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Structure and Dynamics of Phytoplankton Populations in the Black Sea from 2014 to 2017

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Abstract

This study investigated the seasonal variations in phytoplankton communities along the Turkish Black Sea coast (2014-2017). Analyzing data from 20 stations revealed high biodiversity (175 species across 14 classes). Phytoplankton abundance showed distinct seasonality, with a peak in summer (2017, 96.6%) and lows in winter, characterized by dinoflagellate dominance. In terms of biomass, diatoms dominated in half of the sampling seasons, while dinoflagellates dominated in the other half at the surface during the study period. The dominance of dinoflagellates corresponded to the winters and summers of 2015 and 2016. The winter conditions of 2015 were harsh. The surface water community composition sometimes varied from that of the water column. Importantly, 44 potentially toxic species were identified, comprising 25% of the community and significantly contributing to both abundance (73.2-98.6%) and biomass (64-90.2%) throughout the year. These results highlight the unique structure of the Black Sea phytoplankton community, characterized by seasonal dominance of diatoms and a significant presence of potentially toxic species. Season, year, and water depth significantly influenced the phytoplankton assemblages. Water temperature was negatively correlated with dissolved oxygen and nitrogen-based nutrients.

Keywords*:* Black Sea phytoplankton; seasonal patterns; potentially toxic species; monitoring.

Introduction

Phytoplankton form the foundation of the marine food web and play a critical role in ocean biology. Through photosynthesis, phytoplankton convert inorganic nutrients, carbon dioxide, and water into organic matter with the aid of light energy, sustaining higher trophic levels and entire marine ecosystems. As a highly sensitive component of the aquatic biota, phytoplankton also serve as early indicators of environmental disturbances, including those caused by human activities (pollution and eutrophication) and climate change. Therefore, changes in phytoplankton community biodiversity, dominant species, taxonomic structure, abundance, biomass, primary production, seasonal succession, and mode of function are valuable indicators of ecosystem health (Moncheva *et al.*, 2019).

The European Union's Water Framework Directive (EU, 2000), Marine Strategy Framework Directive (EU, 2008), and Black Sea Commission Strategic Action Plan (BS SAP, 2009) all recognize phytoplankton as an essential biological component in assessing the ecological status of marine environments. Plankton indicators provide insight into the condition and health of pelagic habitats, contributing to the evaluation of descriptors D1 (biodiversity), D2 (non-indigenous species), D4 (food web), and D5 (eutrophication).

Marine monitoring is a crucial component of environmental management and scientific research, providing valuable information on the health and dynamics of marine ecosystems. The importance of marine monitoring extends to several key areas, including Ecosystem Health, Water Quality, Pollution, Detection and Management, Climate Change Research, Fisheries Management, Early Warning Systems, Research and Scientific Understanding, Policy and Regulation Support, and Educational and Outreach Purposes (Danovaro *et al.*, 2016).

The significance of national or intergovernmental monitoring studies in transboundary seas such as the Black Sea cannot be overstated. These studies are crucial as they furnish the basin-scale, which comprises comparable datasets that encompass a wide range of essential marine parameters.

The origins of scientific studies in the Black Sea, which is a *"unicum hydrobiologicum"* in the analogy of Russian oceanographer Nikolai M. Knipovich, date back to the first half of the 1800s. R. Gotie conducted the first thorough bathymetric surveys in 1820 and 1821, with findings published in 1822 (Vespremeanu & Golumbeanu, 2018). Since then, the Black Sea has been an important research area for scientists from this region and those interested in the region.

Phytoplankton studies in the Black Sea Turkish coasts

Phytoplankton investigations in the Turkish coastal zone of the Black Sea began in the late 1980s. These investigations primarily consisted of project-funded cruises, scientific theses, and project reports based on the acquired data and articles generated from the data. Notably, most of the studies were short-term and localized, with very few encompassing expansive regions or the entirety of the Turkish coast.

The sample periods, durations, qualitative/quantitative findings, sampling methods, and equipment employed varied across the studies. Notably, most studies acquired species lists from primary sources (dissertations, reports, etc.) and updated them based on the current taxonomic knowledge using relevant databases.

Studies conducted along the Turkish coasts of the Black Sea have revealed that diatoms were the dominant group in species composition until the 1990s (Feyzioğlu, 1990; Uysal, 1993; Feyzioğlu, 1996); however, after the 1990s, dinoflagellates became the predominant group in species composition (Bayrakdar, 1994; Eker, 1998; Eker *et al.*, 1999; Eker-Develi & Kideys, 2003; Ağırbaş, 2010; Koca, 2014; Agirbas *et al.*, 2017).

The phytoplankton community along the Turkish coasts of the Black Sea has experienced notable changes in abundance and biomass over the years. While earlier studies indicated that diatoms dominated phytoplankton biomass until the 1990s, recent data revealed a significant decline in their proportion, supplanted by an increase in dinoflagellates and coccolithophores. Recent research highlights that diatoms constitute approximately 70% of the total phytoplankton abundance during spring, with significant spatial variations influenced by factors such as river outflows. Additionally, seasonal fluctuations affect phytoplankton dynamics, with higher abundance and biomass observed in fall and spring compared to summer. These shifts in community composition underscore the complex interplay of environmental conditions impacting phytoplankton distribution and productivity in the region (Uysal 2002; Eker-Develi & Kideys, 2003; Koca, 2014; Balkis-Ozdelice & Anda Peynirci, 2019).

The dominant phytoplankton species along the Turkish coasts of the Black Sea exhibit a high degree of similarity across various studies, with species such as *Cylindrotheca closterium*, *Dactyliosolen fragilissimus*, and *Gephyrocapsa huxleyi* frequently observed, particularly during spring and fall. Additionally, dinoflagellate species, including those from the genera *Dinophysis*, *Prorocentrum*, and *Tripos*, are notably dominant in summer, highlighting the seasonal variability in phytoplankton community composition in this region. *Pseudosolenia calcar-avis* and *Scrippsiella acuminata* are frequently reported to dominate phytoplankton abundance during blooms. Studies indicate that these species, along with *Emiliania huxleyi* and *Pseudo-nitzschia seriata*, can reach high concentrations, often exceeding 1 million cells/L, particularly in spring and fall, highlighting the algal blooms in this region (Eker *et al.*, 1999; Türkoğlu & Koray, 2002; Eker-Develi & Kideys, 2003; Agirbas *et al.*, 2014; Agirbas *et al.*, 2017).

Aim of the study

This study aimed to identify the structural indicators (taxonomic structure, abundance and biomass, dominant species, blooms, and harmful species) of phytoplankton sampled in six seasonal cruises carried out within the scope of the "Integrated Marine Pollution Monitoring" national program in the region covering the entire Turkish coast of the Black Sea from 2014 to 2017. It also aimed to reveal the relationship between phytoplankton structural indicators and environmental parameters.

Materials and Methods

Study area

The Black Sea, an elongated basin with limited access to the Aegean and Mediterranean Seas via the narrow Istanbul (Bosporus) and Çanakkale (Dardanelles) Straits, stretches approximately 1,200 km in length and varies in width, from 500 km in the west to 250 km in the east. Its surface area of 423,000 square kilometers is roughly one-fifth of the Mediterranean Sea's expanse. The Turkish Straits System both restricts and provides connections to the Aegean Sea. The Black Sea bathymetry is characterized by a narrow shelf, typically less than 20 km wide, that abruptly transitions into a steep topographic slope, generally less than 30 km in length, surrounded by a deep interior basin with a maximum depth of 2,200 m. The northwestern portion of the sea, encompassing approximately 20% of the total area, features a relatively broad shelf and connection to the deep western basin via a broader topographic slope zone. The width of the western shelf gradually diminished southward and eventually disappeared in the east of the Bosphorus Strait exit. Freshwater rivers flow into the Black Sea from all around the basin, with the most significant rivers –the Danube, Dnieper, and Dniester– discharging into the northwestern coastal waters. The Danube, one of Europe's largest rivers, profoundly influences the Black Sea ecosystem (Tuğrul *et al.*, 2014).

Six countries border the Black Sea: Bulgaria, Romania, Ukraine, Russia, Georgia, and Türkiye. The Black Sea coastline is 4,869 km long, with Türkiye having the longest coastline at 1,700 kilometers, extending from İğneada (near the Bulgarian border) in the west to Sarp in the east (Stanchev *et al.*, 2011).

