

ARTICLE

# Influence of coastal upwelling on micro-phytoplankton variability at Valparaíso Bay (~33°S), Central Chile

Influencia de la surgencia costera en la variación del micro-fitoplancton en la bahía de Valparaíso (~33°S), Chile central

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**Resumen.** Se analizaron 10 años de datos (1986-1996) registrados en una estación fija ubicada al norte de la bahía de Valparaíso (33°00'S; 71°35'O), con el objetivo de estudiar la influencia de la surgencia costera en la variación temporal del micro-fitoplancton (20-200 µm) y su relación con las condiciones oceanográficas. La surgencia costera mostró un régimen bi-modal asociado al viento, con dominio de vientos S-SO favorables a la surgencia entre septiembre y marzo, seguido de una disminución en la intensidad del viento y un debilitamiento de la surgencia entre abril y agosto. Las condiciones oceanográficas mostraron el afloramiento de agua fría y salada, con alto contenido de nutrientes en primavera (septiembre-noviembre). Sin embargo, en verano bajo intensa surgencia se registraron condiciones de estratificación térmica. Esta estratificación podría asociarse tanto a la radiación solar como a la presencia de un área de sombra de surgencia en la bahía. El periodo de surgencia activa presentó el máximo en la abundancia del micro-fitoplancton, dominado por las diatomeas. Este periodo también se asoció con un aumento en la biomasa y la riqueza del micro-fitoplancton. Durante el periodo de debilitamiento de la surgencia —bajo condiciones homogéneas de temperatura, salinidad y nutrientes— se registró un incremento en diversidad (pero baja abundancia y riqueza) asociado al aumento de dinoflagelados y silicoflagelados. Los resultados muestran un régimen bi-modal del micro-fitoplancton en la bahía en respuesta a los cambios en las condiciones oceanográficas relacionados con el forzante local del viento y las condiciones de mezcla/estratificación.

**Palabras clave:** Micro-fitoplancton, surgencia, viento, estratificación, bahía Valparaíso

**Abstract.** In this work 10 years of data (1986-1996) from a fixed station located in the northern part of Valparaíso Bay (33°00'S; 71°35'W) were analysed to study the influence of coastal upwelling activity on the temporal variation of micro-phytoplankton (20-200 µm) and their relationship with oceanographic conditions. The upwelling activity at the bay was associated to semi-annual wind regime with an intensification of upwelling-favourable S-SW winds from September to March followed by a decrease and the occurrence of downwelling events from April to August. Oceanographic conditions showed the ascent of cold, nutrient-rich salty water in spring (September-November). However, during summertime under highest upwelling index, thermal stratification conditions were registered. This stratification might be associated to either the solar radiation or the presence of an upwelling shadow area in the bay. The upwelling period had the highest micro-phytoplankton abundance mainly dominated by diatoms. This period was associated with an increase in biomass and richness in the bay. Meanwhile during non-upwelling period —under homogenous conditions of temperature, salinity and nutrients— an increase in diversity (but low abundance and richness) associated to dinoflagellates and silicoflagellates was noted. Therefore, the results suggest the presence of a bi-modal regime of micro-phytoplankton in the bay in response to changes in oceanographic conditions related to local wind forcing and mixing/stratification.

**Key words:** Micro-phytoplankton, upwelling, wind, stratification, Valparaíso Bay

## INTRODUCTION

The central-south Chilean coast (~30°-40°S) is a highly dynamic and biological productivity area supported by the upwelling activity (Thiel *et al.* 2007, Escribano & Morales 2012). The phytoplankton in this coastal zone is characterized by the dominance of the micro-phytoplankton (20-200 µm) under upwelling active conditions, typical in spring-summer periods (Anabalón *et al.* 2007). In several bays along this region (Coliumo, Quintay and Valparaíso), *in situ* observations have shown a seasonal pattern of phytoplankton biomass (Chl-*a*) and cell abundance. These patterns are often coupled with seasonal wind-driven

upwelling, mixing/stratification processes and solar radiation (Avaria 1971, Avaria *et al.* 1989, Anabalón *et al.* 2007, 2016; González *et al.* 2007, Correa-Ramírez *et al.* 2012, Corredor-Acosta *et al.* 2015). The intensification of wind-driven upwelling usually observed in spring-summer (September-February) is considered a crucial factor for phytoplankton growth. During these months, upwelled nutrient-rich water fertilizes the photic layer in response to favourable S-SW wind intensification (Shaffer *et al.* 1999, Sobarzo *et al.* 2007, Pinochet *et al.* 2019). This triggers the phytoplankton response via an increment in biomass and cell abundance and impulse the primary production (PP) (González *et al.* 2007, Testa *et al.* 2018).

In this region, the seasonality of micro-phytoplankton has been characterized by a peak of diatoms in the spring/summer followed by dinoflagellates in the austral autumn and succeeded by high levels of flagellates in winter (Montecino *et al.* 2006, Anabalón *et al.* 2007, González *et al.* 2007). This seasonality in the micro-phytoplankton community has been related to changes in environmental factors (temperature, nutrient concentration and light availability). Small flagellates are usually efficient at acquiring nutrients under low nutrient and stratified conditions. Meanwhile, high nutrient concentrations and turbulence can sustain large phytoplankton cells that are better adapted to these conditions than the smaller ones (Margalef 1978, Smayda 1998).

