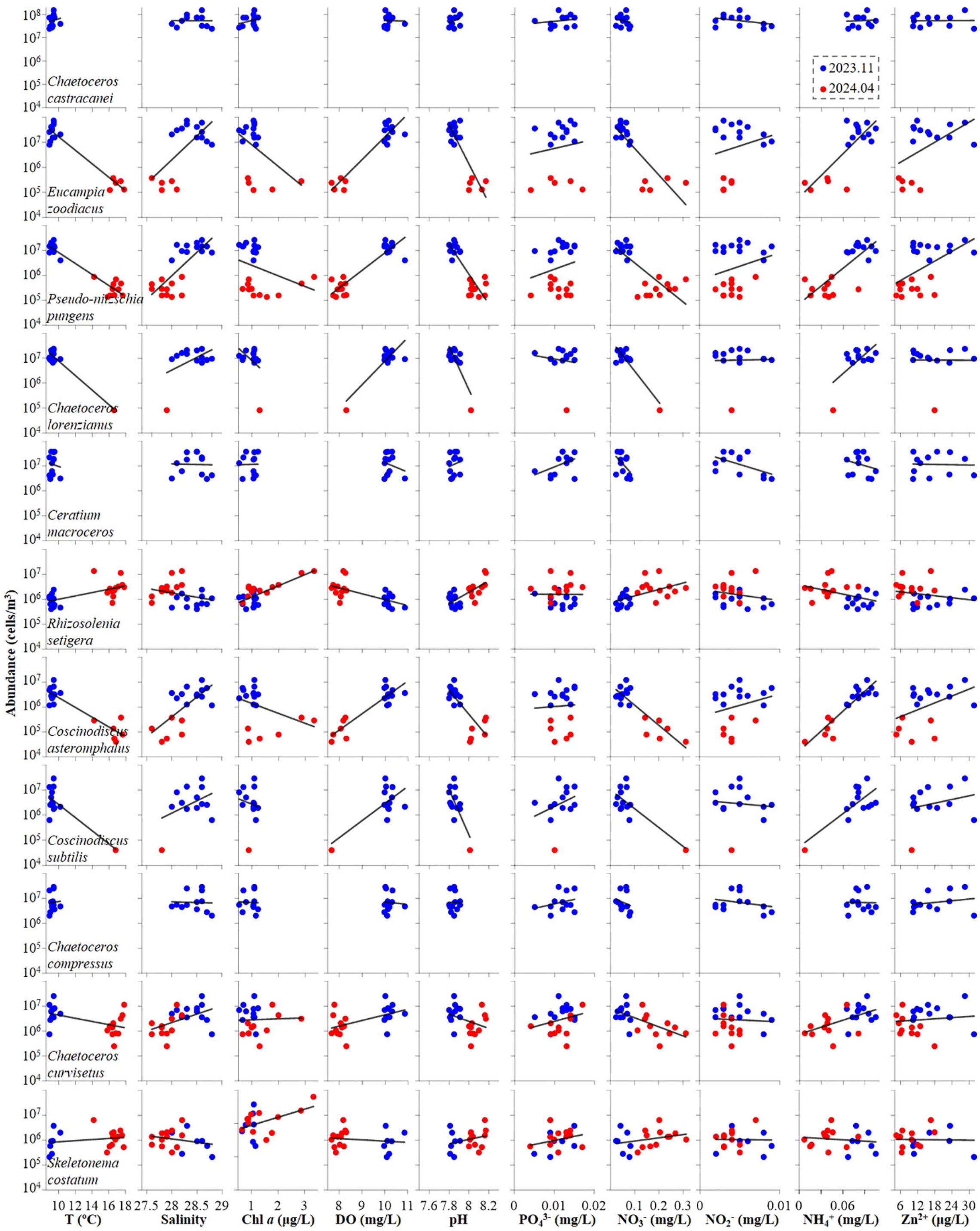

FIGURE 6
Correlation between environmental variables and dominant phytoplankton species at both autumn 2023 and spring 2024.

resilience in marine ecosystem processes (Ibarbalz et al., 2019; Benedetti et al., 2021; Chust et al., 2024). Consistent with observational studies using both optical microscopy (Marić et al., 2012; Godrijan et al., 2013) and metabarcoding (Piredda et al., 2017; Armeli et al., 2019), species diversity of both phytoplankton and zooplankton was higher in autumn 2023 compared to spring 2024 (Table 2), showing clear seasonal variations. Furthermore, considering the significantly higher plankton abundance (Figure 3), it can be logically concluded that the plankton community in autumn 2023 exhibited greater resistance and resilience to harsh environmental conditions than in spring 2024.

