Research Article

Seasonal changes of potentially toxic epiphytic dinoflagellates in Chabahar Bay, Oman Sea

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Abstract

Harmful algal blooms caused by dinoflagellates have significant adverse effects on environmental and public health. This study aimed to investigate the effect of water physicochemical parameters on the annual cycle of epiphytic dinoflagellates in the northern Chabahar Bay coastal waters of the Oman Sea (Iran). The macroalgal samples with associated epiphytes were collected seasonally from 6 coastal sites in spring, summer, atumn 2019 and winter 2020. The water physicochemical parameters were measured, and the data were analyzed using a one-way ANOVA and the principal component analysis (PCA). Twelve potentially toxic dinoflagellate species from five genera were identified during the four sampling seasons. *Amphidinium carterae* with an average of 11.22% and *A. operculatum* with an average of 10.77% of the total abundance of epiphytic dinoflagellates were the dominant species, and *Gambierdiscus australes* showed an average of 6.48%. Based on the PCA, the abundance of certain species was found to be influenced by different environmental factors. The PCA revealed that NO_2, NO_3 and SiO_4 values had the greatest impact at sites with high abundances of *A. operculatum*, *Prorocentrum concavum*, *P. emarginatum*, *P. rhathymum* and *G. balechii*. Furthermore, PO_4 concentration had the greatest impact at the sites with high abundances of *A. carterae*, *P. lima*, *Ostreopsis lenticularis*, *O. heptagona*, *G. balechii*, *G. toxicus*, *G. australes* and *Coolia monotis*. The results obtained highlighted a significant impact of dissolved oxygen, pH, salinity, temperature and nutrients on the epiphytic dinoflagellate species abundances in the study area.

Keywords: Epiphytic Dinoflagellates, Microphytobenthos, Annual Cycle, HABs, Harmful Algal Blooms, Red tide

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Introduction

Epiphytic microalgae are organisms attached to or associated with seaweeds (macroalgae and seagrasses) and growing on their surface. Seaweeds are suitable substrates for the attachment and growth of microalgae in coastal waters (Murphy *et al.*, 2013). Different species of microalgae occupy different habitats based on depth, wave exposure, coastal beds, and other environmental factors. The dynamics, abundance, and community structure of epiphytic microalgae are affected by biotic factors such as age, host seasonal cycle, growth cycle pressure by herbivores, as well as by abiotic factors such as light, temperature, nutrients, and water movement (Sales and Ballesteros, 2009; Lewis *et al.*, 2020; Durán-Riveroll *et al.*, 2023). Epiphytic dinoflagellates, a taxonomic group that contains the majority of toxic species among marine algae, are mostly found in tropical and subtropical regions (Aligizaki *et al.*, 2011; Stanca and Parsons, 2021). Several factors, such as temperature increase, lack of air circulation and rainfall, and enrichment of coastal waters due to sewage and pesticides, may cause harmful algal blooms (HAB) (Enriquez *et al.*, 2010; Hayashida *et al.*, 2020; Cembella *et al.*, 2021) resulting in mortality of invertebrates, fish, and mammals and in acute human poisoning. Recently, different types of algal blooms caused by dinoflagellates have occurred in the south of Iran. For example, *Noctiluca scintillans* (Macartney) Kofoid et Swezy have bloomed mainly after oil spills; the seasonal algal bloom caused by this species is periodically seen in Chabahar waters (Bahri, 2018; Asefi and Attaran-Fariman, 2023). Ershadifar *et al.* (2020) investigated the response of phytoplankton assemblages to variations in environmental parameters in Chabahar Bay, the Northeast of the Oman Sea, the Southeast of Iran. They specifically focused on HAB and coastal hypoxia. Jalili *et al.* (2022) examined short-term variations of phytoplankton communities in response to a *Noctiluca scintillans* bloom in Chabahar Bay. Asefi and Attaran-Fariman (2023) reported a *Noctiluca scintillans* bloom in the southeastern coastal waters of Iran. *Margalefidinium polykrikoides* (Margalef) Gómez, Richlen and Anderson (2017) (= *Cocholodinium polykrikoides* Margalef) is the main species in the neighboring Persian Gulf that causes toxic blooms (Zarshenas *et al.*, 2015). Additionally, *Prorocentrum* Ehrenberg is one of the dominant dinoflagellate genera that contributes to algal blooms and causes mortality of marine fauna. Overall, HAB can cause different syndromes such as paralytic shellfish poisoning (PSP), neurotoxic shellfish poisoning (NSP), ciguatera fish poisoning (CFP), amnesic shellfish poisoning (ASP), and diarrhetic shellfish poisoning(DSP). These human intoxications are produced by various toxins, such as saxitoxin, brevetoxin, dinophysistoxin, ciguatoxin, domoic acid and their analogs. They can cause diarrhea, vomiting, dizziness, and even death of the patient (Van Dolah *et al.*, 2002). Therefore, it is necessary to

investigate the relationship between environmental factors and microalgal assemblages. To date, in Iran and other countries, various studies on different aspects of benthic HAB and epibenthic/epiphytic dinoflagellate assemblages have been conducted (Maso and Garcés, 2006; Kim *et al*., 2011; Makaremi *et al*., 2011; Dhib *et al*., 2013; Okolodkov *et al*., 2014; Zarshenas *et al*., 2015; Akbarzadeh *et al*., 2017; Aquino-Cruz and Okolodkov, 2016; Adam *et al*., 2017; Al-Handal *et al*., 2018; Wilken *et al*., 2018; Isles and Pomati, 2021; Asefi *et al*., 2023; Dai *et al*., 2023). Due to the importance of this issue, this study aims to investigate the effect of physicochemical factors on the annual cycle of epiphytic dinoflagellate assemblage in Chabahar Bay.

Material and methods

Study area

Chabahar Bay is located in an area characterized by hot arid summers and short dry winters. The air temperature usually varies between 16°C and 37°C; it is rarely below 12°C (down to 7°C) or above 40°C (up to 47°C). The climate, in general, is hot and humid, influenced by summer and winter monsoon systems from the Indian subcontinent (Armanfar *et al.*, 2019). Four seasons are distinguished during a calendar year: spring, summer, autumn, and winter. The tidal range in the bay is about 2 m. Station 1(ST1) located in Abshirikon with the sandy mud substrate, station 2(ST2) in Tis region with the sandy rock substrate, station 3(ST3) in Lipar zone with the rock substrate, station 4 (ST4)

is in Shilate coast with the sandy substrate, station 5 (ST5) in the Daryakochic coast with the sandy substrate and station 6 (ST6) in Daryabozorg coast with the rock substrate.