Sampling and analytical procedures of seawater

The research under the Turkish Integrated Marine Pollution Monitoring Program initiated in 2014 as part of the national program by the Ministry of Environment, Urbanization, and Climate Change and coordinated by TÜBİTAK Marmara Research Center was conducted at 20 stations selected from 16 coastal water bodies along the entire Black Sea coast of Türkiye, from the western-most İğneada to the easternmost Hopa (Georgian border), between 2014 and 2017 (Fig. 1). Six cruises (August/Summer 2014; January/Winter and August/Summer 2015; January/Winter and August/Summer 2016; and August/Summer 2017) were implemented in the study area with R/V TÜBİTAK Marmara. The details of the stations in the study area are provided in Supplementary Material Table S1.

A total of 254 phytoplankton samples were collected using 10 L teflon Niskin bottles attached to a CTD (Sea-Bird SBE 25Plus/SBE 27 pH Sensor) Rosette System (SBE 32C 12 universal sampling bottle). Water sampling depths were determined by examining the temperature, salinity, PAR, in-situ fluorescence, dissolved oxygen profiles, and light (PAR) transmittance at the time of sampling using a CTD and water sampler that takes real-time measurements at each station. These depths (Supplementary Material Table S1) included the surface, maximum temperature/salinity gradients, fluorescence maximum (or chlorophyll maximum), and 2 m above the bottom depth. The 1-L samples were fixed with 2.5–5 ml L^{-1} alkaline Lugol's solution and concentrated by the sedimentation method (Moncheva & Parr, 2010). Following this process, microscopic analyses (including species identification, counting, and measurements) began without interruption.

In addition to phytoplankton sampling, the following parameters were measured at the stations: Temperature (^{0}C), salinity (‰), light transmittance (m), pH, dissolved oxygen (mg L^{-1}), chlorophyll-*a* (µg L^{-1}), total phosphorus (µM), dissolved inorganic phosphorus (µM), total inorganic nitrogen (µM), nitrate + nitrite nitrogen (µM), ammonium nitrogen (µM), and silicate (µM). The parameters measured at the stations, the measurement details of the parameters, and the applied methods are presented in Supplementary Material Tables S2 and S3.

Structural components of phytoplankton

Qualitative and quantitative analyses of the samples were performed using a light microscope (Nikon Eclipse Ni with DS-Fi2 cam-NIS Imaging System) and an inverted microscope (Zeiss Axio Vert A.1 with Axiocam 105 color-ZEN Imaging System) in a Sedgewick Rafter counting cell using standard methods. For the nanophytoplankton analysis, 0.01-ml subsamples were scanned using a slide (Moncheva & Parr, 2010).

The biovolume of individual cells (V, µm3) was determined by measuring and approximating the shape of each species (Hillebrand *et al.*, 1999). An average of at least ten measurements per species was considered acceptable for biovolume calculations (MISIS, 2014).

The species identified in the literature were taxonomically updated by examining both the AlgaeBase (Guiry & Guiry, 2023) and the World Register of Marine Species (WoRMS Editorial Board, 2023) online databases.

For the identification of species, printed and digital sources were used, including Kiselev (1950), Proshkina-Lavienko (1955) and Tomas (1997), as well as online databases such as AlgaeBase, nordicmicroalgae.org, planktonnet.avi.de, and WoRMS. The species obtained in this study were classified using the AlgaeBase database (Guiry & Guiry, 2023).

Soyer's (1970) Frequency Index Formula was used to determine the frequency values of phytoplankton species at the stations during the sampling period.

The dominance index (*Y*) method described by McNaughton (1967) was used to determine the most abundant phytoplankton species. Species exceeding a dominance threshold of $Y \geq 0.02$ were classified as "dominant species," with those attaining $Y > 0.1$ designated as "absolute dominant species" (Wu *et al.*, 2021).

To determine potentially toxic species **IOC-HAB:** (harmful algal bloom, or HAB), the Taxonomic Reference List of Harmful Micro Algae was used, which is a resource compiled by the Intergovernmental Oceanographic Commission's Harmful Algal Bloom Program (UNESCO) (Lundholm *et al.*, 2009). **Harmful:** GEOHAB (2001), Hallegraeff *et al.* (2021), Harmful Algal Event Database (2023). **Blooming:** Türkoğlu & Koray (2004), Terenko & Terenko (2005), Vershinin *et al.* (2005), Nesterova *et al.* (2008), Yasakova (2013), Moncheva *et al.* (2019).

Statistical analyses

The Principal Component Analysis (PCA) was applied to the normalized data set of the environmental parameters to elucidate the physiological and chemical

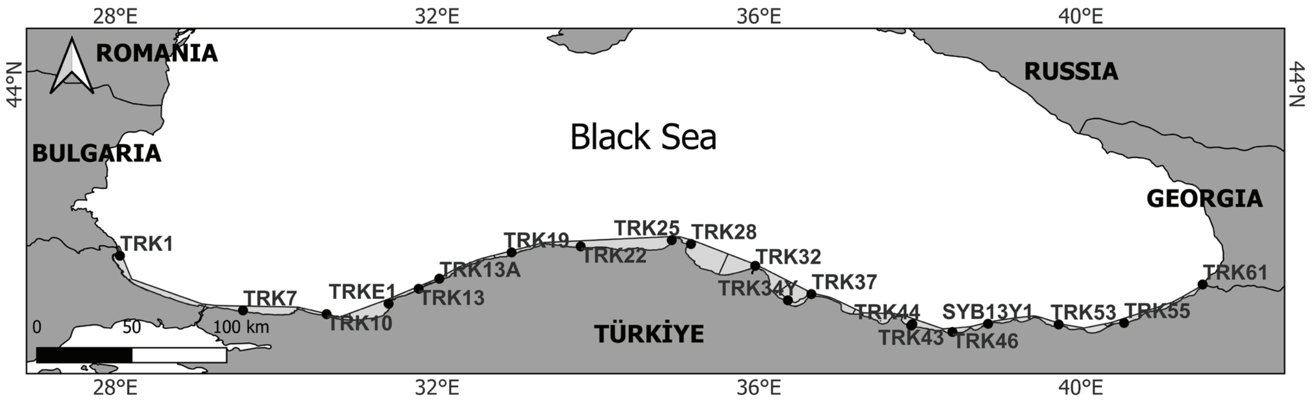

Fig. 1: Sampling stations along the Black Sea coast of Türkiye.

characteristics of the study area by season and year. The inherent floral composition and the phytoplankton assemblages were summarized using non-metric multidimensional scaling (nMDS) subjected to a log10-transformed rectangular matrix of the phytoplankton species abundances. A three-way permutated multivariate analysis of variance (PERMANOVA) was used to test differences in phytoplankton assemblages among years, seasons, and depths. A similarity of percentage (SIMPER) analysis was performed to determine the contributor and discriminator species within year and season and among pairwise years and seasons, respectively. All analyses were performed using PRIMER 6. To understand the phytoplankton–environment relation, a canonical correspondence analysis (CCA) was applied to a log10-tranformed rectangular matrix of the phytoplankton abundances, and discrimination of phytoplankton composition was validated via Monte Carlo testing using CANOCA.

Results

Environmental characteristics of the study area

The physical and chemical parameters were measured and included the minimum, maximum, and mean values, which are presented in Supplementary Material Table S4. The temperatures measured were between 4.42–26.58 ºC. The 2014 summer period had the highest temperature, with a mean of 23 ºC, and the 2015 winter period had the lowest temperature, with a mean of 8 °C. The highest average salinity was calculated during the summer of 2017 at 18.11‰; the other periods had similar average salinity values. The lowest dissolved oxygen values were calculated during the summer period of 2017, with a mean of 7.93 mg L^{-1}, and the highest oxygen values were calculated during the winter period of 2015, with a mean of 10.91 mg L^{-1}. The highest Secchi depth was calculated during the summer of 2014, at 12.1 m, and the lowest was found during the winter of 2016, at 0.5 m. Chlorophyll-a values varied between 0.665-0.889 µg L^{-1}, with the highest values calculated during the summer of 2017, at 4.945 µg L^{-1}. The nitrate + nitrite values varied between 0.061-1.130 µM, with the highest value calculated during the winter of 2016, at 8.227 µM. The highest total phosphorus value was calculated during the winter of 2015, at 0.828 µM, while the reactive silicate values varied between 1.398-5.556 µM, with the highest value calculated during the winter of 2016 (31.680 µM).