The relationship between seasonal upwelling activity and phytoplankton response has been characterized by a bimodal regime of upwelling *versus* non-upwelling conditions along the coastal area of Central Chile (Anabalón *et al.* 2007, 2016; González *et al.* 2007). First, successive upwelling events induce an increase in phytoplankton biomass and promote diatom populations including chain-forming diatoms in spring/summer under mixing and eutrophication conditions (high nutrient content). Second, dinoflagellates are favoured under stratification (non-upwelling) and oligotrophic (low nutrient content) conditions during the autumn/winter period (Anabalón *et al.* 2007, González *et al.* 2007). However, this seasonal pattern has showed temporal and spatial heterogeneity related to episodic wind-forcing regimes and other hydrographic factors (Thiel *et al.* 2007, Anabalón *et al.* 2016, Testa *et al.* 2018).

Changes in coastal upwelling systems can impact the phytoplankton community. These changes are related to wind-driven upwelling activity that promotes the arrival of nutrients to the surface. However, nutrients from rivers in Central Chile can also impact the phytoplankton (Iriarte *et al.* 2012, Anabalón *et al.* 2016, Aparicio-Rizzo & Masotti 2019). Seasonal freshwater discharge can impact coastal systems during weak upwelling activity periods when nutrient input from rivers can help maintain basal phytoplankton biomass (Chl-*a*) and PP (Léniz *et al.* 2012, Masotti *et al.* 2018, Testa *et al.* 2018). In these areas, with quasi-constant high nutrient concentrations year-round, changes in phytoplankton are not just linked to nutrients availability but also other factors (temperature, salinity, stratification/mixing conditions, or solar radiation).

In Central Chile, the coastal area off Valparaíso Bay has been historically defined by quasi-permanent S-SW upwelling-favourable winds (>50%) with no seasonal pattern in upwelling activity, and the stability of the water column connected to solar radiation (Pizarro 1973, 1976; Avaria *et al.* 1989). Furthermore, recent studies have

detected changes in micro-phytoplankton related to the hydrological conditions on the inter-annual scale with an increment in dinoflagellate abundance after high river discharge events (Aparicio-Rizzo & Masotti 2019).

Studies of micro-phytoplankton in this bay have mostly focused on descriptive phytoplankton species composition (Avaria 1971, 1975; Avaria & Orellana 1975). Two types of phytoplankton community have been described: 1) a spring/summer community characterized by frequent bloom events in chain-forming colonies of a few dominant diatom species with high abundance; and 2) an autumn/winter community composed of heterogeneous phytoplankton with low abundance (Avaria 1971, 1975; Avaria & Orellana 1975). However, physical-chemical oceanographic conditions have never been study at this bay and far from this the relationships between these conditions and the micro-phytoplankton variability remain unknown in this area. Thus, the aim of this study was to characterize the annual variation of micro-phytoplankton and their interaction with meteorological (wind), physical (temperature, salinity, UI), and chemical (inorganic nutrients) variables in Valparaíso Bay using an extended time series of *in situ* data (10 years).

## MATERIALS AND METHODS

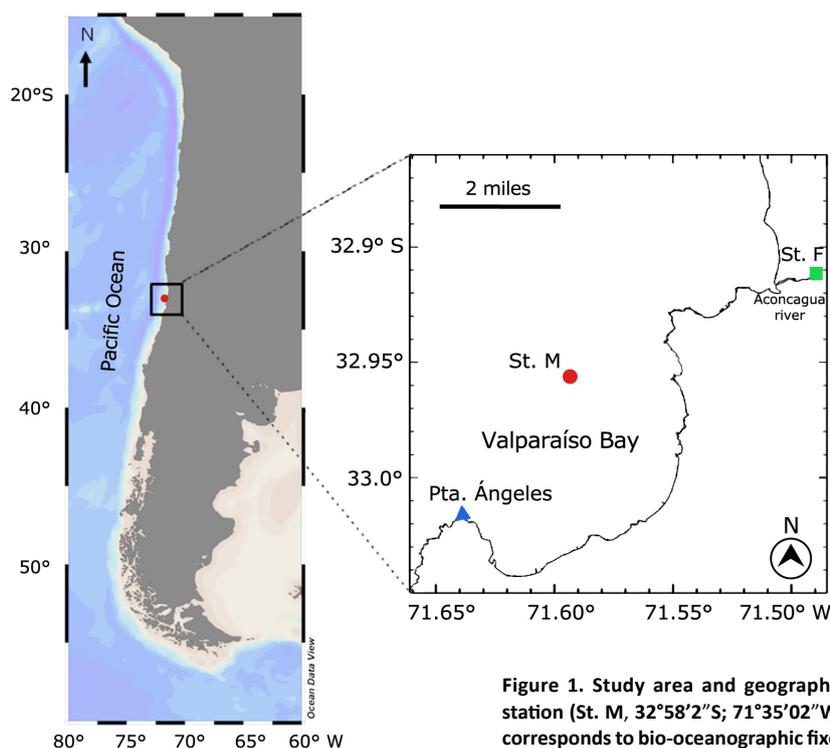
### STUDY AREA

The study area is located in Valparaíso Bay (~32°55'-33°30'S) —a N-NE open embayment flanked by two headlands (Fig. 1). A bio-oceanographic fixed station was located two nautical miles (~3.7 km) from the coast at the north of the bay (St. M; 32°58'2"S; 71°35'02"W); and a depth of ~90 m. Sampling cruises were carried out at this fixed station from October 1986 to December 1996 with intervals of 15 to 30 days. However, no data were registered in February along the time-series.