Sampling and in situ measurements

Samples were taken seasonally (four samplings) in low tide from spring (15 May, 2019), Summer (15 Agust, 2019), atumn (15 November, 2019) to winter (15, March, 2020) at six coastal sites in Chabahar Bay (Fig. 1). The macroalgal samples with associated microalgal epiphytes with three replicates were collected by hand all macroalgae samples from each replicate placed in three 250 ml plastic flasks with surrounding seawater and fixed with stock formaldehyde to a final concentration of 4% and then transported to the laboratory. Water temperature was recorded *in situ* with a thermometer, pH was measured with a WTW portable pH meter, model LF 320 (Weilheil, Germany), and salinity was measured with an ATAGO MASTER-S/MillM (Japan) refractometer.

Laboratory analyses

The samples were shaken vigorously in the flask for 1 min. To separate the attached epiphytic microalgae, they were filtered through 500 µm mesh. The macroalgae were then washed twice with 100 ml of 0.2-µm filtered seawater to recover the maximum amount of microalgae and then weighed (Hachani *et al*., 2018). The water samples for determination of physicochemical parameters were collected in 500 ml plastic flasks.
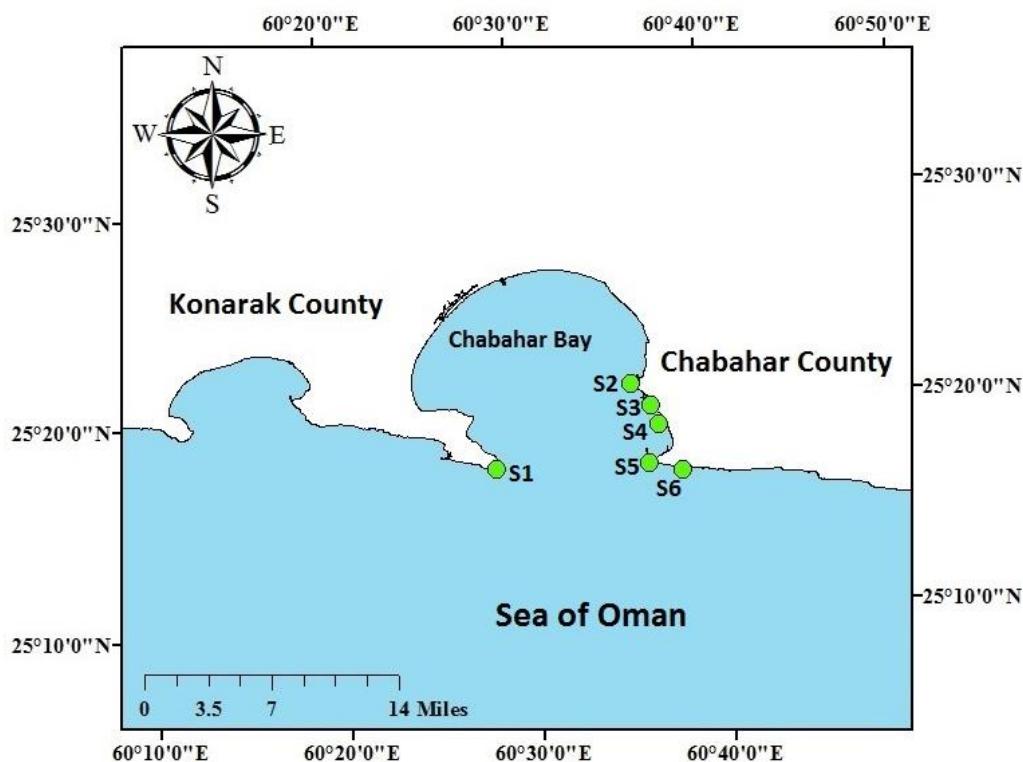
Figure 1: Study area and sampling sites (green-filled circles) of epiphytic dinoflagellates in Chabahar Bay, the Sea of Oman (2019-2020) (S: Station).

Inorganic nutrients (nitrites – NO_2, nitrates – NO_3, orthophosphates – PO_4 and silicates – SiO_4) were determined using a Bran+Luebbe GmbH continuous-flow AutoAnalyzer III (Norderstedt, Germany) with a UV-vis spectrophotometer (JENWAY 6705) (APHA, 2005). Data on meteorological parameters were obtained from specialized weather forecasting websites (www.wunderground.com and www.worldweatheronline.com), and the geographical characteristics of each sampling site were determined using a GPS. The samples were kept in the dark for 14 days to allow sedimentation. The upper layer of water was carefully decanted using a siphon, and the samples were then centrifuged in several steps (Willén, 2000). A 1-ml Sedgewick-Rafter counting chamber, an inverted

Ceti microscope (Belgium) and KE Review imaging software, version 3.71-ml were used. The counted cells were reported as cells/g of macroalgae fresh weight. The identification of dinoflagellate species was carried out using specialized literature (Faust and Gulledge, 2002; Hallegraeff *et al*., 2004).

Statistical analyses
The normality of data was confirmed using the Kolmogorov-Smirnov test, and a one-way analysis of variance (ANOVA) was performed to determine significant differences between treatments. Duncan's test was used to compare means at a significance level of 0.05. Additionally, the impact of physical and chemical parameters on the abundance of phytoplankton was

evaluated using the PCA analysis in the PAST software version 2.13.

Results

Epiphytic dinoflagellate assemblages
In 2019-2020, at six sites in Chabahar Bay, a total of twelve potentially toxic epiphytic dinoflagellate species from five genera (*Amphidinium* Claparède et Lachmann, *Coolia* Meunier, *Gambierdiscus* Adachi et Fukuyo, *Ostreopsis* Johs. Schmidt and *Prorocentrum* Ehrenberg) were identified during the four sampling seasons. The genera *Prorocentrum* (4 species) and *Coolia* (1 species) had the highest and the lowest number of identified species, respectively. Twelve were observed in spring, autumn, and winter, while eleven were observed in summer. The identified seasonal abundance of phytoplankton showed significant differences between the abundance of *Amphidinium carterae*, *Amphidinium operculatum*, *Ostreopsis heptagona*, and *Gambierdiscus australes*, while no significant differences were observed between the abundance of other species ($p<0.05$). *Amphidinium operculatum* (3.13%) had the highest percentage in spring, *Prorocentrum lima* (83.14%) had the highest percentage in summer, *Ostreopsis lenticularis* (4.10%) had the highest percentage in autumn, and *Amphidinium carterae* (95.12%) had the highest percentage in winter (Figs. 2 and 3). The genera *Prorocentrum* and *Coolia* had the highest and lowest percentages of abundance during all four seasons (Figs. 4 and 5) (Table 1 to 5).

Physicochemical variables
The seasonal averages of the measured physicochemical variables in Chabahar Bay in 2019-2020 are shown in Table 6. The results showed that only the seasonal average of salinity in summer and spring had a significant difference between them ($p<0.05$), and no significant differences were observed between the values of the physicochemical parameters in different seasons ($p>0.05$).