PCA1 elucidated seasonal characteristics (winter and summer), with 36.2% of the total variance correlating positively and negatively with water temperature and dissolved oxygen in the water, respectively, followed by N-based nutrients (Fig. 2, Table 1). The negative correla-

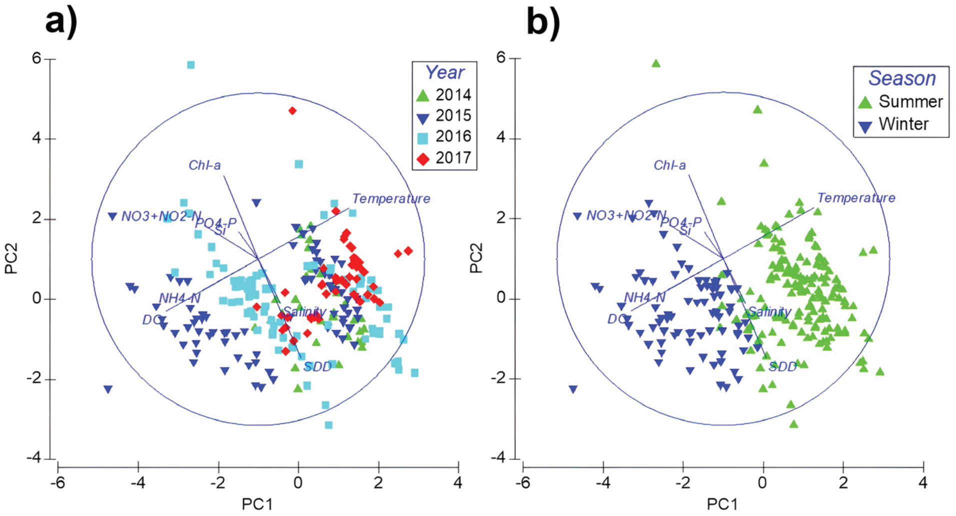

Fig. 2: PCA solution for the physical and chemical parameters of the water at the sampling stations classified by year (a) and season (winter and summer) (b).

Table 1. Summary of physical and chemical characteristics of the study area explained by PCA.

Variable	PC1	PC2	PC3	PC4	PC5
Temperature (ºC)	**0.545**	0.308	0.305	0.027	0.075
Salinity (‰)	0.134	-0.270	**-0.530**	**-0.638**	0.310
DO (mg L^{-1})	**-0.556**	-0.315	0.036	0.024	-0.137
Chl-*a* (µg L^{-1})	-0.209	**0.507**	0.244	**-0.696**	-0.360
PO_4-P (µM^{-1})	-0.116	0.163	-0.068	-0.053	0.219
NO_3+NO_2-N (µM)	**-0.327**	0.205	-0.176	0.205	-0.335
NH_4-N (µM)	**-0.334**	-0.186	**0.621**	-0.152	**0.530**
Si (µM)	-0.182	0.115	-0.279	-0.002	-0.013
SDD (m)	0.259	**-0.600**	0.257	-0.198	-0.555
Variance (%)	36.2	19.0	13.7	10.1	8.5

tion between temperature and nutrients in PCA1 indicated that the nutrients were significantly higher in winter than in summer. The characteristically explained parametric components of PCA1 revealed that the winters of 2015 and 2016 possessed a distinguished structure in the study area; the winter of 2015 had higher nutrients and colder water than the winter of 2016, and there was also an extreme winter condition in 2015 compared to other years (Fig. 2). However, it is important to emphasize that this study lacks winter sampling in 2014 and 2017.

PCA2 characterized the study area with Chl-*a*, followed by optical characteristics derived from the Secchi depth. This component explained 19% of the variance (Table 1). There was a reverse relationship expected between Chl-*a* and the Secchi depth in PCA2 (Fig. 2). However, no determinative component was found for the collinearity of this relationship in the study area in PCA2. Both of the axes of the PCA explained the physical and chemical characteristics of the study area with over half (55.2%) of the total variance.

Species composition

The list of species identified in all sampling seasons in this study is provided in Supplementary Material Table S5.

A total of 175 phytoplankton species (belonging to 14 phytoplankton classes) were identified, with diatoms accounting for the largest proportion (46%, 80 species), followed closely by dinoflagellates (45%, 79 species). The remaining 9% (16 species) consisted of various taxa outside these two dominant groups.

Within the dinoflagellates, 26 genera were identified. The genera *Protoperidinium* (23 species), *Dinophysis* (11 species), *Tripos* (seven species), *Prorocentrum* (five species), and *Gonyaulax* (four species) exhibited the highest species richness, collectively representing 63% of all dinoflagellate species observed. Among the diatoms, 39 genera were identified. The genera *Chaetoceros* (22 species), *Thalassiosira* (five species), and *Coscinodiscus* (four species) were the main contributors to species diversity, accounting for 39% of the total diatom species identified.

Temporal analysis of phytoplankton species diversity revealed a peak in winter abundance in 2015, with 118 species recorded, followed by a summer minimum in 2016 with 62 species. Notably, winter periods consistently exhibited higher species richness in diatoms than in dinoflagellates, while the reverse pattern was true during all summer seasons. Despite the relatively consistent species richness during the first four sampling seasons, a significant decrease in total species diversity was observed during the summers of both 2016 and 2017 (Fig. 3).

Based on the frequency index formula, Supplementary Material Table S6 details the species identified as "constant" across all 20 stations and throughout all sampling periods. Notably, 63 species exhibited inter-station constancy, whereas 65 species exhibited intra-seasonal constancy. Among these, the dinoflagellates *Gyrodinium fusiforme*, *Prorocentrum micans*, *Protoperidinium granii*, *Scrippsiella acuminata*, *Tripos furca*, *Tripos fusus*, and *Tripos muelleri*, the diatom *Chaetoceros affinis*, and the coccolithophorid *Emiliania huxleyi* were consistently present at all 20 stations during each sampling season.

Abundance and biomass

During the summer of 2014, coccolithophores dominated the phytoplankton community in terms of abundance, representing over 50% across all depths (surface: 51.9%, Chl-Max depth: 53%, water column: 53.1%). However, the biomass data painted a different picture, with diatoms being dominant at the surface (63%) and throughout the water column (51.4%), while dinoflagellates dominated at the Chl-Max depth (64.5%). This highlights a divergence between cell abundance and biomass, where larger-celled diatoms contributed more to total biomass despite lower cell numbers (Table 2).

In the winter of 2015, diatoms were the dominant group in terms of abundance, particularly in the water column (70.6%), but the biomass data showed that dinoflagellates dominated across both the surface (67.6%) and the water column (58.9%). The summer of the same year saw dinoflagellates take over in both abundance and biomass. They represented 57.4% of abundance at the Chl-Max depth and 74.6% of the biomass in the water column, indicating a strong dinoflagellate bloom during this period (Table 2).

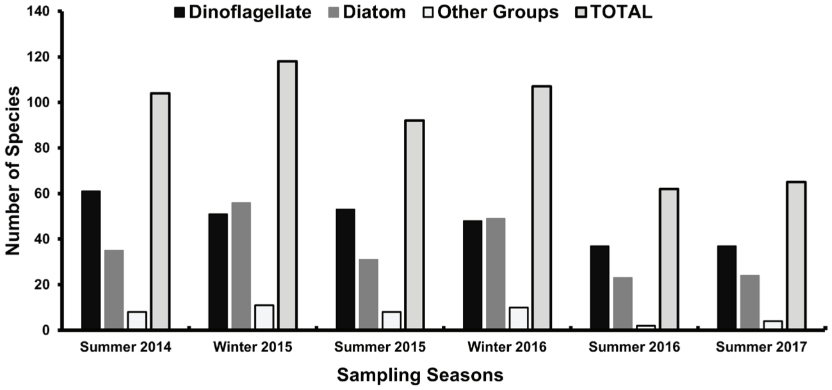

Fig. 3: Distribution of species numbers of phytoplankton groups according to sampling period.

Table 2. Distribution and average abundance/biomass (2014–2017) values of key groups in sampling depths (Dia: Diatoms, Dino: Dinoflagellates, Cocco: Coccolithophorids).