### METEOROLOGICAL AND OCEANOGRAPHIC DATA

Physical-chemical and biological data were examined using a 10 year time-series (1986-1996) to explore the annual variability of micro-phytoplankton and their relationship with meteorological and oceanographic conditions. Daily wind data (speed and direction), registered every 3 hours (8 values per day), at the “Faro Punta Ángeles” station (33°04'00"S; 71°38'00"W) (Fig. 1) were obtained from the Servicio Meteorológico de la Armada de Chile (SERVIMET)<sup>1</sup>. These data were used to calculate an upwelling index (UI) by Bakun's equation (Bakun 1973) on the first 100 km from the coast.

<sup>1</sup><[www.meteoarmada.directemar.cl](http://www.meteoarmada.directemar.cl)>



**Figure 1.** Study area and geographic location of the bio-oceanographic fixed station (St. M, 32°58'2"S; 71°35'02"W) at Valparaíso Bay, Central Chile. Red circle corresponds to bio-oceanographic fixed station (St. M); green square to Aconcagua river DGA station (St. F) and blue triangle to "Faro Punta Ángeles" meteorological SERVIMET station / Área de estudio y localización geográfica de la estación bio-oceanográfica (St. M, 32°58'2"S; 71°35'02"O) en la bahía de Valparaíso, Chile central. El círculo rojo corresponde a la estación bio-oceanográfica (St. M); el cuadrado verde a la estación de la DGA del río Aconcagua (St. F) y el triángulo azul a la estación meteorológica "Faro Punta Ángeles" del SERVIMET

Daily data of Aconcagua river flow were collected from the Chilean Dirección General de Aguas (DGA)<sup>2</sup> at the San Felipe station (32°55'09"S; 71°30'28"W) (Fig. 1, St. F). At the bio-oceanographic fixed station discrete water samples via a Niskin bottle were collected in the upper 60 m (0, 5, 15, 25, 40 and 55 m depth) to study the variability of temperature, salinity, and nutrients (Nitrate-NO<sub>3</sub><sup>-</sup>, Phosphate-PO<sub>4</sub><sup>3-</sup>, and Silicate-SiO<sub>4</sub><sup>4-</sup>). Temperature (°C) was measured *in situ* via protected reverse-calibrated thermometers arranged in pairs in the sampling bottle. A Tsurumi Seiki digital induction salinometer measured salinity. The Brunt-Väisälä frequency was obtained as a derivate variable using the Ocean Data View (ODV) program (Schlitzer 2019). Nutrient concentrations (μM) were determined via spectrophotometry. PO<sub>4</sub><sup>3-</sup> was measured following Koroleff (1983). The Grasshoff methodology (Grasshoff 1983) was employed to measure NO<sub>3</sub><sup>-</sup>, and SiO<sub>4</sub><sup>4-</sup> according to Parsons *et al.* (1984).

#### PHYTOPLANKTON DATA

Water samples obtained from six depth levels (0, 5, 10, 20, 30 and 50 m depth) were analysed for phytoplankton biomass (Chl-*a*; mg m<sup>-3</sup>). Chl-*a* was analysed by spectrophotometry via a combination of techniques from Lohrenz & Jeffrey (1980) and Parson *et al.* (1984). Cells were counted following Utermöhl (1958) using a Wild M-40 inverted microscope.

#### DATA PROCESSING

Monthly variability reconstructions were developed using 10 years of time-series data (1986-1996) to characterize the physical-chemical conditions and phytoplankton at the bay. For the annual reconstruction, the median (Mdn) and its absolute deviation (MAD) were calculated for all variables from the original data compiled. The meteorological (wind), hydrological (river flow), oceanographic (temperature, salinity, nutrients and UI), and micro-phytoplankton data (biomass and abundance) were categorized according to monthly variability (one year from June to May) and seasons [austral summer (December-February), spring (September-November), autumn (March-May) and winter (June-August)].

<sup>2</sup><www.dga.cl>

The micro-phytoplankton (20-200  $\mu\text{m}$ ) was binned into three main classes: diatoms (Bacillariophyceae), dinoflagellates (Dinophyceae), and silicoflagellates (Dictyochophyceae). The total and relative percentage of abundance (cells  $\text{L}^{-1}$ ) and richness (number of taxa) were calculated at 0 and 10 m. In relation to the biodiversity analysis, different types of diversity indexes were explored (Supplementary Table 1). Menhinick's diversity index was the most statistically significant index in relation to micro-phytoplankton abundance ( $P < 0.05$ ). Dominance was calculated (1-Simpson index) using the whole count data (Zar 1999) in tandem with the diversity index.