PCA between environmental factors and the phytoplankton abundance
Based on the PCA test results in components 1 and 2, dissolved oxygen (DO), pH, and salinity had the greatest impact at stations; ST4, ST6 in spring, ST6 in summer, ST2 and ST3 in autumn, ST2 and ST4 in winter the highest abundances of *A. operculatum*, *P. concavum*, *P. emarginatum*, *P. rhathymum* and *O. lenticularis*. Additionally, temperature had the greatest impact at stations; ST3 and ST4 in atumn and ST6 in winter with the highest abundances of *A. carterae*, *P. lima*, *O. heptagona*, *G. balechii*, *G. toxicus*, *G. australes* and *C. monotis* in components 3 and 4 (Fig. 6).
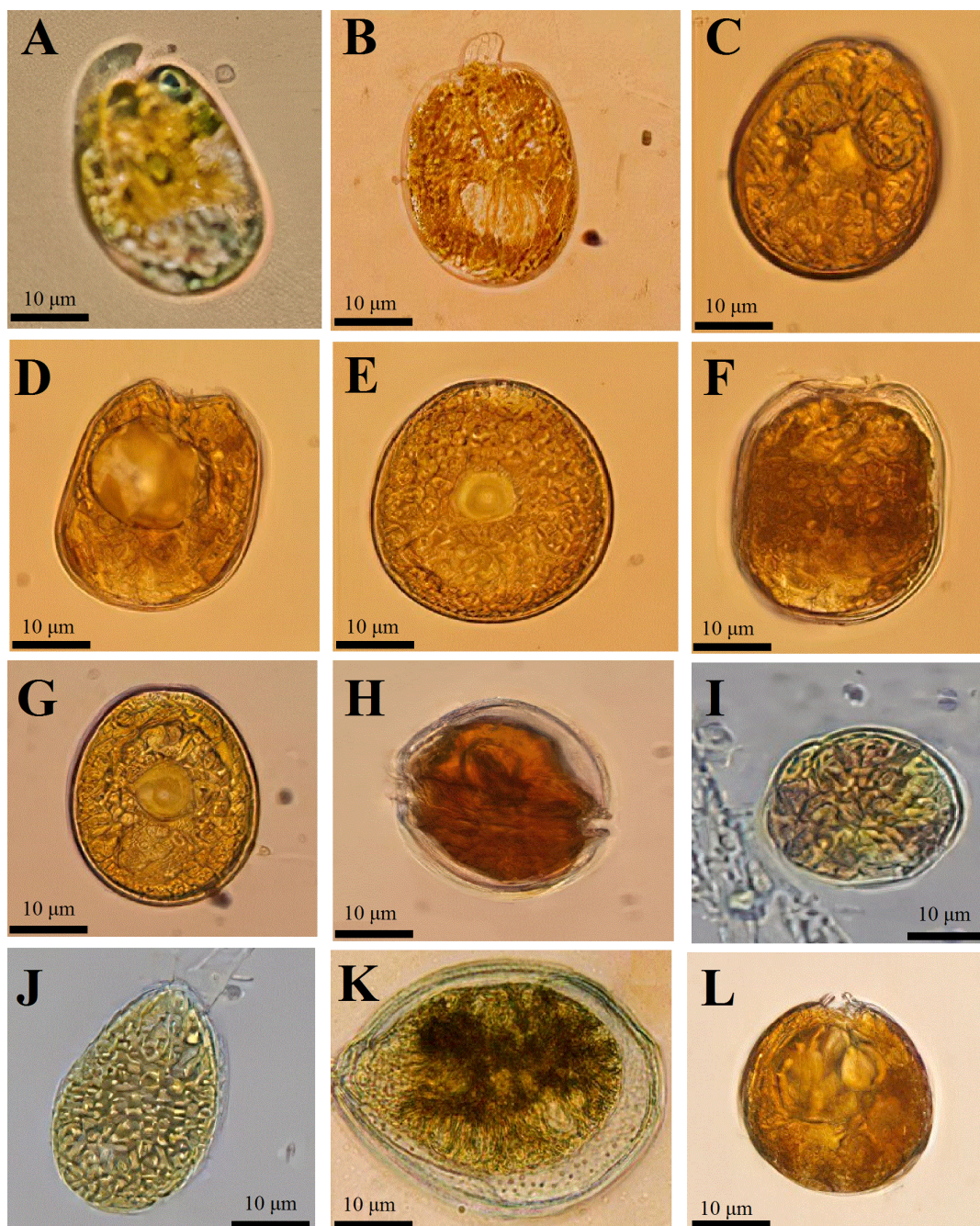
Figure 2: Potentially toxic dinoflagellates in Chabahar Bay in 2019-2020; A: Amphidinium carterae; B: A. operculatum ; C: Prorocentrum concavum; D and F: P. emarginatum; E: P. rhathymum G: P. lima; H: Gambierdiscus toxicus; I: G. australes; J: Ostreopsis heptagona; K: O. lenticularis; L: Coolia monotis.

PCA between nutrients and phytoplankton abundance

Based on the PCA test results, NO_2, NO_3 and SiO_4 had the greatest impact at stations in different season with the highest abundances of *A. operculatum*, *P. concavum*, *P. emarginatum*, *P.*