		Abundance (%)				**Average**
SEASONS	**LAYERS**	Dia	Dino	Cocco	Others	Abundance (cell L^{-1}) (± Conf. Int.)
2014-Summer	*Surface*	24.5	23.5	**51.9**	0.1	61186.85 ± 9986.03
	Chl-Max	15.5	30.9	**53.0**	0.5	61485.80 ± 13055.11
	Water Column	21.0	25.6	**53.1**	0.3	123948.45 ± 24830.95
2015-Winter	*Surface*	**62.0**	11.7	4.0	22.3	59025.25 ± 51368.51
	Water Column	**70.6**	8.9	3.6	16.8	120376.50 ± 128527.53
2015-Summer	*Surface*	40.3	**43.6**	15.6	0.5	71607.00 ± 26241.11
	Chl-Max	31.3	**57.4**	11.0	0.3	28637.86 ± 19768.50
	Water Column	39.3	**44.7**	15.6	0.4	106780.25 ± 42016.77
2016-Winter	*Surface*	34.9	**44.5**	9.2	11.4	12513.00 ± 4625.73
	Water Column	39.1	**40.3**	9.9	10.7	21570.75 ± 7077.29
2016-Summer	*Surface*	**60.4**	27.6	11.9	0.02	19960.75 ± 3688.87
	Chl-Max	34.5	**61.1**	4.4	0.0	19711.07 ± 12827.53
	Water Column	**51.3**	39.5	9.2	0.008	37147.50 ± 12111.16
2017-Summer	*Surface*	**94.2**	3.2	2.5	0.03	68793.25 ± 17682.53
	Chl-Max	**95.1**	3.1	1.8	0.003	35348.00 ± 18516.15
	Water Column	**94.6**	3.1	2.3	0.03	128164.00 ± 41037.72
		Biomass (%)				**Average**
SEASONS	**LAYERS**	Dia	Dino	Cocco	Others	Biomass (μg L^{-1}) (± Conf. Int.)
2014-Summer	*Surface*	**63.0**	35.8	1.1	0.1	426.463 ± 110.791
	Chl-Max	34.4	**64.5**	1.0	0.1	469.738 ± 141.695
	Water Column	**51.4**	47.5	1.1	0.1	873.827 ± 202.606
2015-Winter	*Surface*	29.1	**67.6**	0.3	3.0	115.048 ± 37.815
	Water Column	38.0	**58.9**	0.3	2.7	191.951 ± 77.693
2015-Summer	*Surface*	26.6	**72.8**	0.6	0.1	283.449 ± 123.734
	Chl-Max	18.7	**81.0**	0.3	0.01	158.433 ± 84.711
	Water Column	24.8	**74.6**	0.5	0.1	451.322 ± 179.750
2016-Winter	*Surface*	14.9	**84.3**	0.1	0.7	145.132 ± 92.510
	Water Column	18.9	**80.4**	0.1	0.6	231.843 ± 114.280
2016-Summer	*Surface*	**79.5**	20.4	0.1	0.001	624.073 ± 202.373
	Chl-Max	41.6	**58.3**	0.0	0.0	616.748 ± 369.715
	Water Column	**65.8**	34.2	0.0	0.001	1171.231 ± 434.052
2017-Summer	*Surface*	**66.4**	33.5	0.1	0.003	193.356 ± 104.303
	Chl-Max	**57.4**	42.5	0.1	0.001	101.593 ± 47.502
	Water Column	**62.5**	37.4	0.1	0.003	352.874 ± 161.341

During the winter of 2016, dinoflagellates dominated both abundance (surface: 44.5%, water column: 40.3%) and biomass (surface: 84.3%, water column: 80.4%), reflecting a period of low overall cell numbers but high biomass contribution from dinoflagellates. The summer of 2016 saw a return of diatoms as the dominant group in both abundance and biomass, particularly at the surface (60.4% abundance, 79.5% biomass) and across the water column (51.3% abundance, 65.8% biomass), marking the highest biomass recorded across all years (Table 2).

Finally, the summer of 2017 was marked by overwhelming diatom dominance in terms of abundance, reaching 94.6% in the water column. This was also reflected in biomass, though less pronounced, with diatoms accounting for 62.5% of the total biomass in the water column. This year saw the highest abundance recorded, underlining a significant diatom bloom (Table 2).

In summary, the highest phytoplankton abundance was observed in the summer of 2017 (123948.45 ± 24830.95 cell L^{-1}), driven by a large diatom bloom, while the lowest abundance was recorded in the winter of 2016 (21570.75 ± 7077.29 cell L^{-1}), coinciding with a dominance of dinoflagellates. In terms of biomass, the summer of 2016 recorded the highest values (1171.231 ± 434.052 μg L^{-1}), again led by diatoms, while the lowest biomass (191.951 ± 77.693 μg L^{-1}) was observed in the winter of 2015 during a period of dinoflagellate dominance (Table 2).

Diatoms were dominant in abundance and biomass during the summer periods, especially in 2016 and 2017. In contrast, dinoflagellates often dominated the biomass during winter, even when their abundance was lower. The divergence between abundance and biomass is mainly due to the larger size of dinoflagellates, which allows them to contribute more to biomass even with fewer cells. Dinoflagellates were more dominant during periods of lower overall phytoplankton abundance, particularly in the winter months. They adapted well to colder conditions, while diatoms thrived during nutrient-rich summer periods, driving the higher biomass levels observed in those seasons.

Dominant species

The relative contributions of the dominant species to the total abundance and group abundances at the surface, chlorophyll maximum depth, and in the water column are detailed in Supplementary Material Table S7. Using dominance index values calculated across the entire water column and based on the total abundance at each station, a total of 17 species were identified as dominant (Supplementary Material Table S8). These included six diatoms, nine dinoflagellates, and two other groups. Further analysis revealed several "absolute dominant species" based on seasonality; *Pseudosolenia calcar-avis* held this designation during the summer of 2016, while *Pseudo-nitzschia delicatissima* assumed this role in both the winter of 2015 and the summer of 2017. In addition, *Thalassionema nitzschioides* dominated in the summer of 2015, whereas *Prorocentrum cordatum* exhibited absolute dominance in the summers of 2014 and 2015. Notably, *Prorocentrum micans* achieved this status in the winter of 2015, and *Emiliania huxleyi* dominated during the summers of 2014 and 2015. Finally, *Hillea fusiformis* was identified as the dominant species during the winter of 2015 (Supplementary Material Table S7). Furthermore, *Akashiwo sanguinea* and *Tripos muelleri* showed unique summer dominance patterns in 2016. *Akashiwo sanguinea* dominated the surface waters, while *Tripos muelleri* peaked at the chlorophyll maximum depth.

During the study period, a significant dominance of diatom species in both intra-group and total phytoplankton abundance values was observed along the Turkish coast of the Black Sea. *Pseudo-nitzschia delicatissima* dominated, making up 58.1% of the total phytoplankton abundance during the winter of 2015, 32.3% during the summer of 2015, and 91.5% during the summer of 2017. *Pseudosolenia calcar-avis* constituted 39% of the total phytoplankton abundance during the summer of 2016. Diatoms did not dominate the total phytoplankton in the summer of 2014 and winter of 2016. The coccolithophore *Emiliania huxleyi* accounted for 53.1% of the total phytoplankton abundance during the summer of 2014. In the winter of 2016, dinoflagellates accounted for 40.3% of the total phytoplankton abundance. While *Prorocentrum micans* represented 38.6% of the dinoflagellate abundance, it only comprised 15.6% of the total phytoplankton abundance in the entire water column in the winter of 2016. The species *Prorocentrum cordatum* contributed 23.1% of the total phytoplankton abundance during the summer of 2015. Among groups other than diatoms, dinoflagellates, and coccolithophores, only *Hillea fusiformis* constituted 15.7% of the total phytoplankton abundance in the winter of 2015 (Supplementary Material Table S7).

During a four-year study encompassing multiple seasons, 14 phytoplankton species (Diatoms: 4 species, Dinoflagellates: 8 species, Others: 2 species) exceeded the abundance threshold of 10.000 cell L^{-1} (Supplementary Material Table S9). Among them, *Pseudo-nitzschia delicatissima* was the most conspicuous, peaking at 4.7 × 10^{5} cell L^{-1} in surface waters during the winter of 2015, the highest recorded single-species abundance at any depth throughout the entire study. In the summer of 2017, the *Pseudo-nitzschia delicatissima* abundance was calculated as 2.4 × 10^{5} cell L^{-1} at the surface. Notably, *Pseudo-nitzschia delicatissima* exceeded the 10,000 cell L^{-1} threshold at 18 of the 20 stations in summer 2017, six in winter 2015, and 12 in summer 2015. In addition to this species, the abundance of the diatom *Thalassionema nitzschioides* was calculated as 9.5 × 10^{4} cell L^{-1} at the surface of the water in the summer of 2015.

The highest abundance recorded for a dinoflagellate species was 4.8 × 10^{4} cell L^{-1}, observed in *Prorocentrum cordatum* during the summer of 2015. This species exceeded the 10,000 cell L^{-1} threshold at 15 of the 20 stations. Compared to diatoms, dinoflagellate species were generally less abundant, with no species surpassing the 5 × 10^{4} cell L^{-1} threshold throughout the study. Except for *Prorocentrum cordatum*, no other dinoflagellate species exceeded the threshold of 10,000 cell L^{-1} at more than one station during the sampling periods.