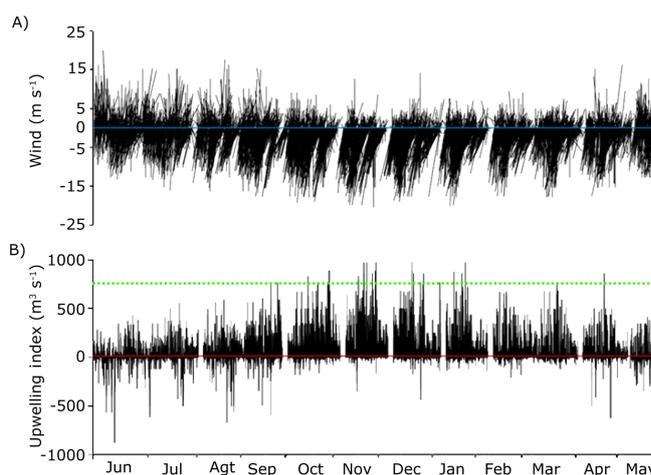
All statistical analysis were performed using data registered in first 15 m with PAST v 3.11 software (Hammer *et al.* 2001). These statistics were based on the uniform phytoplankton vertical distribution described in the bay with cellular density concentrated in the first meters of the water column (0-20 m; Avaria & Orellana 1975) as well as the availability of micro-phytoplankton abundance data only at 0 and 10 m during the study period. Cluster analysis evaluated the similarity in micro-phytoplankton and oceanographic conditions throughout the year. The Bray-Curtis coefficient was used to determine the similarity. Finally, a non-parametric permutational multivariate test of variance (one-way PERMANOVA) assessed the significance differences among groups using a bi-modal regime model based on similarity matrix cluster results.

## RESULTS

### WIND FORCING AND UPWELLING INDEX (UI)

Prevailing equatorward winds (S-SW, Fig. 2) were observed almost through the year in the study area (monthly values  $>50\%$ , Table 1); speeds were  $\sim 2.1$ - $5.7 \text{ m s}^{-1}$  (monthly values 44-57%, Table 2). These equatorward winds (S-SW) intensified between October and February (spring and summer, Mdn  $\sim 70\%$ , Table 1) in coincidence with the highest speed values. During this period an increment of wind up  $11 \text{ m s}^{-1}$  was registered (Table 2; Mdn  $>15\%$ ). The eastward winds (N-NE and E-ES) frequency increased in winter when the S-SW winds decrease ( $\sim 50\%$ , Table 1; Fig. 3).

The upwelling index (UI) at the bay showed persistent upwelling favourable conditions especially from September to March (Fig. 2). In fact, a progressive increase in monthly UI is seen from August to November (Mdn from  $\sim 4.5$  to  $35 \text{ m}^3 \text{ s}^{-1}$ , Table 3). The highest UI values were reached between October and January ( $>750 \text{ m}^3 \text{ s}^{-1}$ , Fig. 2).



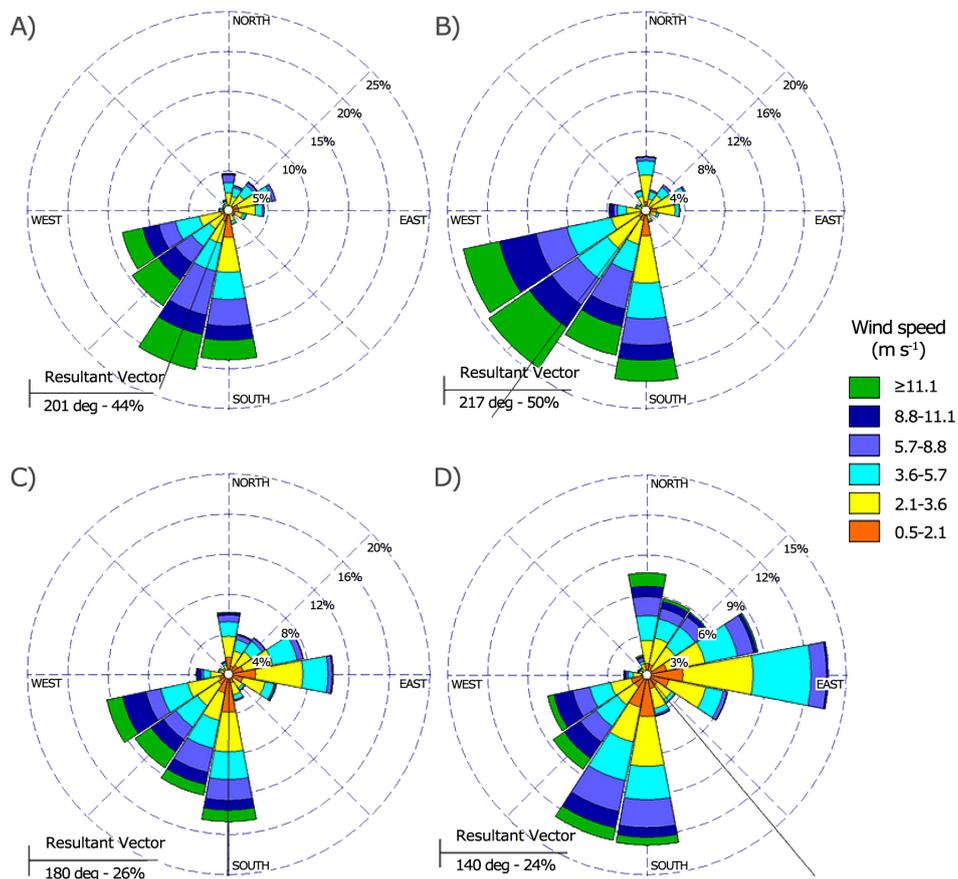
**Figure 2. Monthly variability through daily data of: A) wind vector (speed and direction) and B) upwelling index (UI). Negative direction is equatorward and positive direction is poleward. Green line corresponds to UI values over  $750 \text{ m}^3 \text{ s}^{-1}$  / Variabilidad mensual del: A) viento (velocidad y dirección) y B) índice de surgencia (UI). Valores negativos indican dirección ecuatorial y positivos dirección polar. Línea verde corresponde a valores del UI superiores a  $750 \text{ m}^3 \text{ s}^{-1}$**