rhathymum, and *G. balechii*. Additionally, PO_4 had the greatest impact at stations in different seasons with the highest abundances of *A. carterae*, *P. lima*, *O. lenticularis*, *O. heptagona*, *G. balechii*, *G. toxicus*, *G. australes*, and *C. monotis* (Fig. 7).
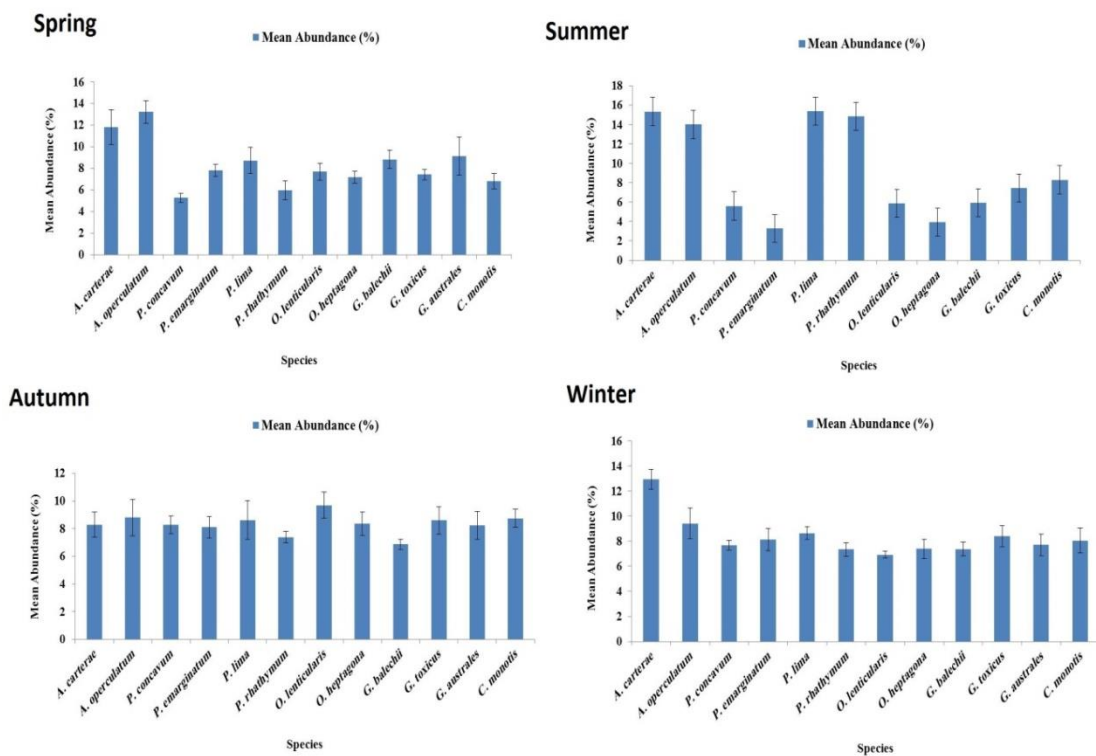
Figure 3: Abundance (%) of the total dinoflagellate of potentially toxic epiphytic dinoflagellates in Chabahar Bay, 2019-2020.
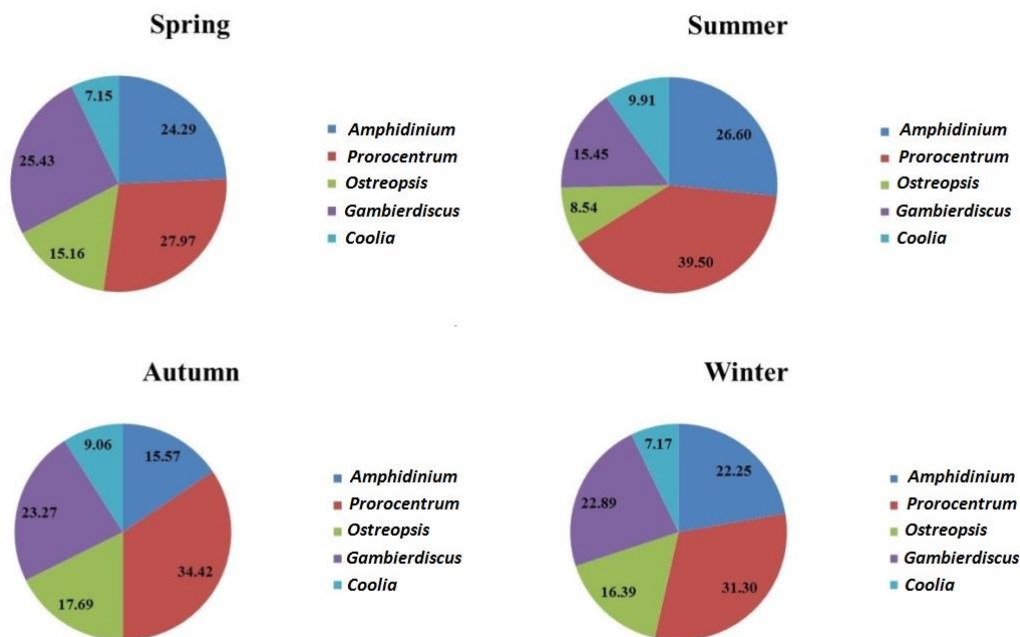
Figure 4: Abundance (%) of the potentially toxic epiphytic dinoflagellate genera in Chabahar Bay, 2019-2020.
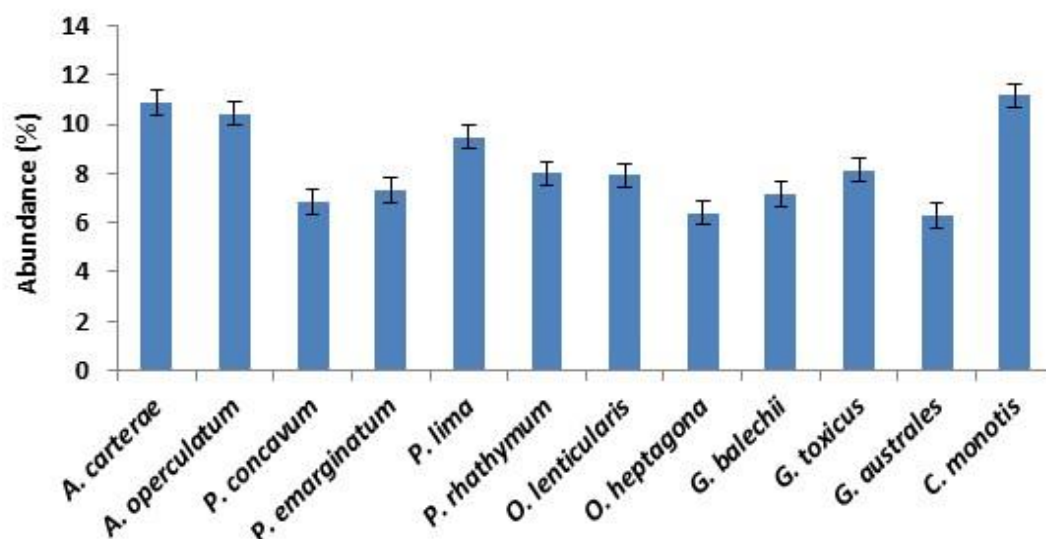
Figure 5: **Average abundance (%) of the total dinoflagellate of potentially toxic epiphytic dinoflagellates in Chabahar Bay, 2019-2020.**

Table 1: Species composition and cell abundances (mean ± standard error; cells g^{-1}) of potentially toxic dinoflagellates at six sampling sites/stations in Chabahar Bay, the Sea of Oman Sea (2019-2020) in spring.

