ARTICLE

Variability of microphytoplankton community composition in response to oceanographic drivers in the coastal upwelling area off central Chile

Variabilidad de la composición de la comunidad microfitoplanctónica en respuesta a los forzantes oceanográficos en la zona de surgencia costera de Chile central

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Resumen.- En los sistemas de surgencia costera la comunidad microfitoplanctónica la integran principalmente diatomeas y dinoflagelados. Sin embargo, ninguno de ellos constituye grupos uniformes, ya que las interacciones físico-químicas y biológicas afectan a la estructura de la comunidad. En este trabajo se analizó la comunidad microfitoplanctónica en una estación fija ubicada en la bahía de Valparaíso (32°-33°S) bajo el modelo C-S-R de Reynolds. Cambios mensuales en la comunidad se asociaron con la disponibilidad de nutrientes (nitrato-NO_3^-, silicato-SiO_4^{4-} y N/Si), y la temperatura, relacionados a su vez con la actividad de la surgencia, pudiendo describir tres comunidades. Una primera constituida por diatomeas neríticas R estrategas como *Asterionellopsis glacialis, Chaetoceros radicans* y *Chaetoceros tortissimus* detectadas desde finales de invierno hasta verano (agosto-diciembre), asociada al ascenso de agua fría y rica en nutrientes bajo surgencia activa. Así mismo, dinoflagelados como *Protoperidinium brochii, Protoperidinium pellucidum* y *Preperidinium meunieri*, fueron identificados como parte de esta comunidad. Entre verano y otoño (enero-abril) bajo condiciones de estratificación térmica dominaron dinoflagelados S/R-S como *Tripos furca* var. *berghii, Ceratium tripos* f. *tripodioides, Prorocentrum gracile,* y *Protoperidinium steinii* junto con diatomeas pennadas C-R como *Navicula* sp. y *Thalassionema nitzschioides*. Finalmente, diatomeas R-C/R como *Leptocylindrus danicus, Guinardia delicatula, Detonula pumila, Pseudo-nitzschia australis, Skeletonema costatum, Thalassiosira mendiolana* y *Chaetoceros* sp. estuvieron presentes todo el año sin mostrar relación con las condiciones oceanográficas. Aunque la surgencia desempeña un papel determinante en la sucesión del microfitoplancton en la bahía, las interacciones biológicas parecen jugar un rol, siendo necesario abordar el estudio desde una perspectiva ecológica.

Palabras clave: Microfitoplancton, composición de la comunidad, diatomeas, dinoflagelados, surgencia

Abstract.- In coastal upwelling areas, the microphytoplankton community comprises two main groups, diatoms and dinoflagellates. However, neither group is uniform because physical-chemical and biological interactions can affect the community structure. In this work, the composition of the microphytoplankton community was analyzed at a fixed station located in Valparaíso Bay (~32°-33°S) using the Reynolds C-S-R model. In the bay, monthly variation of the microphytoplankton community occurred due to nutrient availability (nitrate-NO_3^-, silicate-SiO_4^{4-}, and N/Si ratio), and water temperature, driven by upwelling activity. Three main communities were observed. The first one comprised neritic R diatoms such as *Asterionellopsis glacialis, Chaetoceros radicans,* and *Chaetoceros tortissimus* from late winter to early summer (August-December), when upwelling activity occurred with the ascent of cold and nutrient-rich water. In addition, dinoflagellates such as *Protoperidinium brochii, Protoperidinium pellucidum,* and *Preperidinium meunieri* were identified as part of this community. Secondly, S/R-S dinoflagellates such as *Tripos furca* var. *berghii, Ceratium tripos* f. *tripodioides, Prorocentrum gracile,* and *Protoperidinium steinii* were predominant under thermal stratification conditions from summer to autumn (January-April) together with C-R pennate diatoms such as *Navicula* sp. and *Thalassionema nitzschioides*. Finally, a community including neritic R-C/R diatoms such as *Leptocylindrus danicus, Guinardia delicatula, Detonula pumila, Pseudo-nitzschia australis, Skeletonema costatum, Thalassiosira mendiolana,* and *Chaetoceros* sp. was present throughout the year with no remarkable connection to any oceanographic conditions. Although upwelling activity constitutes the main driver of microphytoplankton community succession in the bay, biological interactions appear to play also a role, being necessary a deeper study under an ecological perspective.

Key words: Microphytoplankton, community composition, diatoms, dinoflagellates, upwelling

INTRODUCTION

The central coast of Chile (~30°-40ºS) is characterized as a dynamic and productive region where upwelling activity is considered a key driver of phytoplankton fluctuations (Daneri *et al*. 2000, Montecino *et al*. 2004, Anabalón *et al*. 2007, 2016; González *et al*. 2007, Aparicio-Rizzo *et al*. 2020). In this region, variability in the phytoplankton community composition has shown temporal and spatial heterogeneity, which is related to not only local wind forcing but also solar radiation and freshwater inputs, which are associated with changes in the community structure (Anabalón *et al*. 2007, 2016; Iriarte *et al*. 2012, Aparicio-Rizzo & Masotti 2019).

In Valparaíso Bay (Central Chile, ~33°S), the microphytoplankton variability has been characterized as following a bi-modal regime in response to changes in oceanographic mixing/stratification processes (Avaria *et al*. 1989, Aparicio-Rizzo *et al*. 2020). High biomass and diatoms abundance occur under upwelling (mixing conditions), while low biomass and the presence of dinoflagellates have been linked to a more stratified water column following Margalef's classical "mandala" model (Margalef 1978). This model is based on the linear and co-dependent relationship between turbulence and nutrient concentration and was postulated to represent the succession of diatoms and dinoflagellates in the bay (Avaria *et al*. 1989). However, it cannot explain changes in the phytoplankton community under different scenarios and dinoflagellates' non-exclusive presence in stratified waters (Smayda & Reynolds 2001, Smayda 2002, Reynolds 2006). In this sense, the Reynolds C-S-R model (Reynolds 1988) could help to better explain the changes in the microphytoplankton community in this upwelling coastal region. This model is based on the coexistence of diverse species with different characteristics under the same environmental conditions and divides species based on their primary strategies into invasive-colonist (C), stress-tolerant (S), and ruderal (R) species. Changes in phytoplankton community have mainly been described based on the transition from diatoms to dinoflagellates, which is insufficient since changes in abiotic factors affect phytoplankton at not only the group level (diatoms and dinoflagellates), but also at the specific composition level. Furthermore, neither diatoms nor dinoflagellates are uniform groups; they change at the species level according to not only abiotic factors (*e.g.*, temperature, salinity, radiation, nutrients), but also biotic factors like cell size, growth rates, efficiency in resource acquisition and use, anti-predator defenses, or the ability to produce resistance cysts and remain in the water column (Margalef 1978, Kiørboe 1993, Kiørboe *et al*. 1994, Reynolds *et al*. 2002, Reynolds 2006, Alves de Souza *et al*. 2008a, b), in addition to the interactions among the species that constitute the community (Alves de Souza *et al*. 2008a).