**Table 1. Monthly and seasonal frequency (%) of wind direction / Frecuencia (%) mensual y estacional de la dirección del viento**

	N-NE ( $350^{\circ}$ - $90^{\circ}$ )	E-SE ( $90^{\circ}$ - $170^{\circ}$ )	S-SW ( $170^{\circ}$ - $270^{\circ}$ )	N-NW ( $270^{\circ}$ - $350^{\circ}$ )
Jan	16.6	4.5	71.4	7.5
Feb	18.7	7.7	66.0	7.6
Mar	18.6	13.4	60.7	7.3
Apr	27.1	16.0	51.0	5.9
May	29.1	24.3	42.3	4.3
Jun	33.0	24.8	38.2	4.0
Jul	29.3	25.7	40.1	4.9
Agt	27.1	19.9	48.3	4.7
Sep	22.8	12.0	60.7	4.5
Oct	19.8	8.3	67.1	4.8
Nov	13.6	7.0	75.7	3.7
Dec	12.8	6.5	74.6	6.1
Spring (Sep/Oct/Nov)	18.9	9.2	67.5	4.4
Summer (Dec/Jan/Feb)	15.9	6.2	70.8	7.1
Autumn (Mar/Apr/May)	24.9	17.9	51.4	5.8
Winter (Jun/Jul/Agt)	29.9	23.6	42.0	4.5

**Table 2. Monthly and seasonal frequency (%) of wind speed ( $m s^{-1}$ ) / Frecuencia (%) mensual y estacional de la velocidad del viento ( $m s^{-1}$ )**

	Calm	0.5-2.1	2.1-3.6	3.6-5.7	5.7-8.8	8.8-11.0	=/>11.0	Range 2.1-5.7
Jan	-	9.5	27.4	22.9	14.7	10.6	14.9	50.3
Feb	-	15.6	31.6	21.6	13.0	8.8	9.5	53.2
Mar	-	17.7	33.8	22.3	10.2	8.3	7.8	56.0
Apr	0.2	24.1	33.2	20.8	9.5	6.3	9.8	53.0
May	0.1	21.2	31.7	24.9	12.3	6.2	3.7	56.5
Jun	0.1	21.8	30.8	25.1	12.7	6.0	3.6	55.9
Jul	0.1	18.5	32.9	24.1	13.5	7.3	3.5	57.0
Agt	0.2	18.6	29.2	21.9	14.8	8.4	7.0	51.1
Sep	0.1	16.4	25.9	22.5	16.1	9.6	9.5	48.4
Oct	-	15.0	27.2	20.3	15.9	8.3	13.3	47.5
Nov	-	11.1	23.6	20.4	16.4	9.9	18.7	44.0
Dec	-	9.9	25.7	21.1	15.2	11.4	16.7	46.8
Spring (Sep/Oct/Nov)	0.02	14.3	25.6	21.1	16.1	9.24	13.6	46.7
Summer (Dec/Jan/Feb)	-	11.6	28.2	21.8	14.4	10.29	13.8	50.0
Autumn (Mar/Apr/May)	0.1	20.9	32.6	22.7	10.7	6.98	6.1	55.2
Winter (Jun/Jul/Agt)	0.1	19.7	31.0	23.8	13.7	7.19	4.6	54.8



**Figure 3. Seasonal pattern of wind data off Valparaíso Bay: A) Spring, B) Summer, C) Autumn and D) Winter / Patrón estacional del viento en la bahía de Valparaíso: A) Primavera, B) Verano, C) Otoño y D) Invierno**

The lowest UI values were registered from April to August (Mdn  $\sim 1.7$ - $4.5 \text{ m}^3 \text{ s}^{-1}$ , Table 3), with an increment in downwelling events occurrence (Fig. 2). Likewise, an increase in the frequency of poleward winds were seen during this period (N-NE; Mdn  $\sim 30\%$ , Table 1, Fig. 3) along with relaxation periods (Fig. 2, Table 2). Besides there was an increment in weak wind speed values ( $\sim 0.5$ - $2.1 \text{ m s}^{-1}$ ) during this period (Table 2; Mdn  $\sim 20\%$ ). On the seasonal scale, the UI showed the highest values in spring and summer. Minimum value was registered in winter with an UI median value almost ten-fold lower than summer (Table 3).