Apart from diatoms and dinoflagellates, the coccolithophorid *Emiliania huxleyi* reached its highest abundance value (9.2 × 10^{4} cell L^{-1}) in the summers of 2014 and 2015 (4 × 10^{4} cell L^{-1}). Except for the winter of 2015, this species did not exceed the threshold of 10,000 cell L^{-1} during winter.

Potentially toxic (harmful and bloom-forming) species

A total of 44 potentially toxic species constituted 25% of the phytoplankton community. These species were categorized based on established frameworks: 17 species were classified within the IOC-HAB taxonomic list, 12 species were recognized as harmful, and 15 species exhibited bloom-forming tendencies in the Black Sea. Notably, the potentially toxic species exhibited a striking dominance over the total phytoplankton abundance and biomass in all sampling periods. Additionally, 21 potentially toxic species were present in all sampling periods, suggesting that they were well adapted to the environmental conditions of the study area (Table 3).

In all sampling periods, the abundance values of the potentially toxic species dominated the total phytoplankton abundance values, from 73.2% in winter 2016 to 98.6% in summer 2017. Except for the winter of 2015, the total biomass values were dominated by potentially toxic species, from 64% in winter 2016 to 90.2% in summer 2016 (Table 4).

Phytoplankton assemblages

Phytoplankton assemblages based on either abundance or biomass were significantly different by year,

Table 3. Potentially toxic species and their frequency in the 2014–2017 sampling periods.

Status	Species	Frequency
IOC-HAB	*Pseudo-nitzschia delicatissima*	Constant (100)
	Pseudo-nitzschia pungens	Constant (67)
	Akashiwo sanguinea	Constant (83)
	Alexandrium minutum	Constant (67)
	Dinophysis acuminata	Constant (83)
	Dinophysis acuta	Common (50)
	Dinophysis caudata	Constant (100)
	Dinophysis fortii	Constant (100)
	Dinophysis ovum	Constant (83)
	Dinophysis sacculus	Constant (100)
	Gonyaulax spinifera	Common (50)
	Karenia mikimotoi	Frequent (17)
	Karenia sp.	Frequent (33)
	Lingulodinium polyedra	Constant (100)
	Phalacroma rotundatum	Constant (100)
	Prorocentrum cordatum	Constant (100)
	Prorocentrum lima	Frequent (33)
Harmful	*Asterionellopsis glacialis*	Frequent (17)
	Cylindrotheca closterium	Constant (83)
	Leptocylindrus danicus	Constant (100)
	Tryblionella compressa	Constant (100)
	Dinophysis hastata	Frequent (17)
	Gonyaulax polygramma	Constant (83)
	Kryptoperidinium triquetrum	Constant (100)
	Prorocentrum micans	Constant (83)
	Scrippsiella acuminata	Constant (100)
	Tripos furca	Constant (100)
	Tripos fusus	Constant (100)
	Tripos muelleri	Constant (100)
Bloom-forming	*Cerataulina pelagica*	Common (50)
	Chaetoceros affinis	Constant (100)
	Chaetoceros curvisetus	Constant (100)
	Chaetoceros danicus	Frequent (17)
	Chaetoceros socialis	Common (50)
	Ditylum brightwellii	Constant (67)
	Melosira moniliformis	Frequent (33)
	Nitzschia longissima	Frequent (17)
	Proboscia alata	Constant (100)
	Pseudosolenia calcar-avis	Constant (100)
	Skeletonema costatum	Common (50)
	Thalassionema nitzschioides	Constant (100)
	Prorocentrum balticum	Frequent (17)
	Protoperidinium steinii	Constant (100)
	Emiliania huxleyi	Constant (100)

Table 4. The contribution ratios of potentially toxic species groups in total abundance and biomass.

			Abundance (%)			
Season	**14-S**	**15-W**	**15-S**	**16-W**	**16-S**	**17-S**
IOC-HAB	14.4	**59.2**	28.4	21.9	11.8	**92.2**
Harmful	10.7	6.8	9.3	31.6	27.5	2.0
Bloom-forming	**67.8**	8.9	**51.2**	19.7	**52.3**	4.4
PTS Total	**93.0**	**74.9**	**88.8**	**73.2**	**91.6**	**98.6**
			Biomass (%)			
Season	**14-S**	**15-W**	**15-S**	**16-W**	**16-S**	**17-S**
IOC-HAB	8.8	7.3	26.5	5.8	3.6	12.5
Harmful	25.7	17.4	21.6	**53.1**	22.0	13.4
Bloom-forming	46.2	13.3	20.7	5.1	**64.5**	**51.9**
PTS Total	**80.7**	38.0	**68.8**	**64.0**	**90.2**	**77.8**

season, and depth, and by year/season interaction at $p < 0.05$ (Supplementary Material Table S10, Fig. 4).

Assemblages of the phytoplankton composition were distinguished by season and year (Fig. 4). This distribution of NMDS coincided well with the distribution of the PCA collinearities of the environmental parameters of the study area (Fig. 2, Fig. 4) There was an apparent separation in the phytoplankton assemblages between winter and summer. However, there were different floral compositions in summer each year. The assemblages were abruptly discriminated against from the summers of 2015 to 2017. There was a similar phytoplankton composition between the summers of 2014 and 2016 compared to that between 2015 and 2017 (Fig. 4). However, the winter conditions in 2015 were different from other years, and this affected the phytoplankton assemblage.

Unlike the winter composition, the diatom/dinoflagellates ratio elucidated the summer variation in the phytoplankton composition, particularly in 2017 (Supplementary Material Figure S1). This ratio was rather higher in 2017 than other years when the diatom dominance was less pronounced in summer. However, few species were found to be contributor species to the similarity of phytoplankton assemblages in seasons. The common contributor species between seasons were *Emiliania huxleyi* and *Chaetoceros affinis* in winter and *Emiliania huxleyi*, *Tryblionella compressa*, and *Tripos furca* in summer (Supplementary Material Table S11). All these species shaped seasonal phytoplankton assemblages. The percentage dissimilarity between seasons was estimated to be 58.93%. The differences in seasonal phytoplankton composition was mainly dictated by five species (*Hillea fusiformis*, *Cylindrotheca closterium*, *Skeletonema costatum*, *Thalassionema nitzschioides*, *Octactis speculum*), which abundantly predominated in winter compared to summer (Supplementary Material Table S12). Additionally, one summer species (*Protoperidinium divergens*) was the discriminator species between seasons.

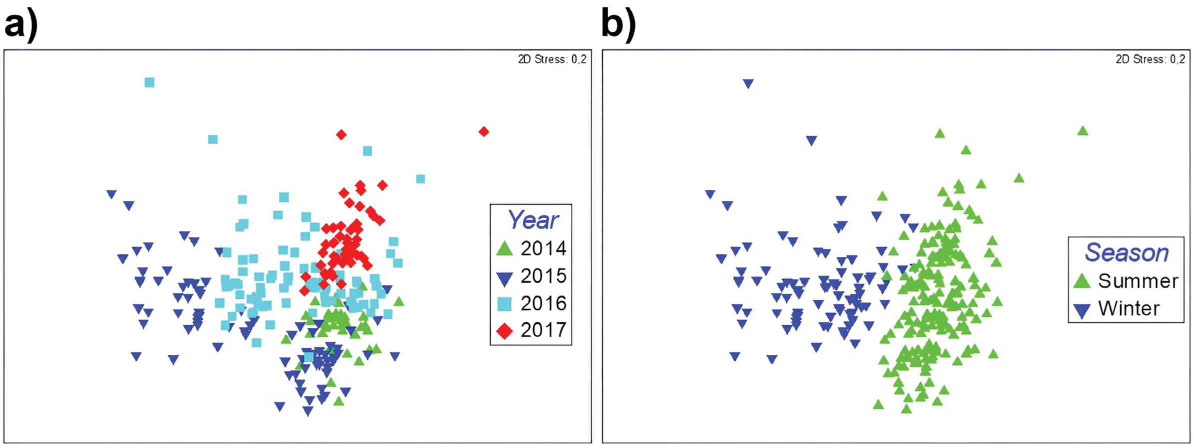

Fig. 4: Based on the Bray–Curtis similarity index solving $\log_{10}$(abundance+1) of phytoplankton nMDS solution showing the distribution of the sampling stations classified by year (a) and season (b).