Descriptive specific composition studies from the 1970s used short-term data (around one year) to characterize the microphytoplankton in Valparaíso Bay as a diatom-dominated community, which is typical of temperate upwelling systems (Avaria & Orellana 1975, Avaria *et al*. 1989). Two main communities throughout the year have been indicated: 1) a spring-summer community with high abundance but low richness characterized by frequent blooms of few chain-forming diatoms species and 2) a low-abundance autumn-winter community composed of heterogeneous phytoplankton with the presence of dinoflagellates (Avaria 1971, Avaria & Orellana 1975, Avaria *et al*. 1989). From spring to summer, diatoms species such as *Detonula pumila*, *Leptocylindrus danicus*, *Skeletonema costatum*, and *Thalassiosira aestivalis*, together with small species of *Chaetoceros*, such as *Chaetoceros socialis*, *Ch. radicans*, and *Ch. debilis*, have been described as characteristic in the bay. Between autumn and winter months, this is followed by *Guinardia delicatula*, *Hobaniella longicruris* (referred as *Biddulphia longicruris),* *Corethron pennatum*, and other *Chaetoceros* sp. such as *Chaetoceros convolutus* and *Ch. compressus*, together with some dinoflagellates (Avaria 1971, Avaria & Orellana 1975, Avaria *et al*. 1989). Dinoflagellates in the bay have generally been described from late summer to autumn and have mainly been represented by *Tripos muelleri*, *T. furca*, *T. azoricus*, *Diplopsalis lenticula*, *Prorocentrum micans*, *Protoperidinium pellucidum,* and *P. oceanicum*. However, no research has been done to determine the connections between the specific composition of the microphytoplankton community and the oceanographic drivers in this coastal upwelling area. Therefore, the aim of this study was to explore and understand the response of microphytoplankton community composition to oceanographic conditions (temperature, salinity, nutrients, and upwelling activity) throughout the year by analysing an extensive time series of data from a 10-year period (1986 to 1996), collected in coastal waters at Montemar station in Valparaíso Bay.

MATERIALS AND METHODS

STUDY AREA AND DATASET

Valparaíso Bay is an N-NW oriented open embayment located at central Chile, in Valparaíso Region (~33ºS), characterized by intense coastal upwelling activity. Montemar fixed station (St. M), directly exposed to S-SW upwelling favourable winds (Aparicio-Rizzo & Masotti 2019, Aparicio-Rizzo *et al*. 2020), was located at approximately 2 nautical miles (~4 km) from the coast, at the north part of the bay (Fig. 1; 32º58'2"S-71º35'2"W).
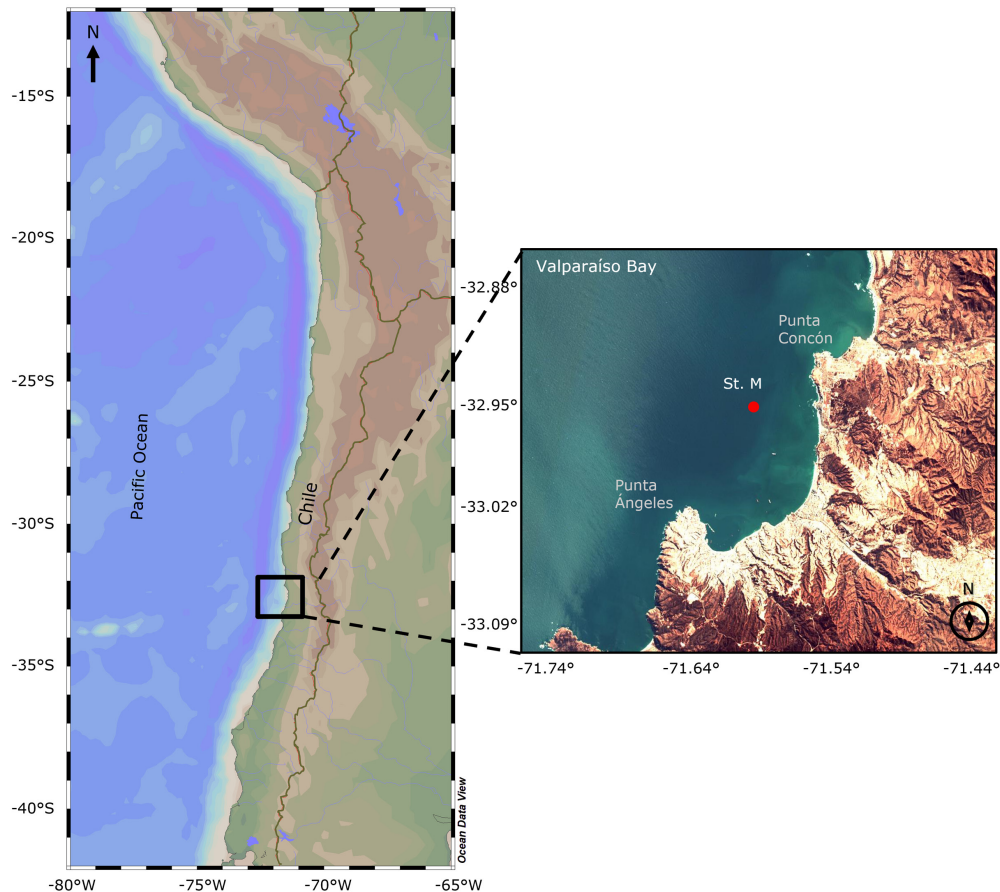
Figure 1. Location of the study area in Central Chile and position of the time series fixed Montemar station at Valparaíso Bay (St. M) / Ubicación del área de estudio y posición de la estación fija de Montemar en la Bahía de Valparaíso (St. M), Chile central

This study uses a time series data, including *in situ* samplings from October 1986 to December 1996 with intervals of 15 to 30 days. Biological (microphytoplankton abundance), chemical (nitrate-NO_3^-, phosphate-PO_4^{3-}, and silicate-SiO_4^{4-}) and physical (temperature and salinity) variables, were registered each sampling date at the station in the first 55 m of water column.

Hourly wind data (8 values per day; from 3 a.m. to 24 p.m.) recorder at Punta Angeles weather station located ~10 km at the south of the Montemar fixed station (Fig. 1) were obtained from Servicio Meteorológico de la Armada de Chile (SERVIMET)[1].

Microphytoplankton composition and abundance

The phytoplankton was analyzed in terms of species abundance in the microphytoplankton range (~20-200 μm).

Discrete water samples were obtained at 0 and 10 m depth in plastic bottles (~250 mL) and preserved in 1% Lugol's iodine solution. Phytoplankton cell-counts analyses were carried out in the laboratory, using a Wild M-40 inverted microscope following the method described by Utermöhl (1958). Abundances were expressed in number of cells L^{-1}. To facilitate taxonomic identification, qualitative analyses were made from net samples. Horizontal net tows were carried out for 15 min using a standard net of 62 mesh size to obtain the net samples that were fixed in neutralized 5% formaldehyde. Taxonomic identification was accomplished by direct observation of the preserved samples with a phase contrast microscope Leitz Dialux 20, to the lowest level (species or genus), using the descriptions in Avaria (1965) and Tomas (1997). Finally, using algabase.org database (Guiry & Guiry 2024) an updating of species name was performed (Table 1 & Table S1 illustrate also species name synonyms).