#### HYDROLOGICAL AND OCEANOGRAPHIC CONDITIONS

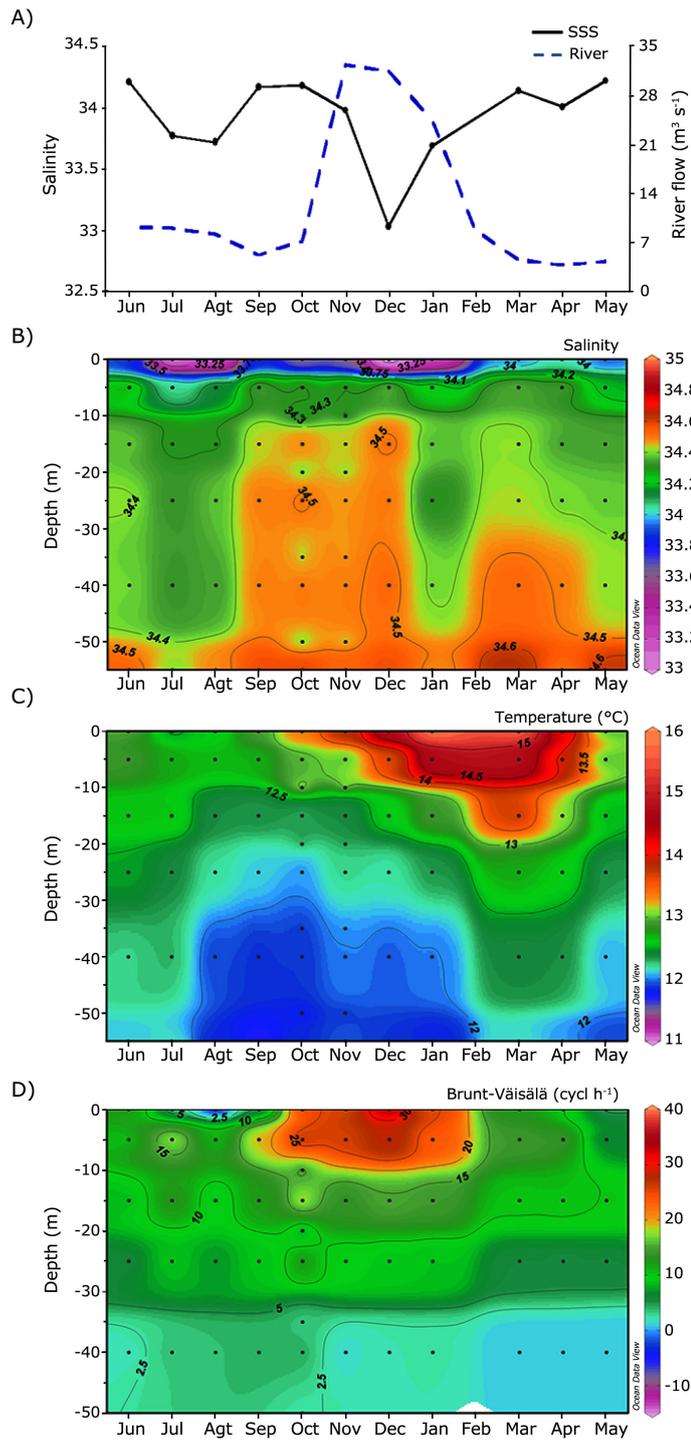
The Aconcagua River displayed high discharge values from November to January (Mdn from  $\sim 32.4$  to  $24.5 \text{ m}^3 \text{ s}^{-1}$ , Table 3); lower values were seen from June to August (Mdn  $\sim 9 \text{ m}^3 \text{ s}^{-1}$ , Table 3) and the minimum was in March to May (Mdn  $\sim 4 \text{ m}^3 \text{ s}^{-1}$ , Table 3). In this sense, a low surface salinity (Mdn  $\sim 33.0$ - $33.2$ ) was seen from November-January and June-August at the fixed station with a sea surface salinity (SSS, Fig. 4A and B) associated with Aconcagua River discharge influence in the bay.

The water column's salinity minimum occurred in July (0-60 m), and the maximum was during September-December with the arrival of salty and cold deep water (Fig. 4B). However, not important differences between seasons were seen in the first 15 m of water column salinity (Table 3). The temperature was low during August-November (Mdn  $\sim 12.4$ - $12.8 \text{ }^\circ\text{C}$ , Table 3) (Fig. 4C). Meanwhile, progressive warming in the upper layer ( $\sim 0$ - $10 \text{ m}$ ) was observed from November to April (Fig. 4C) with a noticeable thermal stratification in January-April (Fig. 4C) when the highest temperatures were registered (Mdn  $\sim 13.5$ - $14.8 \text{ }^\circ\text{C}$ , Table 3). Summer and autumn had the highest temperature median values *versus* spring and winter when the lowest values were registered (Table 3).

The Brunt-Väisälä frequency showed high values from October to January in the upper layer ( $<10 \text{ m}$ ) (Fig. 4D), whereas a vertical homogenization was detected from March to August (Fig. 4D). Therefore, autumn and winter had a mixed water column, and late spring and summer showed a more stratified condition (Fig. 4D).