Species	Station 1	Station 2	Station 3	Station 4	Station 5	Station 6
Amphidinium carterae (Hulburt, 1957)	10.79±4.67	5.60±2.08	14.24±7.12	11.79±0	4.65±0	8.47±3.60
Amphidinium operculatum (Claparède and Lachmann, 1859)	10.79±0	5.60±2.08	7.12±0	19.66±6.80	10.85±2.60	10.25±2.60
Prorocentrum concavum (Fukuyo, 1981)	5.40±4.04	1.87±1.06	4.12±2.37	7.86±6.80	2.60±1.55	4.47±3.60
Prorocentrum emarginatum (Fukuyo, 1981)	6.74±2.33	1.87±1.06	7.12±0	11.79±0	6.20±2.60	6.35±0
Prorocentrum lima (Stein, 1878)	9.44±2.33	4.67±3.23	7.12±0	7.86±6.80	6.20±2.60	4.23±3.60
Prorocentrum rhathymum Loeblich III *et al.*, 1979)	4.04±2.33	1.06±0.93	4.12±2.37	11.79±0	4.65±0	6.35±6.35
Ostreopsis lenticularis (Fukuyo,1981)	5.40±0	3.73±1.06	7.12±0	11.79±0	3.20±2.60	6.35±0
Ostreopsis heptagona (Norris *et al.*, 1985)	5.40±0	1.87±1.06	7.12±0	11.79±0	4.65±0	6.35±0
Gambierdiscus balechii (Fraga *et a*l., 2016)	5.40±0	4.67±3.23	7.12±0	11.79±0	6.20±0	6.35±0
Gambierdiscus toxicus (Adachi *et al.*, 1979)	6.74±2.33	2.80±0	7.12±0	11.79±0	4.65±0	4.23±3.60
Gambierdiscus australes (Chinain and Faust,1999)	6.74±2.33	1.06±0.93	7.12±0	11.79±0	11.60±3.20	8.23±3.60
Coolia monotis (Meunier, 1919)	4.05±2.33	1.87±1.06	7.12±0	11.79±0	6.20±0	4.23±3.60

Table 2: Species composition and cell abundances (mean ± standard deviation; cells g^{-1}) of potentially toxic dinoflagellates at six sampling sites/stations in Chabahar Bay (the Sea of Oman) in summer.

Species	Station 1	Station 2	Station 3	Station 4	Station 5	Station 6
Amphidinium carterae	7.60±4.23	6.33±5.49	8.60±4.63	7.6±4.59	7.84±6.60	5.35±0
Amphidinium operculatum	7.60±4.23	5.49±3.33	8.60±4.63	7.6±4.59	7.84±6.60	3.60±1.70
Prorocentrum concavum	7.60±4.23	6.33±5.49	8.60±4.63	0	0	0
Prorocentrum emarginatum	7.60±4.23	5.49±3.33	0	0	0	0
Prorocentrum lima	12.79±0	6.34±5.49	8.60±4.73	7.6±4.59	7.84±6.60	3.70±3.60
Prorocentrum rhathymum	7.60±4.23	5.49±3.33	8.60±4.63	9.11±7.6	7.84±6.60	3.70±3.60
Ostreopsis lenticularis	7.60±4.23	0	0	0	6.70±3.90	3.60±1.70
Ostreopsis heptagona	0	5.49±3.33	0	0	0	3.60±1.70
Gambierdiscus balechii	8.23±7.26	0	8.60±4.63	0	0	3.60±1.70
Gambierdiscus toxicus	7.60±4.21	5.49±3.33	8.60±4.63	0	6.70±3.80	0
Coolia monotis	7.60±4.21	6.33±5.49	9.63±8.60	0	7.74±6.60	0

Table 3: Species composition and cell abundances (mean ± standard error; cells g^{-1}) of potentially toxic dinoflagellates at six sampling sites/stations in Chabahar Bay (Oman Sea, Iran) in autumn.

Species	Station 1	Station 2	Station 3	Station 4	Station 5	Station 6
Amphidinium carterae	7.76±0	2.35±0	5.60±4.63	8.06±7.60	3.20±2.60	5.60±5.50
Amphidinium operculatum	5.33±4.49	3.60±1.7	3.75±0	8.05±7.60	4.60±4.20	7.20±3.60
Prorocentrum concavum	5.33±4.49	1.70±1.6	5.63±4.60	12.76±0	4.76±0	5.35±0
Prorocentrum emarginatum	5.33±4.49	1.70±1.6	3.76±0	16.06±7.60	4.76±0	5.35±0
Prorocentrum lima	7.76±0	1.60±0.7	3.76±0	20.14±14.60	4.76±0	3.6±3.2
Prorocentrum rhathymum	5.33±4.49	1.70±1.6	4.59±2.60	8.06±7.60	4.76±0	5.35±0
Ostreopsis lenticularis	10.04±4.49	1.60±0.7	5.63±4.60	12.76±0	4.76±0	7.20±3.60
Ostreopsis heptagona	5.80±4.49	2.80±2.49	3.76±0	8.06±7.60	6.2±2.6	5.35±0
Gambierdiscus balechii	4.49±2.33	1.60±0.7	3.76±0	8.06±7.60	4.76±0	5.35±0
Gambierdiscus toxicus	7.76±0	1.60±0.7	2.49±2.33	12.76±0	6.20±2.6	7.20±3.60
Gambierdiscus australes	4.49±2.33	2.80±2.49	3.76±0	8.06±7.60	6.80±2.6	5.35±0
Coolia monotis	7.76±0	1.60±0.7	5.63±4.60	12.76±00	4.76±0	5.35±0

Table 4: Species composition and cell abundances (mean ± standard error; cells g^{-1}) of potentially toxic dinoflagellates at six sampling sites/stations in Chabahar Bay (Oman Sea, Iran) in winter.

Species	Station 1	Station 2	Station 3	Station 4	Station 5	Station 6
Amphidinium carterae	6.22±4.6	4.63±3.6	9.5±7.4	13.49±11.8	8.6±8.06	4.5±0
Amphidinium operculatum	6.22±4.6	4.63±3.6	7.5±5.2	8.35±0	4.4±0	2.63±2.6
Prorocentrum concavum	3.63±3.6	2.76±0	4.5±0	8.35±0	4.5±0	4.5±0
Prorocentrum emarginatum	4.63±2.6	2.76±0	7.5±2.2	8.35±0	4.5±0	2.63±2.6
Prorocentrum lima	4.63±2.6	2.76±0	4.5±0	5.6±5.3	5.63±2.6	4.5±0
Prorocentrum rhathymum	2.62±2.6	2.76±0	4.5±0	8.35±0	4.5±0	4.5±0
Ostreopsis lenticularis	3.35±0	2.76±0	6.2±2.6	8.35±0	4.5±0	2.63±2.6
Ostreopsis heptagona	3.35±0	1.6±1.4	4.5±0	5.6±5.4	5.63±2.6	4.5±0
Gambierdiscus balechii	3.35±0	3.7±1.6	3.2±2.6	5.6±5.5	4.5±0	5.63±2.6
Gambierdiscus toxicus	3.63±3.6	2.76±0	4.6±4.2	5.6±5.5	4.5±0	2.6±1.4
Gambierdiscus australes	4.63±2.6	1.7±1.6	6.2±2.6	11.8±5.49	4.5±0	4.5±0
Coolia monotis	3.35±0	2.76±0	4.5±0	5.6±5.5	4.5±0	4.5±0

Table 5: Seasonal average abundance (mean ± standard error; cells g^{-1}) of potentially toxic dinoflagellates from six sampling sites in Chabahar Bay (the Sea of Oman) in 2019-2020.