Table 1. Selected microphytoplankton species. Life strategy classified as the Reynolds C-S-R model / Especies seleccionadas del microfitoplancton. Estrategia de vida en base al modelo C-S-R de Reynolds

Species	Name synonym	Code	Group	Life strategy	Habitat	Periods
Cerataulina pelagica	*Zygoceros pelagicus*	Cpel	Diatom	R	Neritic	Recurrent
Chaetoceros cinctus	-	Ccin	Diatom	R	Neritic	Recurrent
Chaetoceros compressus	-	Ccom	Diatom	R	Neritic	Recurrent
Chaetoceros debilis	-	Cdeb	Diatom	R-C	Neritic	Recurrent
Chaetoceros didymus	-	Cdid	Diatom	R-C	Neritic	Recurrent
Detonula pumila	*Lauderia pumila*	Dpum	Diatom	R-C	Neritic	Recurrent
Dinophysis fortii	-	Dfor	Dinoflagellate	S	Neritic/oceanic	Recurrent
Guinardia delicatula	*Rhizosolenia delicatula*	Gdel	Diatom	R-C	Neritic	Recurrent
Guinardia striata	*Eucampia striata*	Gstr	Diatom	S	Neritic	Recurrent
Leptocylindrus danicus	-	Ldan	Diatom	R-C	Neritic	Recurrent
Neomoelleria cornuta	*Eucampia cornuta*	Ncor	Diatom	R	Neritic/oceanic	Recurrent
Pseudo-nitzschia australis	-	Paus	Diatom	-	Neritic	Recurrent
Skeletonema costatum	*Melosira costata*	Scos	Diatom	R-C	Neritic	Recurrent
Thalassiosira mendiolana	-	Tmen	Diatom	R-C	Neritic	Recurrent
Asterionellopsis glacialis	*Asterionella glacialis*	Agla	Diatom	R	Neritic	PCA-1
Chaetoceros constrictus	-	Ccon	Diatom	R-C	Neritic	PCA-1
Chaetoceros radicans	-	Crad	Diatom	R	Neritic	PCA-1
Chaetoceros teres	-	Cter	Diatom	R	Neritic/oceanic	PCA-1
Chaetoceros tortissimus	-	Ctor	Diatom	R	Neritic	PCA-1
Protoperidinium brochii	*Peridinium brochii*	Pbro	Dinoflagellate	C	-	PCA-1
Thalassiosira subtilis	*Podosira subtilis*	Tsub	Diatom	R-C	Neritic/oceanic	PCA-1
Ceratium tripos f. *tripodioides*	*Tripos muelleri*	Ctri	Dinoflagellate	R-S	Neritic/oceanic	PCA-2
Leptocylindrus mediterraneus	*Dactyliosolen mediterraneus*	Lmed	Diatom	R	-	PCA-2
Navicula sp.	-	Nav	Diatom	R-C	Benthic	PCA-2
Prorocentrum gracile	-	Pgra	Dinoflagellate	R-C	Neritic/estuarine	PCA-2
Protoperidinium steinii	*Peridinium steinii*	Pste	Dinoflagellate	S	Neritic/oceanic	PCA-2
Tripos furca var. *berghii*	*Ceratium furca* var. *berghii*	Tfur	Dinoflagellate	R-S	Neritic/estuarine/oceanic	PCA-2
Chaetoceros lorenzianus	-	Clor	Diatom	R-C	Neritic	PCA-1 & 2
Chaetoceros socialis	-	Csoc	Diatom	R	Neritic	PCA-1 & 2
Eucampia biconcava	*Climacodium biconcavum*	Ebic	Diatom	-	Oceanic	PCA-1 & 2
Nitzschia longissima	*Ceratoneis longissima*	Nlon	Diatom	R	Neritic	PCA-1 & 2
Preperidinium meunieri	*Diplopsalis minor*	Pmeu	Dinoflagellate	C-R	Oceanic	PCA-1 & 2
Protoperidinium pellucidum	-	Ppel	Dinoflagellate	C	Neritic	PCA-1 & 2
Thalassionema nitzschioides	*Synedra nitzschioides*	Tnitz	Diatom	R-C	Neritic	PCA-1 & 3

C (invasive-colonist), S (stress-tolerant), R (ruderals)

DATA ANALYSES

Oceanographic conditions in the water column were characterized at monthly scale. To calculate the upwelling index (UI) (Bakun 1973), only wind data registered between 12 h and 24 h p.m. were used, and from them a daily maximum value of UI was selected.

Phytoplankton abundances and nutrients concentration were integrated by the trapezoidal rule and transformed logarithmically [log (x+1)]. Nutrient ratios (N/P, N/Si, Si/P) were determined using nutrient's concentration.

Prior to the statistical analysis, a selection of phytoplankton species and oceanographic variables was performed. 34 species, from the total identified (Table S1) along the study period, were selected based on frequency of occurrence (> 30%). Concern to the oceanographic variables a selection was developed based on cross-correlation analysis results (r > ± 0.60, P < 0.05), after examining the data distribution by a Shapiro-Wilk test. Seven variables were selected: Upwelling Index (UI), Sea Surface Temperature (SST), Sea Surface Salinity (SSS), nitrate-NO_3^-, phosphate-PO_4^{3-}, and silicate-SiO_4^{4-} concentrations, together with N/Si ratio.

A principal component analysis (PCA) was performed to study the temporal pattern of the oceanographic variables (UI, SST, SSS, nitrate-NO_3^-, phosphate-PO_4^{3-}, silicate-SiO_4^{4-}, and the N/Si ratio) in the study area, and a permutational analysis of variance (One-way PERMANOVA) to determine the differences among the groups identified.

Microphytoplankton data were grouped based on the oceanographic monthly characterization and classified by Reynolds life strategy categories as C, R and/or S (Table 1) (Smayda & Reynolds 2001, Reynolds 2006). To distinguish temporal changes in the community composition a non-metric multi-dimensional scaling (NMDS) was used. To assess the differences between groups, an analysis of similarity (One-way ANOSIM test) was applied to the microphytoplankton matrices, and a similarity distance analysis (SIMPER) was applied to identify the taxa that contribute most to the similarity and/or differentiation between groups.

Finally, to explore the relationship between microphytoplankton composition and the oceanographic conditions, a Canonical Correspondence Analysis (CCA) was performed. The statistical relationship among oceanographic variables and the axis of CCA was evaluated by a correlation test.

RESULTS

MONTHLY VARIABILITY OF OCEANOGRAPHIC CONDITIONS

The upwelling index (UI) revealed upwelling favourable conditions throughout the year, which were especially notable in spring to summer (October to January), when the highest values were registered (Fig. 2A). By contrast, downwelling events showed an increase in the autumn and winter seasons, particularly from April to September (Fig. 2A).