As for prey-predator interactions, the fatty acid composition of phytoplankton is recognized as a crucial factor influencing food quality for higher trophic levels (Becker and Boersma, 2003;

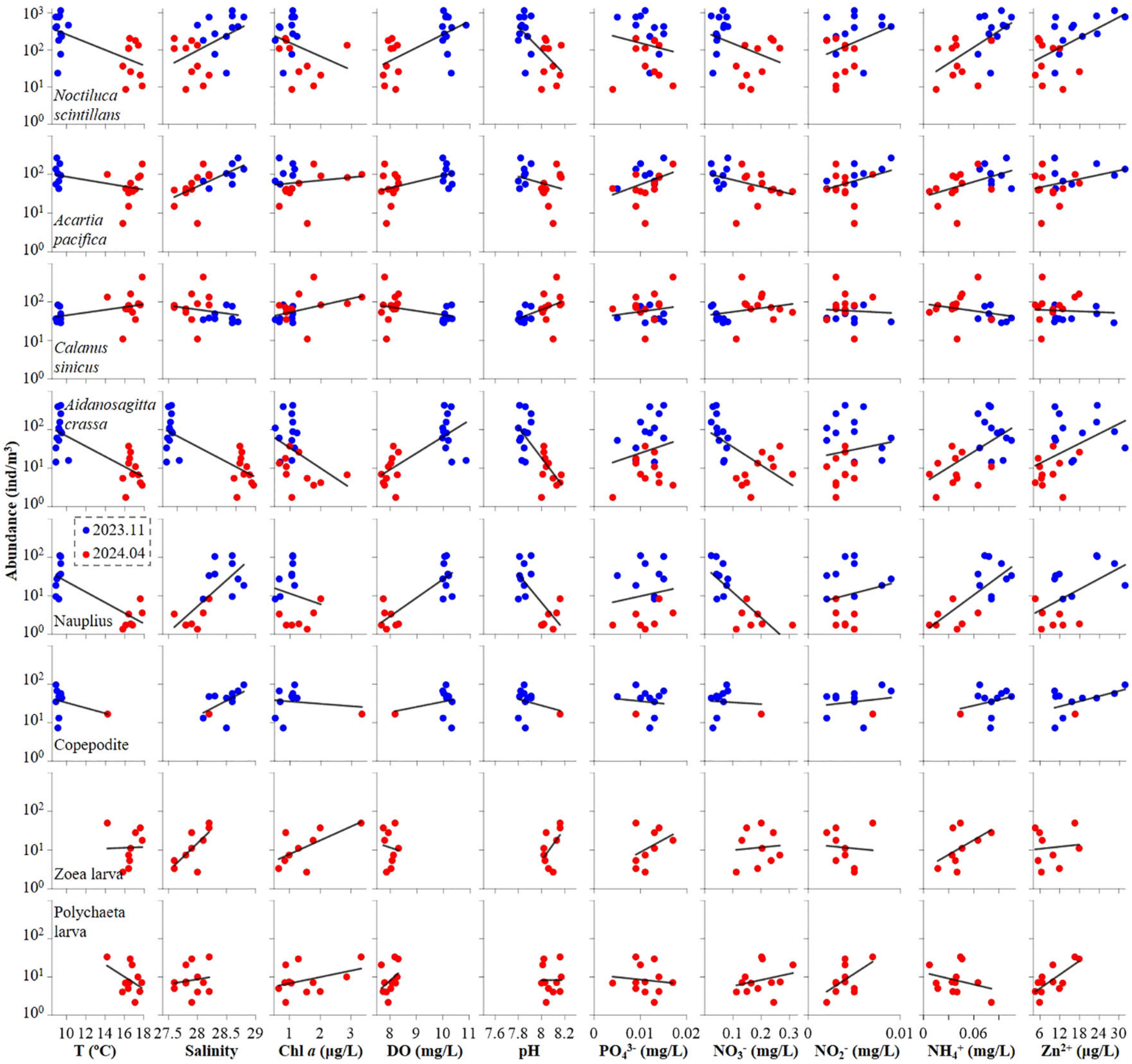

FIGURE 7
Correlation between environmental variables and dominant zooplankton species at both autumn 2023 and spring 2024.