The highest average percent similarity was assessed in 2017, followed by 2014. Relatively, other years had less pronounced similarity of the annual phytoplankton composition compared to that in 2014 and 2017 (Supplementary Material Table S13). In all years, *Emiliania huxleyi* was the predominant contributor species, except in 2017 when *Pseudo-nitzschia delicatissima* was the first contributor species. The significant contributor species were *Emiliania huxleyi*, *Tryblionella compressa*, *Prorocentrum micans,* and *Tripos furca* in 2014, *Emiliania huxleyi*, *Gyrodinium fusiforme,* and *Chaetoceros affinis* in 2015, *Emiliania huxleyi*, *Prorocentrum micans*, *Tripos furca*, and *Protoperidinium steinii* in 2016, and *Pseudo-nitzschia delicatissima*, *Emiliania huxleyi*, *Phalacroma rotundatum*, *Tryblionella compressa*, *Prorocentrum micans*, *Tripos furca*, and *Tripos muelleri* in 2017.

In terms of pairwise dissimilarity between years, the highest dissimilarity was found between 2015 and 2017, followed by 2016 (Supplementary Material Table S14, Fig. 4a). Excluding *Prorocentrum micans* (more abundantly found in 2016), phytoplankton species, which were more abundantly estimated in 2015, were the discriminator species between 2015 and 2016. Followed *Pseudo-nitzschia delicatissima* by *Prorocentrum micans* which were outburst species in 2017 compared to 2015 were the discriminator species between 2015 and 2017 besides few species abundantly found in 2015. Two dominant species (*Prorocentrum micans* and *Kryptoperidinium triquetrum*) found in 2014 and *Pseudosolenia calcar-avis* in 2015 were the main discriminator species between 2014 and 2015. *Thalassionema nitzschioides, Kapelodinium vestifici,* and *Gonyaulax spinifera* were the discriminating species in 2014 from 2016. Two species (*Prorocentrum cordatum* and *Thalassionema nitzschioides*) in 2014 and *Pseudo-nitzschia delicatissima* in 2017 were the main discriminator species dictating differences in the phytoplankton assemblages between 2014 and 2017. *Pseudo-nitzschia delicatissima* followed by *Dactyliosolen fragilissimus* predominantly found in 2016 and *Prorocentrum cordatum* in 2017 were the discriminator species between 2016 and 2017.

Phytoplankton species were mainly distributed depending on season, followed by year, as was the case in the NMDS plot (Fig. 4, Fig. 5). CCA1 explained the phytoplankton species derived from season-related environmental parameters with a variance of 38.3% (Table 5). According to CCA1, temperature was negatively correlated with DO and nutrients. CCA2 and CCA3 were presumably explained by annual changes (year) and layers (water depths) with respective variances of 16.7% and 11.6% (Table 5). In CCA2 and CCA3, the phytoplankton composition was correlated with NH_4 and Si, whereas water salinity was an additional correlative parameter in CCA3. This could be elucidated with the annual variation in the terrestrial-sourced nutrients in CCA2 and with layered waters inducing difference in both nutrients and salinity in CCA3 (Table 5). This annual difference reflects abundances of the diatom/dinoflagellate ratio (Fig. 5c). This discrimination in the CCA was significantly confirmed by the Monte Carlo test at $p < 0.05$ (F: 15.85, p: 0.0020 for the first canonical axis and F: 4.63, p: 0.0020 for all canonical axes).

Discussion

Species composition

From 1987, when phytoplankton studies first started on the Turkish coast of the Black Sea, to 2014, a total of 257 diatom species belonging to 99 genera, 233 dinoflagellate species belonging to 63 genera, and 58 species outside these groups were recorded, making a total of 548 species. A total of 91 species belonging to the diatom group and 85 species belonging to the dinoflagellate group were recorded only once during all phytoplankton studies in the southern Black Sea until 2014. Fifty-six genera belonging to the diatom group and 35 genera belonging to the dinoflagellate group were represented by only one species. The genera belonging to the diatom group, *Chaetoceros* (43 species), *Coscinodiscus* (14 species), *Thalassiosira* (12 species), *Nitzschia* (10 species), and *Pseudo-nitzschia* (8 species), constituted approximately 34% of the total diatom species. Genera belonging to the dinoflagellate group, *Protoperidinium* (45 species), *Tripos* (31 species), *Dinophysis* (20 species), *Prorocentrum* (17 species), *Gonyaulax* (14 species), *Gymnodinium* (9 species), and *Gyrodinium* (9 species), dominated 62% of the total dinoflagellate species (Benli, 1987; Karaçam & Düzgüneş, 1990; Feyzioğlu, 1990;

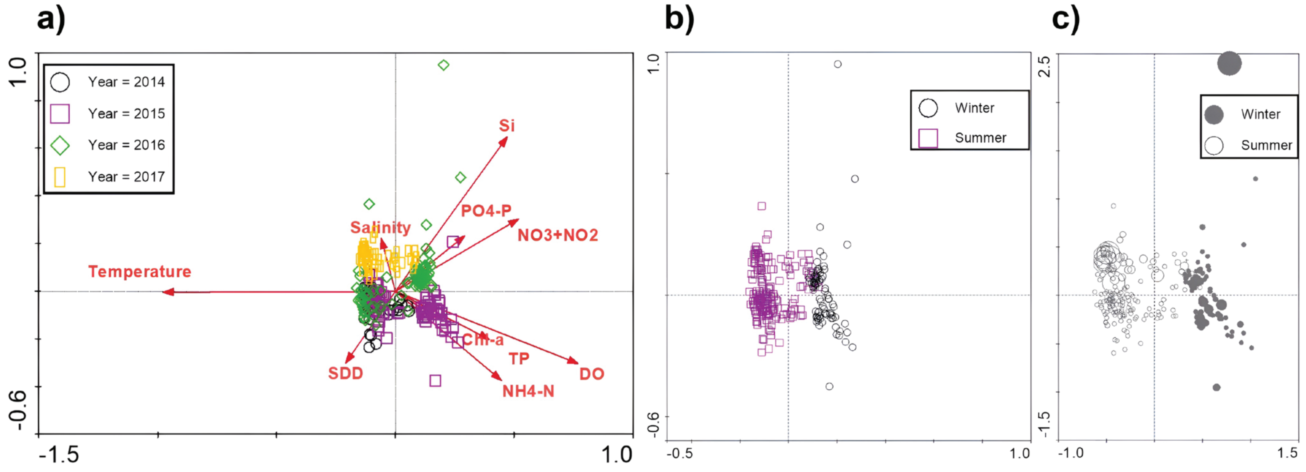

Fig. 5: Biplot of the CCA solution based on the log10-tranformed abundance of the phytoplankton at the sampling stations classified by year (a) and season (b) and correlation with environmental parameters. Ratio of abundances of diatom/dinoflagellates overlapped on the CCA plot (c).

Table 5. Results of the CCA solution based on the log10-tranformed abundance of the phytoplankton correlated with the environmental parameters.

Variables	CCA1	CCA2	CCA3
Temperature	**-0.8763**	-0.0034	0.0796
Salinity	-0.0533	0.1800	**-0.3648**
DO	**0.6892**	-0.2474	0.1002
Chl-*a*	0.1538	-0.0897	0.1910
PO_4-P	0.2622	0.1891	0.2645
TP	**0.3540**	-0.1642	0.1764
NO_3+NO_2-N	**0.4648**	0.2467	0.0501
NH_4-N	**0.3998**	**-0.3043**	**0.3583**
Si	**0.4222**	**0.5274**	**0.3393**
SDD	-0.1871	-0.2443	-0.0305
Eigen values	0.204	0.089	0.062
Species-environment correlations:	0.897	0.813	0.728
Cumulative percentage variance			
of species data	6.1	8.8	10.7
of species-environment relation:	38.3	55.0	66.6

Uysal, 1993; Bayrakdar, 1994; Feyzioğlu, 1996; Gönlügür, 1995; Eker, 1998; Türkoğlu, 1998; Uysal *et al.*, 1998; Eker-Develi & Kideys, 2003; Feyzioğlu & Seyhan, 2007; Büyükhatipoğlu *et al.*, 2002; Seyhan *et al.*, 2005; Bircan *et al.*, 2005; Soydemir, 2004; Baytut, 2004; Şahin, 2005; Taş & Okuş, 2006; Ağırbaş, 2010; Agirbas *et al.*, 2014; Balkis-Ozdelice & Anda Peynirci, 2019; Esensoy, 2014; Koca, 2014).