In the water column (0-55 m), the temperature indicated progressive surface warming (values over 13.5 ºC) in the first meters (~0-20 m) from austral spring to early autumn (November to April), with highest temperatures in summer (January to March), under a clear development of thermal stratification conditions (Fig. 2B). From late winter to early summer (August to January), an ascent of cold, salty water (~34.4) reaching 10 m depth was detected (Fig. 2B-C). The salinity showed slightly lower values at the surface layer from winter to summer (June to February), which was especially pronounced in July-August and December-January (Fig. 2C).
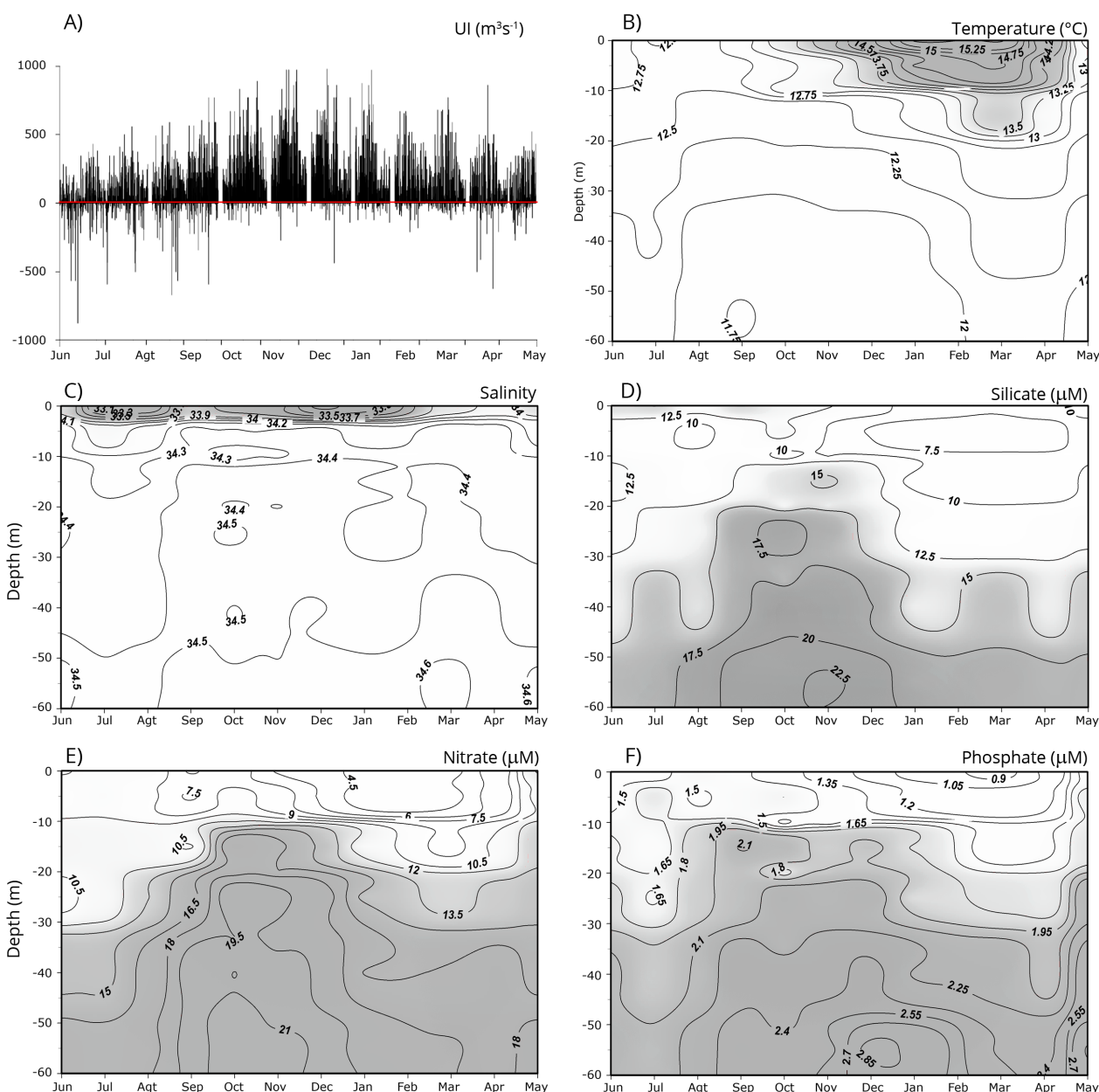

Figure 2. Monthly variability of: A) Upwelling Index (UI), B) Temperature, C) Salinity, D) Silicate-SiO$_4^{4-}$, E) Nitrate-NO$_3^-$, and F) Phosphate-PO$_4^{3-}$ / Variabilidad mensual de: A) Índice de surgencia (IS), B) Temperatura, C) Salinidad, D) Silicato-SiO$_4^{4-}$, E) Nitrato-NO$_3^-$, y F) Fosfato-PO$_4^{3-}$

Nutrients' concentrations (NO_3^-, PO_4^{3-}, SiO_4^{4-}) displayed lower values in the upper layer (0-10 m) with a progressive increase in depth (Fig. 2D-F). From late winter to early summer, the ascent of nutrients rich water was associated with salty, cold deep-water rises (Fig. 2). From summer to early autumn (January to April), in association with thermal stratification conditions, a deepening of the low nutrients' concentrations detected in the upper layer was registered (Fig. 2B and D-F).

PCA analysis of oceanographic variables showed two principal components explaining 64.4% of the total variability (Fig. 3). The first component (PC1) showed the highest eigenvectors for the integrated nutrient concentrations (PO_4^{3-}, NO_3^-, and SiO_4^{4-}) and SST, which were significantly associated with PC1 scores ($P < 0.01$). UI had the most relevant eigenvector in the second component (PC2), followed by the N/Si ratio, but only UI was significantly correlated to the axis of PC2 scores ($P < 0.01$).

This analysis revealed three periods of the year. The first one (PCA-1) was from late winter to early summer and included the months of August to December (Fig. 3). This period was associated with high UI, low temperature, and high salinity and nutrients according to values assessed over the period of 1986-1996 (Table 2, Fig. 3). The second period (PCA-2) was significantly different ($P < 0.05$) and occurred from summer to autumn, including the months of January, March, and April (Fig. 3). This period was characterized by a low nutrient concentration and the highest temperature (Table 2). Finally, the third period (PCA-3, Fig. 3) was from late autumn to winter (May to July) and had the lowest salinity and UI values (Table 2).
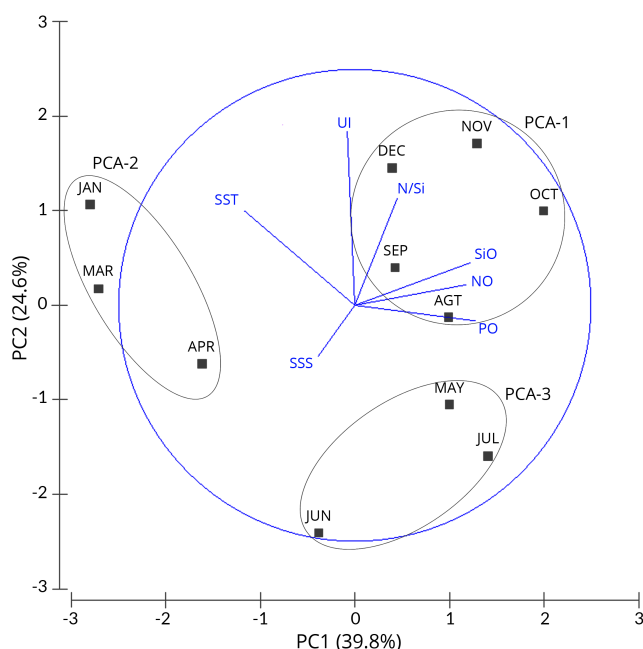

Figure 3. Temporal ordination diagram of oceanographic variables (SST, SSS, Nitrate-NO_3^-, Phosphate-PO_4^{3-}, Silicate-SiO_4^{4-} and N/Si ratio) and the UI resulting from a Principal Component Analysis (PCA) / Diagrama de ordenación temporal de las variables oceanográficas (SST, SSS, Nitrato-NO_3^-, Fosfato-PO_4^{3-}, Silicato-SiO_4^{4-} y relación N/Si) y el IS resultante de un Análisis de Componentes Principales (PCA)

Table 2. Time series data of oceanographic variables at the Montemar station (1986-1996). Mean, standard deviation (SD) and median (Mdn) in the first 55 m / Datos de series temporales de variables oceanográficas en la estación de Montemar (1986-1996). Promedio, desviación estándar (SD) y mediana (Mdn) en los primeros 55 m