Boersma et al., 2009; Chen et al., 2010; Peng et al., 2024). Among various phytoplankton species, diatoms are particularly noted for their high levels of unsaturated fatty acids, which are essential for the cell differentiation, growth, reproduction, immune function, and other biological processes of zooplankton (Wichard et al., 2008; Yeung et al., 2020; Peng et al., 2024). Thus, it is reasonable to suggest that higher diatom abundance contributes to increased zooplankton populations, as observed in autumn 2023 (Figure 3). Additionally, our findings indicate that all phytoplankton species in spring 2024 belonged to the phylum Bacillariophyta (Table 2), aligning with Murphy et al. (2020), which found that warming significantly enhances the ecological importance of diatoms. Moreover, the minimal variation in both total and dominant zooplankton species between autumn 2023 and spring 2024 (Figure 3; Table 2) may be attributed to their strong selective feeding abilities (Serandour et al., 2023).

Ecological role of environmental parameters played in seasonal plankton variations

Physicochemical factors, e.g., temperature, salinity, Chl *a*, nutrients, pH, dissolved oxygen, heavy metal, are crucial in reshaping complex plankton compositions through bottom-up control (resource limitation) (Power, 1992; Pörtner and Farrell, 2008; Wang et al., 2023c, 2024b; Lennartz et al., 2024). Specifically, temperature enhances species biodiversity by modulating temperature-dependent metabolic processes (Vázquez-Domínguez et al., 2007; Archibald et al., 2022). However, our results indicate that only a few phytoplankton and zooplankton species showed a positive correlation with temperature (Figure 8). We speculate that in specific locations, the surrounding environmental conditions may exceed the temperature thresholds for these species (Holding et al., 2013; Stuart-Smith et al., 2015), potentially