This study, which investigated phytoplankton assemblages along the Turkish Black Sea coast from 2014 to 2017, revealed a strong alignment with previous surveys in the region. Consistent with previous findings, the diatom species richness surpassed that of other taxonomic groups. Notably, several genera emerged as dominant contributors to the phytoplankton community, including *Chaetoceros*, *Thalassiosira,* and *Coscinodiscus* among diatoms and *Protoperidinium*, *Dinophysis*, *Tripos*, *Prorocentrum*, and *Gonyaulax* among dinoflagellates. This study further enriched the species list of the Turkish Black Sea phytoplankton by reporting 14 first records: *Achnanthes armillaris*, *Entomoneis alata*, *Gyrosigma fasciola*, *Halamphora holsatica*, *Lennoxia faveolata*, *Planktoniella sol*, *Dinophysis amandula*, *Dinophysis cuneiformis*, *Dinophysis vertex*, *Gyrodinium fusus*, *Karenia mikimotoi*, *Protoperidinium latidorsale*, *Pyrocystis robusta*, and *Torodinium robustum*.

Prior to the 2000s, approximately 800 phytoplankton species were documented in the Black Sea (Sorokin, 2002). After this period, a surge in research activities has paralleled a rapid increase in species identification. Consequently, recent estimations by the BSPC Editorial Board (2013) suggest a revised total of approximately 1,700 phytoplankton species residing in the Black Sea. Interestingly, the data revealed comparatively lower species diversity in the southern region, encompassing the Turkish coastlines. This discrepancy may be due to the earlier initiation of monitoring and research efforts in other areas of the Black Sea compared to the south, contributing to a more comprehensive historical record of biodiversity in these regions.

Abundance and biomass

It is challenging to make a direct comparison between the current study and other studies conducted on the Turkish coast of the Black Sea in terms of both abundance and biomass. While abundance has been a calculated parameter in many previous studies, the small scale of these studies, their short-term duration, and the fact that they were conducted in different seasons and utilized different methodologies make it difficult to compare abundance data. Furthermore, while several researchers have calculated biomass in recent years (Büyükhatipoğlu *et al.*, 2002; Eker-Develi & Kideys, 2003; Soydemir, 2004; Bircan *et al.*, 2005), it was either not calculated or was based on pigment content in previous studies (Agirbas *et al.*, 2014; Koca, 2014).

Eker *et al.* (1999) found that abundance and biomass values were lower in March-April than October 1995. Values for the northwestern region were higher than those for the southerly regions, possibly due to the influence of the Danube River. In March-April, dinoflagellates were the most important groups, whereas in October, diatoms and coccolithophores were dominant. Nanophytoplankton constituted a higher percentage of the total abundance and a lower percentage of the total biomass in spring than in fall.

The study of the net phytoplankton abundance in the southern Black Sea during spring revealed several key findings. Diatoms are the predominant phytoplankton group in terms of cell abundance, comprising about 70%

of the total abundance of all species. Dinoflagellates form the second major group, contributing about 22% of the total abundance of all species. Net phytoplankton (species > 55 µm) was observed to be more abundant in the southwestern sector, particularly near the mouths of Bosporus and Sakarya rivers. The spatial distribution indicated the presence of four distinct patches along the coast, with differences in species number and diversity. The study also found notable differences in phytoplankton abundance and species distribution between the western and eastern regions of the Black Sea during the spring (Uysal, 2002).

Eker-Develi & Kideys (2003) reported that average total phytoplankton abundance and biomass varied across seasons, with higher values in the fall and spring of 1998 compared to the summer of 1996. The most abundant species was the coccolithophorid *Emiliania huxleyi*, with its contribution to the total abundance ranging from 43% to 73% across seasons. Diatoms were the dominant species in terms of biomass in spring and fall, whereas dinoflagellates were dominant in summer. The dominant species showed remarkable similarities between the western and eastern regions of the southern Black Sea, suggesting the transport of phytoplankton within the basin.

The phytoplankton community in the Black Sea has changed significantly since the early 1990s. Diatoms, which comprised 60–80% of the total phytoplankton biomass between 1970 and 1990, decreased to 15–25% after 1995. This decline was accompanied by an increase in dinoflagellates and phytoflagellates. Coccolithophorids became the dominant group in the community during May-June, while dinoflagellates decreased from 60–80% to 15–25% during the same period (Mikaelyan, 2008).

Research conducted by Silkin *et al.* (2021) provides valuable information regarding the makeup and prevalence of phytoplankton in the Black Sea. According to their findings, coccolithophores, small flagellates, and diatoms play a significant role in determining the abundance of phytoplankton, while diatoms, coccolithophores, and dinoflagellates are responsible for determining the total biomass in the northeastern Black Sea. The annual dynamics of phytoplankton follow a pattern of small diatoms in spring, coccolithophores in late spring and early summer, and large diatoms in summer and fall. This pattern was also observed in previous decades.

The results of this study are consistent with those of previous studies performed in Türkiye and other areas of the Black Sea in terms of abundance and biomass values. However, it should be noted that this study was conducted during both winter and summer, and as a result, the dominance of *Emiliania huxleyi* on the total phytoplankton abundance was not observed in comparison to other studies, except for the summer of 2014.

Dominant species

The degree of similarity between the studies conducted in the Turkish coasts of the Black Sea in terms of the dominant species is remarkably high, both among themselves and in relation to this study. Species such as *Cylindrotheca closterium*, *Dactyliosolen fragilissimus*, *Ditylum brightwellii*, and *Proboscia alata* are particularly prevalent during spring (Benli, 1987; Uysal & Sur, 1995; Feyzioğlu, 1996; Eker-Develi& Kideys, 2003; Agirbas *et al.*, 2015). Similarly, during spring and winter, species belonging to the *Pseudo-nitzschia* genus (Türkoğlu & Koray, 2002; Uysal, 2002; Agirbas *et al.*, 2015) were observed. Species of the *Chatoceros* genus were primarily observed during the winter period, whereas *Pseudosolenia calcar-avis*, *Rhizosolenia styliformis*, and *Thalassionema nitzschioides* were observed during each season, albeit in different years (Benli, 1987; Uysal & Sur, 1995; Feyzioğlu, 1996; Uysal, 2002; Türkoğlu & Koray, 2002; Eker-Develi & Kideys, 2003; Agirbas *et al.*, 2015). Among dinoflagellates, species belonging to the *Dinophysis*, *Prorocentrum*, and *Tripos* genera, as well as *Kryptoperidinium triquetrum* and *Scrippsiella acuminata*, have been reported to be particularly dominant, especially during the summer (Benli, 1987; Feyzioğlu, 1996; Eker *et al.*, 1999; Türkoğlu & Koray, 2002; Agirbas *et al.*, 2015; Balkis-Ozdelice & Anda Peynirci, 2019). Furthermore, the coccolithophore *Emiliania huxleyi* was found to be highly dominant in terms of abundance, particularly during the fall and spring seasons (Benli, 1987; Feyzioğlu, 1990, 1996; Eker *et al.*, 1999; Türkoğlu & Koray, 2002; Eker-Develi & Kideys, 2003; Agirbas *et al.*, 2017).

The northwestern part of the Black Sea experiences three peaks in the annual dynamics of dominant species abundance and biomass: one in spring dominated by diatoms (*Skeletonema costatum*, *Thalassiosira* spp.), one in early summer dominated by dinoflagellates (*Prorocentrum cordatum*), and the highest one in fall due to diatoms (*Cerataulina pelagica*, *Pseudo-nitzschia* spp., *Leptocylindrus danicus*) and dinoflagellates (*Prorocentrum cordatum*, *Linglodinium polyedra*) (Mikaelyan, 2008; Nesterova *et al.*, 2008).

On the northeastern shelf, winter begins with dominance of small diatoms (*Pseudo-nitzschia* spp., *Skeletonema costatum*, *Dactyliosolen fragilissimus*, *Cerataulina pelagica*, *Hemiaulus hauckii*, and *Chaetoceros* spp.) and nanophytoplankton flagellates. The spring peak of phytoplankton diversity and abundance occurs in spring, with large diatoms (*Pseudosolenia calcar avis*, *Proboscia alata*) and heterotrophic dinoflagellates dominating the community abundance and biomass. The diversity and abundance decreased in May-June, except for cases of coccolithophore (*Emiliania huxleyi*) proliferation or re-intensified growth of specific diatom (*Pseudo-nitzschia* spp., *Thalassiosira* spp.) populations. The most intensive and longest period of phytoplankton growth and maximum diversity occurs in spring, culminating in summer when dinoflagellates (*Dinophysis* spp., *Kryptoperidinium triquetrum*, *Prorocentrum* spp., *Tripos* spp. and *Scrippsiella acuminata*) dominate the phytoplankton abundance (Nesterova *et al.*, 2008; Moncheva *et al.*, 2019).