		UI ($m^3 s^{-1}$)	Temperature (ºC)	Salinity	NO_3^- (μM)	PO_4^{3-} (μM)	SiO_4^{4-} (μM)
PCA-1	Mean	194.75	12.49	34.25	13.93	1.96	15.20
(Agt-Dec)	SD	211.85	1.39	0.72	7.79	0.82	9.88
	Mdn	170.25	12.03	34.44	14	2.03	13.90
PCA-2	Mean	154.80	13.33	34.31	10.72	1.65	11
(Jan-Mar-Apr)	SD	179.83	1.55	0.57	7.15	0.82	7.46
	Mdn	117.48	12.78	34.37	10.10	1.66	9.75
PAC-3	Mean	55.73	12.47	34.23	13	1.84	13.38
(May-Jul)	SD	146.03	0.73	0.70	6.26	0.96	7.26
	Mdn	42.56	12.29	34.33	12.80	1.70	12.20

Monthly variability of microphytoplankton community

The microphytoplankton community (diatoms and dinoflagellates) displayed an acceptable ordination level (nMDS stress < 0.1). Two main communities with a dissimilarity of 75% were identified (Fig. 4). The first one (G-1, Fig. 4) exclusively comprised diatoms species that were classified as recurrent (present all the year) or were detected exclusively from August to April (PCA-1 and PCA-1&2, Fig. 4). The second community (G-2, Fig. 4) was mainly constituted by dinoflagellates species (> 75%) that were detected from summer to autumn in January, March, and April (PCA-2 period, Fig. 4). The first community (G-1) had a division with similarities over 50%. A small subgroup constituted by diatoms species that were exclusively present during late winter to early summer from August to December (PCA-1 period, Fig. 4). Another subgroup contained diverse species were detected during the whole year (recurrent species) or from August to April (PCA-1 & 2, Fig. 4).

At the specific composition level, the group of species that were recurrent throughout the year were represented broadly by *Leptocylindrus danicus, Guinardia delicatula, Detonula pumila, Pseudo-nitzschia australis, Skeletonema costatum, Thalassiosira mendiolana*, and diverse *Chaetoceros* species (Table 1). This particular group principally constituted neritic diatoms R-C and R strategists (Table 1). Exclusive species were also identified among PCA periods (Table 1). Exclusive neritic R-strategy diatoms such as *Asterionellopsis glacialis, Chaetoceros constrictus, Chaetoceros radicans*, and *Chaetoceros tortissimus* were observed during late winter to early summer (PCA-1) from August to December (Table 1). During summer to autumn in January, March, and April (PCA-2), cosmopolitan S dinoflagellates and R-S strategists such as *T. furca* var. *berghii, Ceratium tripos* f. *tripodioides*, or *Protoperidinium steinii* were predominant in the community (Table 1).

The results from SIMPER analysis showed high similarity percentages in the specific composition of microphytoplankton among PCA periods (> 55%) due to the contribution of recurrent species (Fig. 4; Table 3). The highest dissimilarity of 45.1% was detected between late winter to early summer (August-December, PCA-1) and late autumn to winter (May-July, PCA-3) periods. There were significant differences in the microphytoplankton composition (ANOSIM, R= 0.487, P = 0.036) in these periods, which were caused by the contribution of species that were present exclusively from
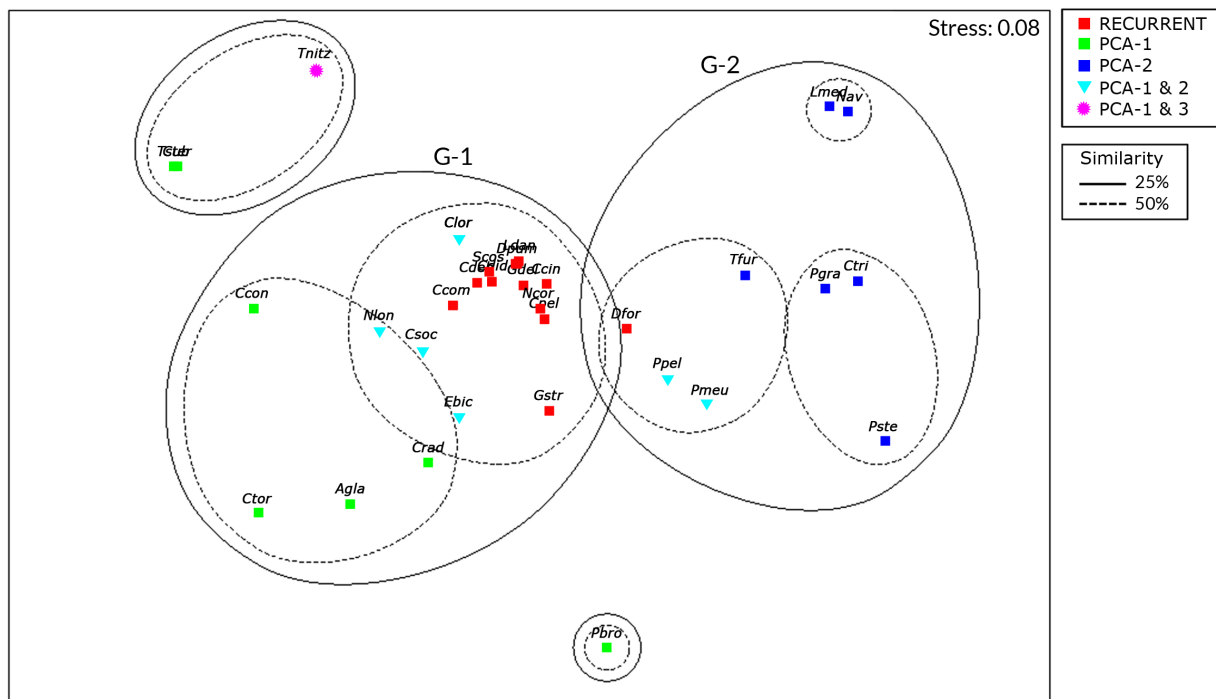

Figure 4. Microphytoplankton community composition ordination plot (NMDS) classified under oceanographic variables periods / Diagrama de ordenación de la composición de la comunidad microfitoplanctónica (NMDS) en base a los periodos de las variables oceanográficas

Table 3. SIMPER analysis of microphytoplankton community composition. PCA-1 species bold, PCA-2 species italics bold, PCA-1&2 species in parentheses and bold and PCA-1&3 species in brackets and bold. Species ordered according to the percentage of contribution to similarity / Análisis SIMPER de la composición de la comunidad microfitoplanctónica. Especies del periodo PCA-1 en negrita, especies del periodo PCA-2 en negrita y cursiva, especies del periodo PCA-1&2 en negrita y entre paréntesis, y especies del periodo PCA-1&3 en negrita y entre corchetes. Especies ordenadas en base al porcentaje de contribución a la similitud de la comunidad

Periods	Similarity & dissimilarity (%)	Contribution of main species (%)
PCA-1	71.78	Scos, Cdeb, Ldan, Cdid, Paus, Tmen, Ccom, Dpum, Gdel, **(Csoc)**, **(Clor)**, **Ncor**, Cpel, **Crad**, Ccin
PCA-2	69.82	Ldan, Gdel, Dpum, Paus, Tmen, Ccin, Cpel, Ecor, Dfor, **(Ppel)**, *Tfur*, Scos, Cdeb, **(Clor)**
PCA-3	55.97	Tmen, Dpum, Ldan, Paus, Scos, Cdid, Gdel, Ncor
PCA-1 *vs.* PCA-2	36.23	Ccom, Csoc, *Tfur*, *Pgra*, **Crad**, Gstr, Ebic, Ccin, Scos, Nlon, Cdeb, Ppel, Cdid, Dfor, **[Tnitz]**, *Ctri*, Pmeu, Clor, **Ccon**, **Agla**, Cpel, Ncor, *Pste*, *Lmed*, **Ctor**
PCA-1 *vs.* PCA-3	45.09*	Cdeb, **(Csoc)**, Ccom, **(Clor)**, **Crad**, Scos, Ccin, Cdid, **(Ebic)**, Cpel, **[Tnitz]**, Gstr, Gdel, **(Nlon)**, Ncor, **Ccon**, **Agla**, Dfor, **(Pmeu)**, **(Ppel)**, **Cter**
PCA-2 *vs.* PCA-3	45.01	Ccin, Cpel, **(Ppel)**, Cdeb, *Pgra*, **(Clor)**, Gdel, Scos, Gstr, **(Pmeu)**, Cdid, *Tfur*, Ccom, Ncor, *Ctri*, **(Csoc)**, **[Tnitz]**, **(Ebic)**, Dfor, **(Nlon)**, Ldan