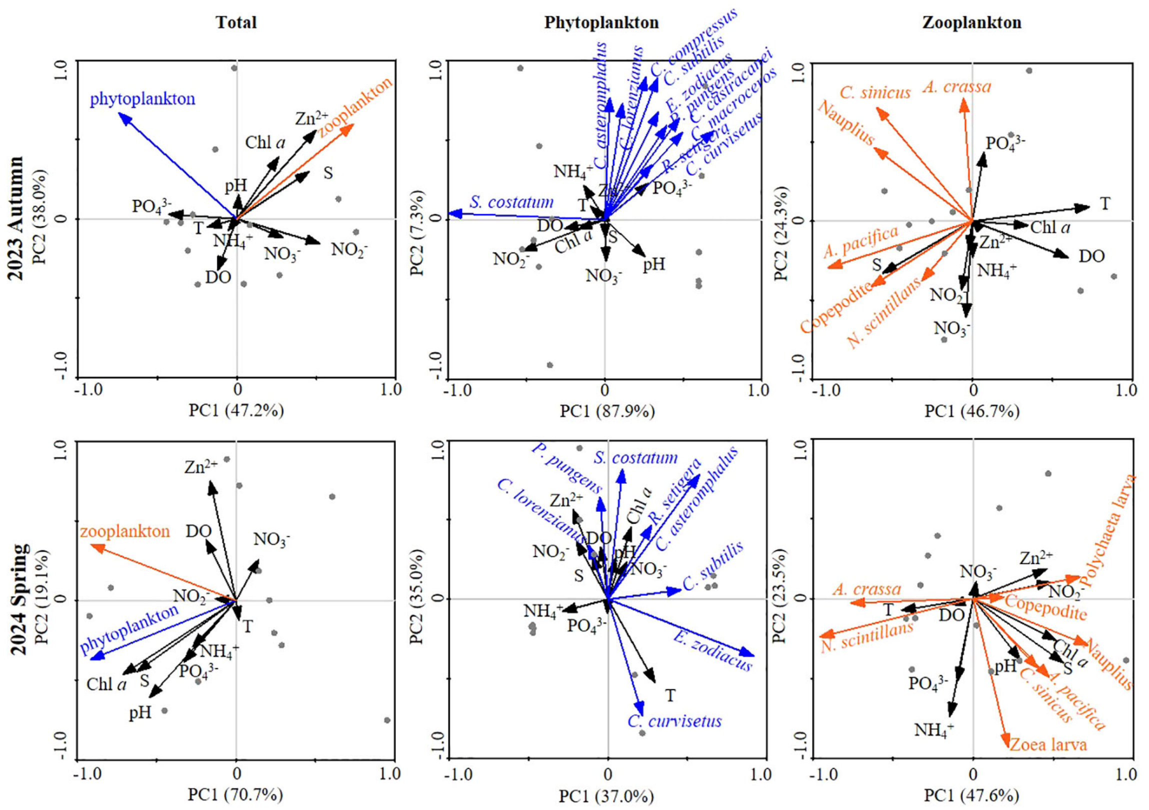

FIGURE 8
Variations in principal component analysis (PCA) between environmental parameters and plankton (including phytoplankton, zooplankton, and dominant species) at both autumn 2023 and spring 2024. The *x*-axis is the first PCA axis, and the *y*-axis is the second PCA axis. Environmental variables and ciliates are indicated by black and green (phytoplankton)/orange (zooplankton) lines, respectively. Grey dots are sampling points.

explaining the observed loss of both biodiversity and abundance in spring 2024. Moreover, previous studies suggest that higher trophic levels are generally more vulnerable to elevated temperatures, as the metabolic demands of consumers are more sensitive to warming, leading to decreased consumer fitness (Lopez-Urrutia et al., 2006; Rall et al., 2010). However, our findings do not align with aforementioned viewpoint, as both species composition and total abundance of zooplankton showed little variation between autumn 2023 and spring 2024 (Figure 3), despite an average temperature increase of 7.3°C from autumn 2023 to spring 2024 (Figure 2).

Nutritional availability is crucial for influencing phytoplankton concentrations, as it is closely linked to increased primary productivity in terms of both quantity (abundance) and quality (lipid unsaturation) (Premakumari et al., 2024). This productivity then transfers to higher trophic levels through essential prey-predator interactions (Šolić et al., 2010; Våge and Thingstad, 2015; Holm et al., 2022). Our results indicate that dominant phytoplankton species exhibited distinctly different trends in response to nutrients in autumn 2023 and spring 2024 (Figure 6). This variability can be explained by two factors: 1) each species has a unique nutrient affinity (Strom and Fredrickson, 2008), and 2) avoid harmful competition (Sommer, 1989; Litchman et al., 2004; Kenitz et al., 2013). Regarding zooplankton, DO is a vital limiting factor for survival and growth, as heterotrophs must oxidize large compounds from their environment to release energy for biological processes (Fenchel, 2014; Qian et al., 2023). Our findings support this perspective (Figure 7).

In recent decades, anthropogenic CO_2 emissions have induced global warming, triggering unprecedented and lasting impacts on marine ecosystems worldwide (Yasumiishi et al., 2020; Carvalho et al., 2021; Wang and Wu, 2022). This poses threats to biodiversity and ecological functions, particularly through poleward dispersal (Ershova et al., 2015; Hastings et al., 2020; Møller and Nielsen, 2020; Wang et al., 2022), changes in phenology and adaptation (Poloczanska et al., 2013; Atkinson et al., 2015), and mean body size miniaturization (Li et al., 2009; Daufresne et al., 2009; Qian et al., 2023). For surface-dwelling species in large marine environments, poleward dispersal is a prominent aspect of plankton's response to global warming (Hastings et al., 2020). Whereas at a specific location, plankton face two options: 1) enhance their temperature tolerance through long-term adaptive evolution (Ward et al., 2019) or 2) extirpation. In this perspective, our study on plankton seasonal variations provides a fundamental benchmark for understanding the adaptive strategies of phytoplankton and zooplankton to rapid warming. Meanwhile, our results indicate that several dominant plankton species exhibited a positive correlation with temperature during the warmer spring of 2024 (Figures 6, 8). Thus, we deduce that these "winner" plankton species, with strong adaptation abilities (Casoli et al., 2020; Boutin et al., 2023), are likely to dominate the neritic area of the Bohai Sea in the future.

TABLE 3 Spearman's rank correlation between dominant plankton (including phytoplankton and zooplankton) species and environmental parameters (T, S, Chl *a*, DO, pH, PO_4^{3-}, NO_3^-, NO_2^-, NH_4^+, Zn^{2+}) in autumn 2023.