Species	Spring	Summer	Autumn	Winter
Amphidinium carterae	9.26±1.38[a]	7.22±0.48[ab]	5.43±0.95[b]	7.82±1.41[ab]
Amphidinium operculatum	10.71±1.82[a]	6.79±0.77[b]	5.42±0.75[b]	5.62±0.87[b]
Prorocentrum concavum	4.39±0.79[a]	3.76±1.70[a]	5.92±1.49[a]	4.71±0.78[a]
Prorocentrum emarginatum	6.68±1.18[a]	2.18±1.41[a]	6.16±2.06[a]	5.06±0.97[a]
Prorocentrum lima	6.59±0.73[a]	7.81±1.22[a]	6.94±2.77[a]	4.60±0.43[a]
Prorocentrum rhathymum	5.34±1.34[a]	7.06±0.84[a]	4.97±0.83[a]	4.54±0.84[a]
Ostreopsis lenticularis	6.27±1.15[a]	2.98±1.44[a]	7.00±1.62[a]	5.42±1.90[a]
Ostreopsis heptagona	6.20±1.22[a]	1.52±0.99[b]	5.33±0.76[a]	4.48±0.84[ab]
Gambierdiscus balechii	6.92±0.94[a]	3.41±1.68[a]	4.67±0.86[a]	4.63±0.92[a]
Gambierdiscus toxicus	6.22±1.18[a]	4.73±1.55[a]	6.34±1.65[a]	5.01±0.74[a]
Gambierdiscus australes	7.76±1.47[a]	0	5.21±0.80[ab]	4.20±0.62[b]
Coolia monotis	5.88±1.28[a]	5.22±1.70[a]	6.31±1.52[a]	4.33±0.45[a]

Different lowercase letters(ab) indicate a significant difference between seasons ($p>0.05$).

Table 6: Seasonal average (mean±standard error) of the measured physicochemical variables from six sampling sites in Chabahar Bay, 2019-2020.

Parameters	Spring	Summer	Autumn	Winter
NO$_2$ (mg L^{-1})	2.27±0.43[a]	2.99±0.68[a]	3.85±0.47[a]	4.17±0.96[a]
NO$_3$ (mg L^{-1})	0.06±0.02[a]	0.07±0.02[a]	0.07±0.05[a]	0.21±0.10[a]
PO$_4$ (mg L^{-1})	0.31±0.05[a]	0.34±0.12[a]	0.30±0.12[a]	0.21±0.11[a]
SiO$_4$ (mg L^{-1})	0.31±0.04[a]	0.26±0.09[a]	0.48±0.15[a]	0.29±0.09[a]
Temperature (°C)	32.38±0.24[a]	32.53±0.16[a]	32.22±0.09[a]	32.18±0.08[a]
Salinity	37.72±0.20[a]	37.18±0.07[b]	37.65±0.17[ab]	37.40±0.15[ab]
pH	6.92±0.14[a]	6.83±0.11[a]	7.17±0.11[a]	7.00±0.13[a]
Oxygen (mg L^{-1})	8.31±0.54[a]	8.75±0.58[a]	9.48±1.28[a]	9.43±0.39[a]

Different lowercase letters(ab) indicate a significant difference between seasons ($p>0.05$).
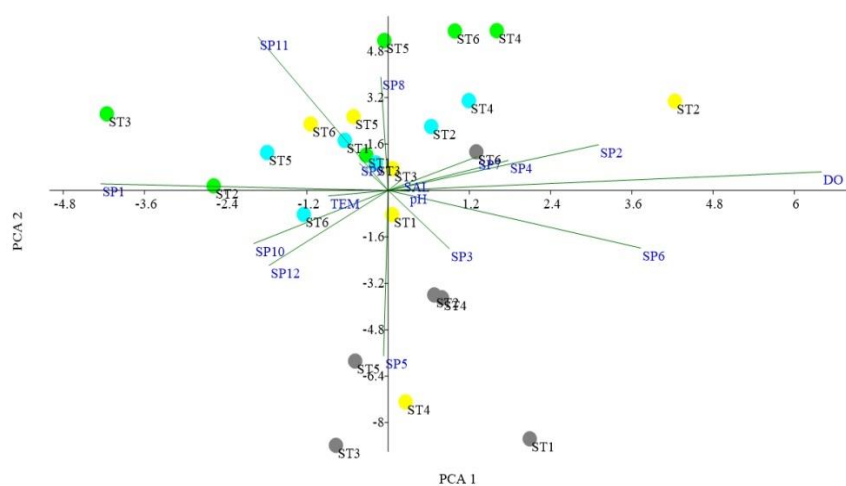