*Significant difference ($P < 0.05$)

August to December and the highest abundance values that occurred during this period (two to five times higher). Species such as *Chaetoceros socialis*, *Chaetoceros lorenzianus*, *Chaetoceros radicans*, *Eucampia biconcava*, *Nitzschia longissima*, and *Chaetoceros constrictus* were present from late winter to early summer (PCA-1) but not in late autumn to winter (PCA-3) and contributed to more than 75% of the differentiation between microphytoplankton communities (Table 3). Although no statistically significant difference was detected in the microphytoplankton communities' composition between summer to autumn (PCA-2) and late autumn to winter (PCA-3), the dissimilarity of 45.01% was related to dinoflagellate species that are present exclusively during summer to autumn (PCA-2).

The relationship between the microphytoplankton composition and oceanographic variables, explored according to a CCA analysis, showed that the first two axes explained 60.88% of the variation (Fig. 5). The phosphate concentration, N/Si ratio, SST and SSS were associated with the compositional first axis. Nutrient variables displayed a statistically significant positive correlation with the first axis (PO_4^{3-} r= 0.752; N/Si ratio r= 0.603; $P < 0.05$) (Fig. 5). SSS and SST showed a non-significant inverse correlation ($P > 0.05$). On the second axis, the UI was the most explanatory variable and the only one that was statistically correlated to the axis (r= 0.827, $P < 0.01$) (Fig. 5).

Species that had no strong association with any oceanographic variable are shown at the centre in Fig. 5 (black circle), which coincides with the presence of recurrent species. A group of dinoflagellates associated with SSS and SST was mainly detected from late summer to autumn (January to April, PCA-2 period), including species such as *Protoperidinium steinii*, *Prorocentrum gracile*, *Ceratium tripos* f. *tripodioides*, *Tripos furca* var. *berghii*, *Preperidinium meunieri*, and *Protoperidinium pellucidum* (left side, Fig. 5). Diatoms identified from August to April (PCA-1 and PCA-1&2 periods) were related to UI and nutrients (NO_3^-, SiO_4^{4-}, and N/Si ratio) (right side, Fig. 5), including species such as *Chaetoceros tortissimus*, *Asterionellopsis glacialis*, and *Chaetoceros radicans* associated with intense upwelling conditions (Fig. 5). These differences were verified by a PERMANOVA test, which showed significant differences (F= 7.717; $P < 0.05$) between PCA-1 and PCA-2 periods associated with different oceanographic conditions and communities.
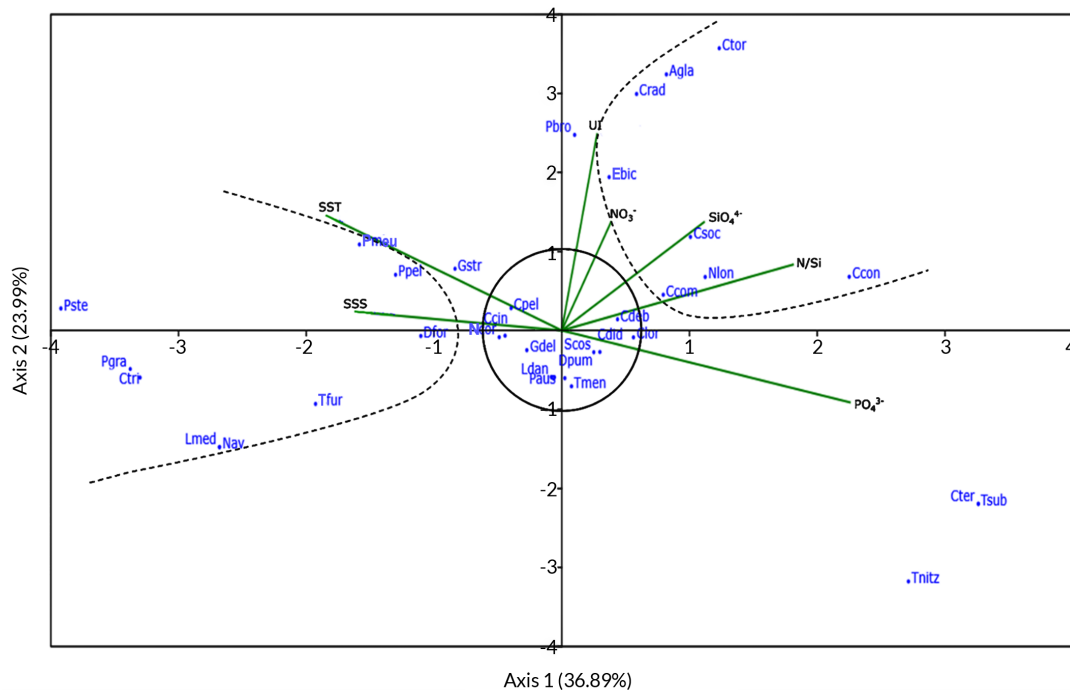
Figure 5. Selected species-oceanographic variables biplot resulting from a Canonical Correspondence Analysis (CCA) / Diagrama del Análisis de Correspondencias Canónicas (CCA) de las especies y variables oceanográficas seleccionadas

Discussion

Microphytoplankton community in coastal upwelling areas

In the coastal upwelling area at Valparaíso Bay, the microphytoplankton community is clearly characterized by a predominance of diatoms (> 75% of total species identified) according to the results. This community composition does not differ significantly from that reported previously in the bay (Avaria 1971, Avaria *et al*. 1989) and in other coastal upwelling ecosystems where diatoms are the main contributor to the microphytoplankton community (in terms of presence, richness, or abundance) (Pitcher *et al*. 1991, Rodríguez *et al*. 1996, Casas *et al*. 1999, Anabalón *et al*. 2007, 2016; González *et al*. 2007, Silva *et al*. 2009, Ochoa *et al*. 2010, Du & Peterson 2014, Wang *et al*. 2016).

In upwelling ecosystems around the world, the predominance of diatoms is well known. In these coastal areas, the microphytoplankton community is mainly composed of cosmopolitan and eurytopic species with an annual succession associated with upwelling activity characterized by diatom blooms during upwelling seasons and dinoflagellates in non-upwelling conditions (Anabalón *et al*. 2007, 2016; González *et al*. 2007, Silva *et al*. 2009, Ochoa *et al*. 2010, Du & Peterson 2014, Wang *et al*. 2016). In this sense, this upwelling coastal area not only shares similar oceanographic conditions, but also some distinctive diatom

genera, such as *Chaetoceros*, *Thalassiosira*, *Pseudo-nitzschia*, or *Nitzschia*, and species like *Skeletonema costatum*, or *Asterionellopsis glacialis*, which are especially predominant under upwelling conditions. Concerning dinoflagellates, the genera *Protoperidinium*, *Tripos*, *Dinophysis*, and *Prorocentrum* are the most representative (Avaria *et al*. 1989, Anabalón *et al*. 2007, González *et al*. 2007, Silva *et al*. 2009, Ochoa *et al*. 2010, Wang *et al*. 2016).