Type	species	Environmental variables									
		T (°C)	S	Chl *a* (μg/L)	DO (mg/L)	pH	PO_4^{3-} (mg/L)	NO_3^- (mg/L)	NO_2^- (mg/L)	NH_4^+ (mg/L)	Zn^{2+} (μg/L)
Phytoplankton	*Chaetoceros castracanei*	0.519	-0.131	0.291	0.217	0.380	0.236	-0.287	-0.329	-0.021	0.105
	C. compressus	0.177	-0.106	-0.064	0.021	0.074	0.236	-0.510	-0.198	-0.179	0.252
	C. curvisetus	0.300	-0.201	-0.085	0.266	0.324	0.077	-0.133	-0.400	0.116	-0.014
	C. lorenzianus	0.018	-0.244	-0.106	-0.042	-0.338	0.127	-0.210	-0.280	-0.018	0.007
	Ceratium macroceros	0.145	-0.113	0.163	0.210	0.261	0.282	-0.559	-0.411	-0.235	0.049
	Coscinodiscus asteromphalus	0.198	0.035	-0.064	-0.112	-0.327	0.236	0.252	0.181	0.602*	0.035
	C. subtilis	-0.053	-0.106	-0.284	-0.175	-0.377	0.236	-0.245	-0.212	0.235	0.056
	Eucampia zoodiacus	0.353	-0.470	-0.121	0.119	-0.028	0.254	-0.462	-0.499	-0.109	-0.119
	Pseudo-nitzschia pungens	-0.159	0.074	-0.298	-0.371	-0.254	0.416	-0.259	-0.181	0.161	-0.112
	Rhizosolenia setigera	-0.304	0.187	0.021	-0.343	-0.394	-0.176	0.238	-0.336	0.235	0.336
	Skeletonema costatum	0.136	-0.143	0.074	0.123	-0.215	-0.099	-0.189	0.415	0.022	0.007
Zooplankton	*Acartia pacifica*	-0.673*	0.710**	-0.206	-0.445	0.029	-0.070	0.153	0.521	-0.021	-0.082
	Aidanosagitta crassa	0.269	-0.166	0.078	-0.315	0.116	0.444	-0.825**	-0.301	-0.480	-0.042
	Calanus sinicus	-0.219	-0.105	-0.275	0.138	0.099	0.208	-0.744**	-0.241	-0.281	-0.346
	Copepoda nauplius	0.032	0.249	0.250	-0.416	0.053	0.131	-0.275	-0.146	-0.272	0.310
	Copepodite	-0.362	0.667*	0.206	-0.425	0.187	-0.122	0.456	0.171	-0.007	0.070
	Noctiluca scintillans	-0.028	0.396	0.397	-0.175	-0.063	-0.577*	0.385	0.297	0.256	0.538

**: $p < 0.01$, *: $p < 0.05$, t-test.

TABLE 4 Spearman's rank correlation between dominant plankton (including phytoplankton and zooplankton) species and environmental parameters (T, S, Chl *a*, DO, pH, PO_4^{3-}, NO_3^-, NO_2^-, NH_4^+, Zn^{2+}) in spring 2024.

Type	species	Environmental variables									
		T (°C)	S	Chl *a* (μg/L)	DO (mg/L)	pH	PO_4^{3-} (mg/L)	NO_3^- (mg/L)	NO_2{sp}{/sp}$^-$ (mg/L)	NH_4^+ (mg/L)	Zn^{2+} (μg/L)
Phytoplankton	*Chaetoceros curvisetus*	0.588*	0.170	0.214	-0.280	0.242	0.460	-0.448	-0.556	-0.091	-0.608*
	C. lorenzianus	0.044	0.000	0.044	0.480	-0.263	0.177	0.131	0.091	0.306	0.480
	Coscinodiscus asteromphalus	0.131	0.309	0.458	0.306	0.448	0.081	0.019	0.169	0.060	-0.090
	C. subtilis	0.131	-0.221	-0.262	-0.480	-0.394	-0.133	0.480	0.091	-0.480	0.044
	Eucampia zoodiacus	0.336	-0.265	-0.094	-0.008	-0.078	-0.028	0.000	-0.308	-0.226	-0.250
	Pseudo-nitzschia pungens	-0.221	-0.222	-0.088	0.238	0.012	-0.371	0.599*	0.378	-0.263	0.193
	Rhizosolenia setigena	0.361	0.770**	0.743**	0.014	0.523	0.425	-0.133	-0.134	0.336	-0.063
	Skeletonema costatum	0.039	0.273	0.385	0.531	0.284	0.142	0.343	0.185	0.189	0.210
Zooplankton	*Aidanosagitta crassa*	0.067	-0.638*	-0.641*	0.168	-0.407	0.021	0.580*	-0.025	-0.077	-0.014
	Acartia pacifica	0.459	0.688*	0.701*	0.154	0.463	0.443	-0.287	-0.280	0.441	0.063
	Brachyura zoea larva	0.141	0.543	0.310	-0.113	0.389	0.307	0.056	-0.132	0.606*	-0.077