Potentially toxic (harmful and bloom-forming) species

According to Benli (1987), *Pseudosolenia calcar-avis* blooms occur in the southern Black Sea region. Uysal & Sur (1995) reported that *Chateceros* sp. constituted 90% of the total phytoplankton abundance, with species exceeding 1 million cells/L. In a study conducted in the southeastern Black Sea region, Feyzioğlu (1996) reported excessive reproduction of *Cylindrotheca closterium*, *Pseudosolenia calcar-avis*, and harmful *Scrippsiella acuminata*. In their study in the western and eastern Black Sea, Eker *et al.* (1999) reported that the harmful *Scrippsiella acuminata* species dominated the phytoplankton abundance in spring, while *Pseudosolenia calcar-avis* and *Emiliania huxleyi* species dominated in fall. Uysal (2002) reported that the toxic *Pseudo-nitzschia seriata* species, along with *Thalassiosira decipiens* and *T. fallax*, constituted 70% of the total abundance. Eker-Develi & Kideys (2003) found that the *Emiliania huxleyi* species dominated 73% of the total phytoplankton abundance in the fall period, while *Pseudosolenia calcar-avis* species constituted 73% of the total biomass value in the same period in the southern Black Sea region. They also reported that *Proboscia alata* constituted 97% of the total biomass in spring. Turkoglu & Koray (2004) recorded the blooming of 17 species in a study conducted in the Sinop region (central southern Black Sea). Eleven of these cells reached 1 million cells/L. *Pseudo-nitzschia delicatissima* was reported as the species reaching the highest bloom concentration (with 9.0×10^7 cell L^{-1}). Agirbas *et al.* (2014) reported that 50% of the total abundance in the southeastern Black Sea was dominated by *Emiliania huxleyi*.

Upon analyzing all studies conducted in the southern Black Sea region, it is evident that the majority of the 44 potentially toxic species identified in this study have been documented in previous research. It is accurate to assert that these species have been present in the southern Black Sea historically and currently, displaying a high level of adaptation to the region's environmental conditions. Their ability to proliferate easily was further illustrated by their dominance over both total abundance and biomass.

Phytoplankton–environment interactions

The present study's analysis of Black Sea environmental parameters, including seasonal changes and the extreme winter of 2015, shows a striking interplay between local dynamics and large-scale atmospheric effects. While seasonal patterns determine the overall rhythm of the ecosystem, with warm summers favoring high oxygen levels and cold winters increasing nutrient availability, 2015 was a clear outlier. Mikaelyan *et al.* (2018), who investigated the annual succession of phytoplankton in the open waters of the Black Sea based on a database covering 30 years from 1985 to 2014, did not assess 2015 as a cold period. This discrepancy could be attributed to variations in sea surface temperatures between coastal and open waters, influenced by different coastal factors such as the early melting of snow in the southern Black Sea. This unusual winter, characterized by records of low temperatures, elevated nutrient concentrations, and a surprising dominance of diatoms, appears to be closely related to the prevailing state of the North Atlantic Oscillation (NAO). Mikaelyan *et al.* (2018) noted a strong positive trend in winter sea air temperature (SAT) and sea surface temperature (SST) observed over the last 25 years, leading to a decrease in the frequency of cold winters from 30% to 15%.

Çokacar (2023) reported that positive NAO phases are associated with colder-than-average winter temperatures in the Black Sea. The observed synchronicity between the extreme winter of 2015 and the strong positive NAO phase lends credence to the notion that large-scale climatic patterns may exert significant control over the winter symphony in the Black Sea. This aligns with research by Oguz *et al.* (2006), highlighting the tendency for colder Black Sea winters associated with positive NAO phases to witness increased nutrient upwelling and subsequent phytoplankton blooms.

Pseudo-nitzschia delicatissima played an important role in differentiating the 2015 and 2017 populations, highlighting the ecological impacts of annual changes in phytoplankton communities. The winter community showed significant differences over the sampling years, suggesting greater adaptability to environmental fluctuations than the summer community, which showed significant annual fluctuations. This is consistent with previous research that highlighted the stabilizing effects of cold winter temperatures and potentially higher nutrient availability (Nesterova *et al.*, 2008). The diatom/dinoflagellate ratio further highlighted changes during summer, with a major shift in diatom dominance in 2017. This finding may reflect the environmental conditions, as the diatoms may have utilized available nutrients more effectively during the sampling period compared to previous summer sampling periods, possibly related to changes in nutrient ratios or light availability (Moncheva *et al.*, 2019).

Overall, this study highlights multiple drivers of phytoplankton dynamics, with both seasonal and interannual variability influencing the community composition. Further research focusing on the specific environmental drivers behind the observed changes, particularly the unique conditions in 2015 and factors affecting diatom dominance in 2017, will be crucial for predicting future phytoplankton trajectories and ensuring the sustainable management of the ecosystem.

Uysal (2002) and Agirbas *et al.* (2017) also emphasized the significant variations in Black Sea phytoplankton communities based on seasonal patterns, wherein the winter and summer communities differ due to alterations in temperature, light, and nutrient availability. The findings of this study, which demonstrate the correlation between phytoplankton composition, water temperature, and dissolved oxygen, are corroborated by research conducted by Nesterova *et al.* (2008) and Seyhan *et al.* (2005), who also emphasized the influential role of these factors in the reproduction and succession patterns of phytoplankton. In a similar vein, the Black Sea literature has already established the significance of nutrients (Eker-Develi & Kideys, 2003; Agirbas *et al.*, 2015), particularly Si and NH_4 (Oguz *et al.*, 2006; Moncheva *et al.*, 2019), in shaping phytoplankton communities, especially diatoms (Uysal, 2002). This study aligns with existing knowledge on the dynamics of Black Sea phytoplankton and highlights the important role of seasonality, temperature, oxygen, and nutrients on phytoplankton assemblages.

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Supplementary Material

The following supplementary material is available for this article:

Table S1. Information on phytoplankton sampling stations and sampling depths.

Table S2. Sampling methods utilized for different parameters.

Table S3. Measurement and analysis methods utilized for different parameters.

Table S4. The physicochemical parameters were examined at stations during the period of 2014 to 2017.

Table S5. Phytoplankton species identified during the 2014-2017 sampling period.

Table S6. Frequency values of species observed "constantly" at stations and between seasons, according to the results of frequency index analysis.

Table S7. The relative contributions of dominant species to the total abundance and group abundances at the surface, chlorophyll maximum depth, and in the water column (S: Summer, W: Winter, Blue highlighted: Species only in surface layer, Yellow highlighted: Species only in Chl-Max layer).

Table S8. Dominance values (*Y*) of the dominant phytoplankton species (S: Summer, W: Winter).

Table S9. The list of species with abundance value exceeding 10.000 cell/L threshold (St: Number of stations, L: Layer, MA: Maximum abundance (cell L^{-1}), S: Surface, B: Bottom, C: Chlorophyll-*a* maximum).

Table S10. Three-way PerMANOVA testing significance of the phytoplankton composition and abundance among years (fixed), seasons (fixed) and layers (fixed). Triangle matrix of Bray-Curtis similarity index solving $\log_{10}$(abundance+1) was subjected to PerMANOVA. Bold P values (P(perm): P value of PerMANOVA, and P(MC): Monte Carlo test) denote that the difference was significant at $p < 0.05$. PerMANOVA solution was iterated 999 times. The df is degrees of freedom.

Table S11. SIMPER analysis to determine the contributor species in season. Avg. Sim: Average similarity in season, Av. Abn: log10-averaged abundance, Av. Sim, average similarity of the species, Sim/SD: average similarity/standard deviation of similarity for the species, Cum%: cumulative percent contribution in similarity in season. * is contributor species in season.

Table S12. SIMPER analysis to determine the discriminator species in pairwise seasons. Avg. Dis.: Average dissimilarity between pairwise seasons, Av. Abn: log10-average abundance for pairwise seasons, Av. Diss, average dissimilarity of the species, Diss/SD: average dissimilarity/standard deviation of similarity for the species, Cum%: cumulative percent contribution in dissimilarity between seasons. * is discriminator species between seasons.

Table S13. SIMPER analysis to determine the contributor species in years. Avg. Sim: Average similarity in year, Av. Abn: log10-averaged abundance, Av. Sim, average similarity of the species, Sim/SD: average similarity/standard deviation of similarity for the species, Cum%: cumulative percent contribution in similarity in year. * is contributor species in year.

Table S14. SIMPER analysis to determine the discriminator species in pairwise years. Avg. Dis.: Average dissimilarity between pairwise years, Av. Abn: log10-average abundance for pairwise years, Av. Diss, average dissimilarity of the species, Diss/SD: average dissimilarity/standard deviation of similarity for the species, Cum%: cumulative percent contribution in dissimilarity between years. * is discriminator species between years.

Fig. S1: Ratio of diatom to dinoflagellates abundance overlapping on nMDS configuration (given in Fig 4).