Although this coastal upwelling area is known to have a distinctive phytoplankton composition, this study provides new explanations about the classical dynamic composition of diatoms and dinoflagellates. In the first studies exploring the microphytoplankton community in Valparaíso Bay (Avaria 1971, Avaria & Orellana 1975), some common species were cited as predominant or abundant, particularly *Skeletonema costatum*, *Detonula pumila*, *Pseudo-nitzschia australis*, *Leptocylindrus danicus*, *Thalassiosira mendiolana*, *Neomoelleria cornuta*, and *Cerataulina pelagica,* together with *Guinardia* spp. and several *Chaetoceros* species. However, the present study clarifies that all of them are not only among the most abundant species (70-90%) in the bay but are also recurrent diatom species that are always present throughout the year. Furthermore, other diatoms species have been identified in this study as part of the microphytoplankton community in the bay in association with particular periods of the year under differentiate oceanographic conditions. These include *Asterionellopsis glacialis* and several *Chaetoceros* spp., which were observed exclusively from late winter to

early summer (August-December or PCA-1 period), as well as *Leptocylindrus mediterraneus,* which was detected from summer to early autumn (January-April or PCA-2 period) when dinoflagellate species prevail.

Dinoflagellate species have been commonly associated with the autumn-winter period in the bay, however, in this study, several species of dinoflagellates have been detected all year around. *Tripos furca* var. *berghii*, *Ceratium tripos* f. *tripodioides*, *Prorocentrum gracile*, and *Protoperidinium steinii* were detected exclusively from summer to early autumn in January to April (PCA-2), while *Protoperidinium brochii*, *Protoperidinium pellucidum*, and *Preperidinium meunieri* were mainly registered during winter and spring (April to December). This temporal pattern shows a monthly succession from not only diatom to dinoflagellate species, but also among diatom and dinoflagellate groups of species throughout the year. Furthermore, species from both groups coexist at once under the same oceanographic conditions.

Chaetoceros spp. that are known to form chains and respond quickly to mixing events were more frequent in the bay. Previous studies in Valparaíso Bay (Avaria 1971) described an annual succession of *Chaetoceros* from small-size species (C*haetoceros radicans*, C*h. cinctus,* and *Ch. debilis*) to large-size species (*Ch. constrictus, Ch. compressus*, and *Ch. didymus*) between spring and summer. Nevertheless, in this study, *Chaetoceros* of both sizes were detected throughout the year. *Chaetoceros cinctus*, *Ch. compressus*, *Ch. debilis*, and *Ch. didymus* were recurrent, while *Ch. constrictus*, *Ch. radicans*, *Ch. teres*, and *Ch. tortissimus* were observed exclusively from August to December (late winter to early summer) under intense upwelling activity. This has been previously reported in other upwelling ecosystems, especially in the coastal systems of Perú and Chile (Avaria *et al*. 1989, Anabalón *et al*. 2007, 2016; González *et al*. 2007, Ochoa *et al*. 2010).

MICROPHYTOPLANKTON COMPOSITION IN RESPONSE TO OCEANOGRAPHIC CONDITIONS

Changes in the microphytoplankton community composition (diatoms and dinoflagellates) in Valparaíso Bay were mainly associated with temperature, nutrients (NO_3^-, SiO_4^{4-}, and N/Si ratio), and upwelling activity (UI). However, several species of the diatom community were not strongly associated with any oceanographic variable and had a permanent presence throughout the year ("recurrent" species). This group mainly constituted neritic R diatoms or R-C strategists such as *Thalassiosira mendiolana*, *Pseudo-nitzschia australis*, *Detonula pumila*, *Skeletonema costatum*, *Leptocylindrus danicus*, and *Chaetoceros* spp. These species have previously been identified as dominant or abundant and classified as "key species" in other coastal upwelling ecosystems (Pitcher *et al*. 1991, Anabalón *et al*. 2007, 2016; González *et al*. 2007, Silva *et al*. 2009, Ochoa *et al*. 2010, Du & Peterson 2014, Wang *et al*. 2016).

Oceanographic conditions in the bay displayed significant differences between late winter to early summer period (August-December or PCA-1 period) and summer to autumn (January-April or PCA-2 period). However, non-significant differences were detected in the microphytoplankton community at the specific composition level, which was probably associated with the continuous presence and high abundance of the "recurrent" species. Nevertheless, two microphytoplankton communities were differentiated between these periods due to the identification of exclusive species and changes in life strategies linked to the singular oceanographic conditions present in this coastal upwelling area.

During late winter to early summer, from August to December (PCA-1), wind-driven upwelling activity was strong, and column water presented high nutrient levels, low temperature, and high salinity. These conditions were associated with the presence of exclusive species characterized especially as R or R-C strategists, such as *Asterionellopsis glacialis*, *Thalassiosira subtilis*, and several *Chaetoceros* species (*Ch. constrictus*, *Ch. radicans*, *Ch. tortissimus*, or *Ch. teres*). This community included non-motile species of diatoms that are favoured under conditions of high nutrient concentrations, radiation availability, and mixing processes in coastal upwelling systems, which are typical from late winter to early summer in the bay (Aparicio-Rizzo *et al*. 2020).

From summer to autumn in January to April (PCA-2), the lowest nutrients concentration was registered, and thermal stratification was induced by heating solar radiation. The microphytoplankton community showed the greatest presence and abundance of dinoflagellates during this time, with species such as *Protoperidinium steinii*, *Prorocentrum gracile*, *Ceratium tripos* f. *tripodioides*, and *Tripos furca* var. *berghii*. Previous studies have described dinoflagellate species as part of the microphytoplankton in the bay between December and January or even in April after autumn diatom blooms, which is typical in coastal upwelling ecosystems (Avaria 1971, Avaria & Orellana 1975, Pitcher *et al*. 1991, Anabalón *et al*. 2007, 2016; González *et al*. 2007, Silva *et al*. 2009, Ochoa *et al*. 2010, Du & Peterson 2014). In these upwelling areas, the classical presence of dinoflagellates from autumn to winter under low nutrient and stratified conditions has been associated with S-R or S adaptive strategies (Smayda & Reynolds 2001, Smayda 2002). However, dinoflagellates encompass a heterogeneous and diverse number of species with a wide range of shapes and sizes, swimming ability, spore and cyst resting phases, and multiple nutrition modes (autotrophy, heterotrophy, and mixotrophy) (Smayda & Reynolds 2001, Smayda 2002, Assmy & Smetacek 2009). These variations make these species efficient by having multiple tools to adapt to different oceanographic environments. In fact, the presence of dinoflagellates in the bay was not exclusive in stratified waters or low nutrient conditions. Species such as *Protoperidinium brochii*,

Protoperidinium pellucidum, and *Preperidinium meunieri* classified as C or C-R strategist were also identified as part of the community under upwelling conditions.

Due to the wide number of species of diatoms and flagellates with different ecological and physiological requirements, a uniform ecological response at the group level cannot be expected. Although diatoms are commonly considered to be a single functional group, their presence throughout the year in coastal upwelling areas under conditions of both weak and strong upwelling and/or nutrient availability shows the plasticity and diversity of this population (Mann 1999, Alves de Souza *et al*. 2008a, Wang *et al*. 2016). In addition, it should be noted how multiple species reported in this study displayed an intermediate position between C and R strategies, particularly diatoms identified at different oceanographic conditions throughout the year, such as *Guinardia delicatula*, *Leptocylindrus danicus*, *Skeletonema costatum*, *Thalassiosira mendiolana*, *Navicula* sp., *Thalassiosira subtilis*, *Thalassionema nitzschioides*, and several *Chaetoceros* species. This pattern could be related to the plasticity of species with capacity to live as single cells and to exploit different habitats (C species) or form large chains (R species) to better adapt to turbulence in the water column (Reynolds 2006, Assmy & Smetacek 2009).