Figure 6: Principal Component Analysis (PCA) between the frequency of identified epiphytic dinoflagellate species and measured physicochemical variables at six sampling stations during different seasons. Physicochemical variables: temperature (TEM), salinity (SAL), and dissolved oxygen (DO). Identified dinoflagellate species: *A. carterae* (SP1), *A. operculatum* (SP2), *P. concavum* (SP3), *P. emarginatum* (SP4), *P. lima* (SP5), *P. rhathymum* (SP6), *O. lenticularis* (SP7), *O. heptagona* (SP8), *G. balechii* (SP9), *G. toxicus* (SP10), *G. australes* (SP11), and *C. monotis* (SP12). The sampling stations are categorized based on seasons, with spring stations represented in green, summer stations in gray, autumn stations in yellow, and winter stations in blue.
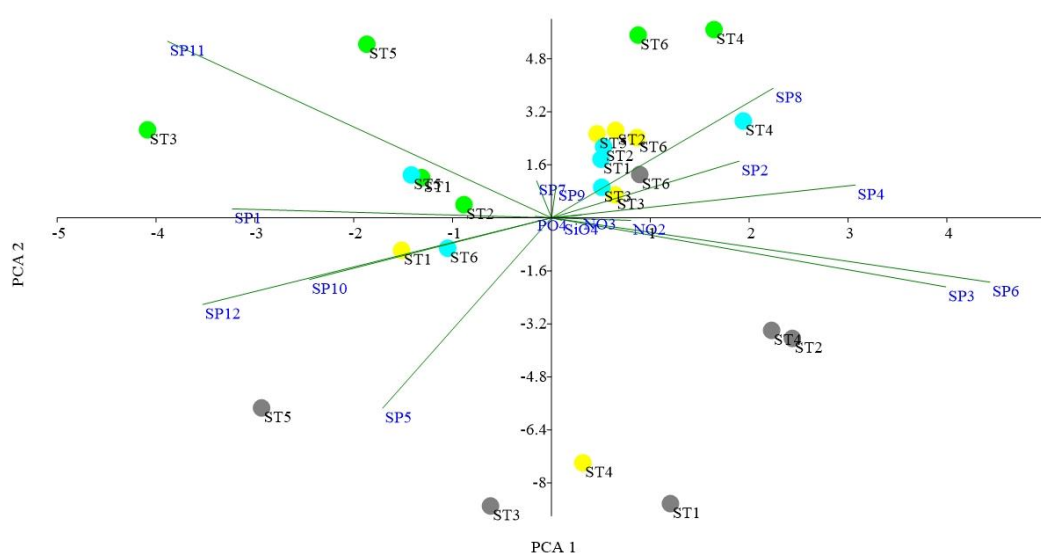
Figure 7: Principal Component Analysis (PCA) between the frequency of epiphytic dinoflagellates and nutrient levels at six sampling stations during different seasons. Studied nutrients: nitrite (NO2), nitrate (NO3), phosphate (PO4), and silicate (SiO4). Identified dinoflagellate species: *A. carterae* **(SP1),** *A. operculatum* **(SP2),** *P. concavum* **(SP3),** *P. emarginatum* **(SP4),** *P. lima* **(SP5),** *P. rhathymum* **(SP6),** *O. lenticularis* **(SP7),** *O. heptagona* **(SP8),** *G. balechii* **(SP9),** *G. toxicus* **(SP10),** *G. australes* **(SP11), and** *C. monotis* **(SP12). The sampling stations are categorized based on seasons, with spring stations represented in green, summer stations in gray, autumn stations in yellow, and winter stations in blue.**

Discussion

It was shown that the species richness, local distribution, and abundance of epiphytic dinoflagellates are affected by several physicochemical variables. Seasonal changes in the surrounding environment of macroalgae cause changes in the abundance of epiphytic organisms (Geddie and Hall, 2019). *Prorocentrum* species are known to produce a range of toxins, including okadaic acid and analogs, dinophysistoxins, and yessotoxins (Hoppenrath *et al*., 2013; Hoppenrath *et al*., 2023). In contrast, *Coolia* species are primarily associated with the production of cooliatoxins (Holmes *et al*., 1995; Wakeman *et al*., 2015; Phua *et al*., 2021). Benthic *Amphidinium* species produce a wide range of toxins, and

amphidinols have been reported more frequently (Wellkamp *et al*., 2020; Hoppenrath *et al*., 2023). *Ostreopsis* species mostly produce palytoxins and their analogs, ovatoxins, and ostreocins. However, the importance of epibenthic dinoflagellates is principally due to ciguatera and its negative impact on human health mainly in tropical countries. At present, at least 18 *Gambierdiscus* species, including the three species identified in the present study (*G. australes, G. balechii* and *G. toxicus*), are known to produce ciguatoxins (Hoppenrath *et al*., 2023). HAB caused by dinoflagellates should not be overlooked due to their negative impacts on environmental and human health (Brosnahan *et al*., 2020). These blooms can deplete oxygen in the water,

harm marine life, and produce toxins that can accumulate in seafood and other marine products, posing a risk to human health (Gárate-Lizárraga *et al*., 2019; Piontkovski *et al*., 2021). HAB can harm or kill organisms that form the basis of the food web. Furthermore, HAB can negatively impact the fishing industry and coastal economies, as well as recreational activities such as swimming and boating. It is therefore crucial to actively monitor and manage HAB to minimize its impacts on the environment, human health, and coastal communities (Zhou *et al*., 2017; Mulholland *et al*., 2018; Açaf *et al*., 2020). In a study by Okolodkov *et al*. (2007) on seasonal variations of epiphytes in the SW Gulf of Mexico, *P. lima* was found to be dominant, with the highest abundances observed on the seagrass *Thalassia testudinum* Banks ex König and the green alga *Ulva fasciata* Delile. The results showed that temperature, salinity, acidity, DO, and other measured parameters did not exhibit a significant correlation with the epiphytic dinoflagellate species (Table 6). In a study by Okolodkov *et al*. (2014) on seasonal variations of epiphytic dinoflagellates in the SE Gulf of Mexico, a total of 20 dinoflagellate species from 12 genera were identified. The genus *Prorocentrum* had the highest abundance, and *P. rhathymum*, *Amphidinium* cf. *carterae*, and *Gambierdiscus* species were dominant. Additionally, the PCA showed a strong correlation between epiphytic dinoflagellates and salinity, nutrients, and water temperature (Fig. 6). In a

study by Hachani *et al*. (2018) on the spatio-temporal distribution of toxic epiphytic dinoflagellates on macrophytes in the Gulf of Tunisia, *Ostreopsis* sp., *P. lima*, and *C. monotis* were dominant. According to the redundancy analyses (RDA), relationships between variables showed that *Ostreopsis* sp. had a direct correlation with ambient temperature and had the highest abundance during summer and the abundance of *P. lima* and *C. monotis* were found to be correlated with nutrient levels (Hachani *et al.,* 2018). In a study by Gharbia *et al*. (2019) on toxic dinoflagellates in the Bizerte Gulf in northern Tunisia, the species *Ostreopsis* spp., *P. lima* and *C. monotis* were found to have positive Pearson correlations with environmental factors. Moreover, the spatial distribution of these dinoflagellates was attributed to changes in the levels of dissolved nutrients in the Gulf. In a study by Kim *et al*. (2021) on toxic epiphytic dinoflagellates in Jeju Island in the Korea Strait, five genera (*Amphidinium, Coolia, Gambierdiscus, Ostreopsis*, and *Prorocentrum*) were identified; the genus *Ostreopsis* had the highest abundance.

Epiphytic dinoflagellates, including those that cause HAB, are known to be influenced by environmental factors and nutrient availability (Anderson *et al*., 2021; Marampouti *et al*., 2021). Nutrients, particularly nitrogen and phosphorus compounds, are known to play a crucial role in the growth and proliferation of dinoflagellates. These elements are essential for the synthesis

of cellular components, such as proteins and nucleic acids, and for energy production through photosynthesis (Hachani *et al*., 2018; Wurtsbaugh *et al*., 2019; Drouet *et al*., 2022). In marine environments, nutrient availability is often limited, and the input of nutrients from external sources, such as agricultural runoff and wastewater discharge, can lead to eutrophication and HAB caused by dinoflagellates. The mechanisms by which nutrients promote the growth and proliferation of dinoflagellates are complex and vary depending on the species and the environmental conditions (Fricke *et al*., 2018). Generally, increased nutrient availability can lead to higher growth rates and cell division rates, leading to an increase in the overall abundance of dinoflagellates. Additionally, high nutrient availability can promote the formation of resting cysts, which can increase the resilience of dinoflagellates to environmental stressors and allow them to persist in the environment for extended periods (Jauzein *et al*., 2017; Sarkar, 2018; Gharbia *et al*., 2019). Moreover, nutrient availability can influence the functioning of dinoflagellates; high nutrient availability can also increase the production of toxins by dinoflagellates, which can have negative ecological and socio-economic impacts (Kim *et al*., 2021; Wang *et al*., 2021). Toxins produced by dinoflagellates can harm marine wildlife, fisheries, and human health, leading to the closure of fisheries and beaches and negatively affecting coastal communities and regional economies

(Accoroni *et al*., 2017; Smith *et al*., 2017; Park *et al*., 2020).