(Continued)

TABLE 4 Continued

Type	species	Environmental variables									
		T (°C)	S	Chl *a* (µg/L)	DO (mg/L)	pH	PO_4^{3-} (mg/L)	NO_3^- (mg/L)	NO_2{sp}{/sp}$^-$ (mg/L)	NH_4^+ (mg/L)	Zn^{2+} (µg/L)
	Calanus sinicus	0.326	0.404	0.501	0.343	0.425	0.336	-0.308	0.073	0.322	0.336
	Copepodite	-0.481	0.443	0.481	0.218	0.351	-0.310	0.044	0.499	0.218	0.393
	Nauplius	0.371	0.158	0.035	-0.403	0.007	0.265	-0.374	-0.106	-0.156	0.054
	Noctiluca scintillans	0.154	-0.378	-0.395	0.203	0.097	0.156	0.102	-0.275	0.231	-0.490
	Polychaeta larva	-0.112	0.069	0.302	0.448	-0.063	-0.096	0.132	0.433	-0.060	0.616*

**: $p < 0.01$, *: $p < 0.05$, t-test.

Conclusions

This study provides a comprehensive assessment of plankton seasonal dynamics in the neritic area of the Bohai Sea, put emphasis on biodiversity, trophic linkages and the biotic-abiotic interplay between phytoplankton and zooplankton. Regarding trophic interactions, abundance ratio of phytoplankton to zooplankton was approximately 10^4: 1 in autumn 2023 and spring 2024, with the former season showing a value 5.5 times higher than the latter, indicating lower feeding pressure on zooplankton in autumn 2023. Incorporate aforementioned higher plankton species richness, a logical conclusion is that the community exhibited greater resistance and resilience to harsh environmental conditions compared to spring 2024. Additionally, both total and dominant zooplankton species showed minimal variation between two seasons, likely due to their strong selective feeding abilities. Each dominant phytoplankton species demonstrated distinct trends in response to nutrients, attributed to their unique nutrient affinities and avoidance of vicious competition. Regarding zooplankton, their close relationship with DO is essential for crucial intracellular metabolic processes. Moreover, several dominant plankton species exhibited significant positive correlations with temperature during the warmer spring of 2024, suggesting that these species may become increasingly dominant in the plankton community under the global warming. To summarize, our results lay a solid foundation for assessing and predicting future changes in plankton seasonal dynamics and their potential responses to rapid climate change.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Author contributions

YZ: Conceptualization, Formal analysis, Writing – original draft, Investigation, Methodology. CW: Conceptualization, Formal analysis, Writing – original draft, Funding acquisition, Project administration, Supervision, Writing – review & editing. XW: Formal analysis, Methodology, Visualization, Writing – original draft. WW: Formal analysis, Visualization, Writing – original draft. TZ: Formal analysis, Writing – original draft. JH: Formal analysis, Investigation, Writing – original draft. WS: Formal analysis, Investigation, Writing – original draft. YS: Formal analysis, Investigation, Writing – original draft. ZH: Formal analysis, Writing – original draft. XZ: Funding acquisition, Project administration, Supervision, Writing – review & editing.

Funding

The author(s) declare that financial support was received for the research, authorship, and/or publication of this article. This research was funded by the Shandong Provincial Natural Science Foundation (Grant Number ZR2022QD022) and the National Natural Science Foundation of China (Grant Number 42206258; 41906084).

Acknowledgments

Special thanks to captain and crews of the fishing-boat “Jintangyu02066” for their great help in sampling periods during the cruises. Meanwhile, we greatly appreciate the constructive comments by two reviewers for dramatically improving the quality of the manuscript.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

Publisher's note

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