**Table 3. Monthly and seasonal variability (Mdn $\pm$ MAD) of: Upwelling index (UI), river flow, temperature, salinity and nutrients (Nitrate- $\text{NO}_3^-$ , Phosphate- $\text{PO}_4^{3-}$  and Silicate- $\text{SiO}_4^{4-}$ ) in the first 15 m depth / Variabilidad mensual y estacional (Mdn $\pm$ MAD) del: Índice de surgencia (UI), caudal del río, temperatura, salinidad y nutrientes (Nitrato- $\text{NO}_3^-$ , Fosfato- $\text{PO}_4^{3-}$  y Silicato- $\text{SiO}_4^{4-}$ ) en los primeros 15 m de profundidad**

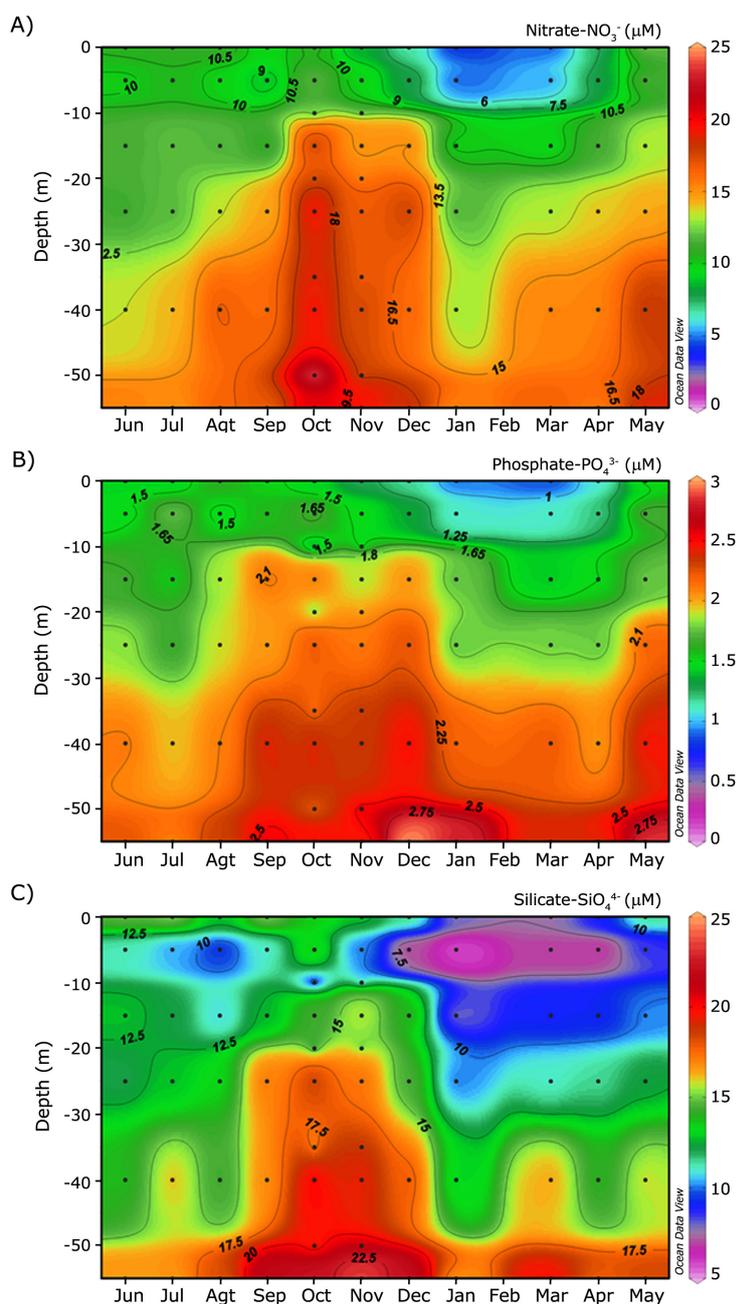
	UI ( $\text{m}^3 \text{ s}^{-1}$ )	River ( $\text{m}^3 \text{ s}^{-1}$ )	Temperature ( $^\circ\text{C}$ )	Salinity	$\text{NO}_3^-$ ( $\mu\text{M}$ )	$\text{PO}_4^{3-}$ ( $\mu\text{M}$ )	$\text{SiO}_4^{4-}$ ( $\mu\text{M}$ )
Jan	22.9 $\pm$ 31.4	24.5 $\pm$ 20.8	14.3 $\pm$ 1.4	34.29 $\pm$ 0.19	2.95 $\pm$ 2.15	1.10 $\pm$ 0.56	5.06 $\pm$ 3.14
Feb	12.0 $\pm$ 20.1	8.8 $\pm$ 6.0	-	-	-	-	-
Mar	8.9 $\pm$ 15.9	4.5 $\pm$ 2.8	14.7 $\pm$ 0.8	34.26 $\pm$ 0.16	5.07 $\pm$ 3.70	0.91 $\pm$ 0.37	7.08 $\pm$ 3.59
Apr	4.3 $\pm$ 10.5	3.8 $\pm$ 1.9	13.5 $\pm$ 0.7	34.24 $\pm$ 0.19	8.65 $\pm$ 4.30	1.25 $\pm$ 0.31	7.77 $\pm$ 1.79
May	2.5 $\pm$ 10.3	4.3 $\pm$ 2.8	12.9 $\pm$ 0.5	34.27 $\pm$ 0.19	12.05 $\pm$ 2.81	1.41 $\pm$ 0.36	9.25 $\pm$ 3.65
Jun	1.7 $\pm$ 10.5	9.2 $\pm$ 5.5	12.8 $\pm$ 0.8	34.30 $\pm$ 0.15	9.60 $\pm$ 3.59	1.23 $\pm$ 0.36	12.90 $\pm$ 4.90
Jul	2.1 $\pm$ 11.8	9.0 $\pm$ 5.9	12.6 $\pm$ 0.6	34.14 $\pm$ 0.25	11.00 $\pm$ 5.55	1.41 $\pm$ 0.44	10.10 $\pm$ 4.95
Agt	4.5 $\pm$ 16.5	8.2 $\pm$ 5.2	12.5 $\pm$ 0.5	34.14 $\pm$ 0.24	9.00 $\pm$ 4.00	1.52 $\pm$ 0.58	9.40 $\pm$ 4.40
Sep	10.0 $\pm$ 23.6	5.2 $\pm$ 4.4	12.4 $\pm$ 0.5	34.39 $\pm$ 0.10	7.14 $\pm$ 4.84	1.62 $\pm$ 0.48	10.59 $\pm$ 6.21
Oct	13.9 $\pm$ 26.9	7.1 $\pm$ 6.8	12.7 $\pm$ 0.8	34.32 $\pm$ 0.14	13.08 $\pm$ 4.53	1.72 $\pm$ 0.52	11.40 $\pm$ 5.35
Nov	35.0 $\pm$ 40.1	32.4 $\pm$ 18.4	12.8 $\pm$ 0.9	34.36 $\pm$ 0.20	9.94 $\pm$ 6.07	1.58 $\pm$ 0.46	11.63 $\pm$ 5.95
Dec	27.8 $\pm$ 34.7	31.5 $\pm$ 20.7	13.4 $\pm$ 1.0	34.35 $\pm$ 0.25	7.48 $\pm$ 5.88	1.36 $\pm$ 0.50	7.32 $\pm$ 5.14
Spring (Sep/Oct/Nov)	17.8 $\pm$ 29.8	11.6 $\pm$ 10.7	12.6 $\pm$ 0.7	34.34 $\pm$ 0.17	10.80 $\pm$ 5.51	1.63 $\pm$ 0.45	11.30 $\pm$ 5.64
Summer (Dec/Jan)	20.0 $\pm$ 28.4	23.2 $\pm$ 18.4	13.7 $\pm$ 1.3	34.31 $\pm$ 0.23	5.43 $\pm$ 4.17	1.26 $\pm$ 0.50	6.10 $\pm$ 4.10
Autumn (Mar/Apr/May)	4.9 $\pm$ 11.9	4.1 $\pm$ 2.4	13.5 $\pm$ 0.9	34.26 $\pm$ 0.18	8.65 $\pm$ 4.45	1.19 $\pm$ 0.38	7.80 $\pm$ 2.73
Winter (Jun/Jul/Agt)	2.2 $\pm$ 11.7	8.9 $\pm$ 5.5	12.6 $\pm$ 0.6	34.18 $\pm$ 0.22	9.40 $\pm$ 4.70	1.41 $\pm$ 0.50	10.26 $\pm$ 4.74