Based on the PCA results, DO had the greatest impact at stations with the highest abundances of the species *A. operculatum*, *P. concavum*, *P. emarginatum*, *P. rhathymum*, and *O. lenticularis* (Fig. 6). DO is an important environmental factor that can affect the growth and distribution of marine organisms, including epiphytic dinoflagellates that cause HAB (Hachani *et al*., 2018; Zou *et al*., 2022). Generally, dinoflagellates require oxygen for respiration, and changes in DO levels can affect their respiration rates and growth rates. Carnicer *et al*. (2019) and Arbeláez *et al*. (2020) stated that changes in DO levels can affect the physical and chemical properties of the marine environment, including the availability of nutrients and other environmental factors, such as temperature, pH and salinity, which can further influence the growth and distribution of dinoflagellates. Low DO levels, also known as hypoxia, can have a significant impact on the abundance of dinoflagellates. Hypoxia can lead to reduced respiration rates and increased mortality rates among dinoflagellates, which, in turn, can lead to a decrease in their overall biomass and abundance (Rodríguez-Gómez *et al*., 2019; Longo *et al*., 2020). Additionally, hypoxia can alter the availability of nutrients and other environmental variables, which can further influence the growth and survival of dinoflagellates. High DO levels can also have a negative impact on

the abundance of dinoflagellates. They can lead to the production of reactive oxygen species, which can cause oxidative stress and damage to dinoflagellate cells (Ghariba *et al*., 2019; Berlinghof *et al*., 2022).

The results showed that salinity had a significant impact on the abundance of several dinoflagellate species, including *A. operculatum*, *P. concavum*, *P. emarginatum*, *P. rhathymum*, and *O. lenticularis*. Some authors observed a notable impact of salinity on dinoflagellate communities that contribute to the formation of algal blooms (Feki-Sahnoun *et al*., 2019; Park *et al*., 2020; Stanca and Parsons, 2021). They reported that an increase in salinity led to a decrease in the abundance of these dinoflagellate species. Generally, dinoflagellates are sensitive to changes in the osmotic pressure of the surrounding environment, and high salinity can lead to cellular dehydration and reduced growth rates (Park *et al*., 2020; Stanca and Parsons, 2021). Abadie *et al*. (2018) and Feki-Sahnoun *et al*. (2019) state that high salinity can limit the availability of nutrients, such as nitrogen and phosphorus compounds, which can further reduce the growth and proliferation of dinoflagellates.

The results showed that temperature had a significant impact on the abundance of several dinoflagellate species, including *A. carterae*, *P. lima*, *O. heptagona*, *G. balechii*, *G. toxicus*, *G. australes*, and *C. monotis* (Figure 6). Similar results have been reported by other authors (Bi *et al*., 2021; Rodríguez-Villegas *et al*., 2021).

Temperature is another environmental factor that can influence the growth and distribution of epiphytic dinoflagellates that cause HAB. Dinoflagellates have optimal temperature ranges for growth and reproduction, and changes in temperature outside of these ranges can lead to reduced growth rates and cell death (Jang *et al*., 2018; Arbeláez *et al*., 2020). Boisnoir *et al*. (2020) state that changes in temperature can affect the availability of nutrients and other environmental parameters, such as DO, pH, and salinity, which can further influence the growth and survival of dinoflagellates.

According to the PCA results, pH had the greatest impact at stations with the highest abundances of *A. operculatum*, *P. concavum*, *P. emarginatum*, *P. rhathymum*, and *O. lenticularis* (Fig. 7). This conclusion is consistent with the results obtained by other authors (Longo *et al*., 2020; Kang *et al*., 2021). The pH level is a crucial environmental variable that can have a significant impact on both the growth and distribution of epiphytic dinoflagellates. Dinoflagellates have optimal pH ranges for growth and reproduction. In particular, an increase in pH can lead to a decrease in the availability of CO_2, which can limit the photosynthetic rates of dinoflagellates (Longo *et al*., 2020). According to Berlinghof *et al*. (2020), high pH can alter the chemical composition of the marine environment, Low pH, also known as acidification, can also have negative impacts on the abundance of dinoflagellates. Acidification can lead to the dissolution

of calcium carbonate structures, which can reduce the availability of this important nutrient for dinoflagellates and other marine organisms (Foo *et al.*, 2018; Berlinghof *et al.*, 2022). Additionally, acidification can lead to the production of hydrogen ions, which can cause cellular damage and reduce the growth and survival of dinoflagellates (Heil and Muni-Morgan, 2021; Berlinghof *et al.*, 2023).

Based on the results of this study, in 2019-2020, twelve potentially toxic epiphytic dinoflagellate species from five genera were identified in Chabahar Bay during the four seasons. *Prorocentrum* and *Coolia* had the highest and lowest number of identified species, respectively. The presence of the three *Gambierdiscus* species (*G. australes, G. balechii*, and *G. toxicus*) identified from Chabahar Bay allows us to consider it a ciguateric area, and the occurrence of ciguatera in this zone is a matter of time. The study also found significant differences in the abundance of certain species between seasons. The results suggested that DO, pH, salinity, and temperature had a significant impact on the abundance of certain species. Moreover, the study examined the relationship between nutrients and dinoflagellate abundance, with NO_2, NO_3, SiO_4, and PO_4 being identified as having the greatest impact on the abundance of certain species. The results on the species composition of the potentially toxic dinoflagellates have implications for various industrial management applications. In aquaculture, they aid in preventing contamination and ensuring seafood safety. In fisheries management, monitoring these organisms helps protect fishery resources. They act as indicators of environmental health and water quality, supporting environmental monitoring and conservation efforts. In coastal areas and recreational waters, understanding toxic dinoflagellates ensures public health and safety. Additionally, they offer potential for pharmaceutical and biotechnological applications. Overall, these findings provide important insights into the dynamics of phytoplankton in Chabahar Bay and can inform management strategies to mitigate the risks associated with harmful algal blooms.

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