In summary, this study has illustrated how oceanographic drivers such as temperature, nutrients (NO_3^-, SiO_4^{4-}, and the N/Si ratio), and upwelling activity (UI) can modulate the microphytoplankton community of diatoms and dinoflagellates in this upwelling coastal region in Valparaíso Bay. In this sense, three main microphytoplankton communities can be described. The first is a community of typically neritic R diatoms observed during late winter to early summer, especially under intense upwelling activity, together with several dinoflagellate species such as *Protoperidinium brochii*, *Protoperidinium pellucidum* and *Preperidinium meunieri*. The second is a community dominated by S and R-S dinoflagellate species, which were predominantly detected in summer to autumn under thermal stratification conditions, along with a few centric diatoms classified as C-R strategists. The third is a community of neritic R-C and R diatoms that are present during the whole year with no remarkable connection to any oceanographic conditions.

However, an in-deep study under an ecological perspective is still needed to relate biotic factors such as morphological (*e.g.*, size, volume) and physiological characteristics (*e.g.*, C biomass, pigments) of species with changes in oceanographic conditions. This information would help to understand not only community dynamics, but also the plasticity and capacity of species to adapt to changing oceanographic scenarios. Furthermore, efforts should be made to understand community composition and changes in Valparaíso Bay to study biotic interactions among phytoplankton species and with other microorganisms, such as bacteria and viruses, as suggested by recent coastal ecological studies on phytoplankton (Arandia-Gorostidi *et al*. 2022, Flynn *et al*. 2022, Le Reun *et al*. 2022).

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SUPPLEMENTARY MATERIAL

Table S1. Microphytoplankton species identified in Valparaíso Bay from 1986 to 1996. Life strategy classified as the Reynolds C-S-R model / Especies del microfitoplancton identificadas en la Bahía de Valparaíso entre 1986 y 1996. Estrategia de vida en base al modelo C-S-R de Reynolds

Group	Species	Name synonym	Life strategy	Habitat
Ciliate	*Mesodinium rubrum*	-	S	-
Diatom	*Asterionellopsis glacialis*	*Asterionella glacialis*	R	Neritic
	Aulacoseira granulata	*Gaillonella granulata*	-	Fresh water
	Bacteriastrum delicatulum	-	-	Oceanic
	Bacteriastrum hyalinum	-	-	Neritic
	Cerataulina pelagica	*Zygoceros pelagicus*	R	Neritic
	Chaetoceros affinis	-	R	Neritic
	Chaetoceros cinctus	-	R	Neritic
	Chaetoceros compressus	-	R	Neritic
	Chaetoceros constrictus	-	R	Neritic
	Chaetoceros convolutus	-	R	Oceanic
	Chaetoceros curvisetus	-	C-R	Neritic
	Chaetoceros debilis	-	C-R	Neritic
	Chaetoceros decipiens	-	R	Neritic/oceanic
	Chaetoceros diadema	*Syndendrium diadema*	R	Neritic
	Chaetoceros didymus	-	C-R	Neritic
	Chaetoceros lorenzianus	-	C-R	Neritic
	Chaetoceros radicans	-	R	Neritic
	Chaetoceros socialis	-	R	Neritic
	Chaetoceros teres	-	R	Neritic/oceanic
	Chaetoceros tortissimus	-	R	Neritic
	Corethron pennatum	*Corethron criophilum*	-	Oceanic
	Coscinodiscus sp.	-	-	Neritic/oceanic
	Coscinodiscus janischii	-	-	Neritic/oceanic
	Cylindrotheca closterium	*Ceratoneis closterium*	R	Neritic
	Dactyliosolen fragilissimus	*Rhizosolenia fragilissima*	C-R	Neritic
	Detonula pumila	*Lauderia pumila*	C-R	Neritic
	Eucampia biconcava	*Climacodium biconcavum*	-	Oceanic
	Fragilariopsis doliolus	*Synedra doliolus*	-	Neritic/coastal
	Grammatophora marina	*Diatoma marina*	-	Neritic/coastal
	Guinardia delicatula	*Rhizosolenia delicatula*	C-R	Neritic
	Guinardia striata	*Eucampia striata*	-	Neritic
	Lauderia annulata	-	-	Neritic
	Leptocylindrus danicus	-	C-R	Neritic
	Leptocylindrus mediterraneus	*Dactyliosolen mediterraneus*	-	-
	Melosira inflexa	*Melosira moniliformis*	-	Neritic/coastal
	Navicula sp.	-	-	-
	Neomoelleria cornuta	*Eucampia cornuta*	-	Neritic/oceanic
	Nitzschia longissima	*Ceratoneis longissima*	R	Neritic/coastal
	Paralia sulcata	*Gaillonella sulcata*	-	Neritic/coastal
	Pseudo-nitzschia australis	-	-	Neritic
	Pseudo-nitzschia delicatissima	*Nitzschia delicatissima*	-	Neritic
	Rhizosolenia imbricata var. *minuta*	-	-	-
	Skeletonema costatum	*Melosira costata*	C	Neritic
	Thalassionema frauenfeldii	*Asterionella frauenfeldii*	-	Oceanic
	Thalassionema nitzschioides	*Synedra nitzschioides*	C-R	Neritic
	Thalassiosira angulata	*Orthoseira angulata*	-	Neritic
	Thalassiosira mendiolana	-	-	Neritic
	Thalassiosira minuscula	-	-	-
	Thalassiosira sp.	-	-	Neritic/fresh water
	Thalassiosira subtilis	*Podosira subtilis*	-	Neritic/oceanic
Dinoflagellate	*Ceratium pentagonum* f. *robustum*	*Ceratium lineatum* var. *robustum*	-	Oceanic
	Ceratium tripos f. *tripodioides*	*Tripos muelleri*	-	Coastal/oceanic
	Dinophysis fortii	-	-	Neritic/oceanic
	Gymnodinium sp.	-	C-S	Neritic/fresh water
	Polykrikos kofoidii	-	-	-
	Preperidinium meunieri	*Diplopsalis minor*	-	Oceanic
	Prorocentrum gracile	-	C	Neritic/estuarine
	Prorocentrum micans	-	C-S→S	Neritic/estuarine/oceanic
	Protoperidinium brochii	*Peridinium brochii*	-	-
	Protoperidinium pellucidum	-	-	Coastal
	Protoperidinium steinii	*Peridinium steinii*	S	Neritic/oceanic
	Scrippsiella acuminata	*Scrippsiella trochoidea*	C-S→S	Neritic/coastal/estuarine
	Tripos azoricus	*Ceratium azoricum*	-	-
	Tripos furca var. *berghii*	*Ceratium furca* var. *berghii*	S-R	Coastal/estuarine/oceanic
	Tripos fusus	*Ceratium fusus* var. *seta*	S-R	Coastal/estuarine/oceanic
	Tripos lineatus	*Ceratium lineatum*	-	Neritic/oceanic
Silicoflagellate	*Dictyocha fibula*	-	-	Oceanic
	Octactis speculum	*Dictyocha speculum*	-	Neritic/coastal/oceanic

C (invasive-colonist), S (stress-tolerant), R (ruderals)

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