**Figure 4. Monthly variability of: A) Aconcagua river flow (blue line) and Sea Surface Salinity (SSS; black line), B) Salinity, C) Temperature and D) Brunt-Väisälä frequency in the water column (0-60 m) / Variabilidad mensual del: A) Caudal del río Aconcagua (línea azul) y la Salinidad Superficial (SSS; línea negra), B) Salinidad, C) Temperatura y D) Frecuencia de Brunt-Väisälä en la columna de agua (0-60 m)**

The inorganic nutrient concentrations ( $\text{NO}_3^-$ ,  $\text{PO}_4^{3-}$ ,  $\text{SiO}_4^{4-}$ ) were lowest under an intensified thermocline (<15 m) from January to April (Fig. 5) especially for nitrate and silicate (Mdn  $\text{NO}_3^-$  ~2.9-8.6  $\mu\text{M}$  and  $\text{SiO}_4^{4-}$  ~5.1-7.8  $\mu\text{M}$ ; Table 3). Furthermore, from September to December, high values of nutrients were associated to salty-cold deep water rises to the surface (Figs. 4 and 5). Nitrate monthly values ranged between 7.1 and 13.1  $\mu\text{M}$  (Spring Mdn ~10.8  $\mu\text{M}$ )

and silicate from 7.3 to 11.6  $\mu\text{M}$  (Spring Mdn ~11.3  $\mu\text{M}$ ) (Table 3). Although phosphate had a similar temporal pattern, this nutrient remained relatively constant with values ranging between 0.9 and 1.7  $\mu\text{M}$  throughout the year (Table 3). At seasonal scale, spring had the highest nutrient concentrations that coincided with active upwelling period but also high river discharges. Summer had the lowest nitrate and silicate concentrations (Table 3).



**Figure 5. Monthly variability of nutrients concentration in the water column (0-60 m): A) Nitrate- $\text{NO}_3^-$ , B) Phosphate- $\text{PO}_4^{3-}$  and C) Silicate- $\text{SiO}_4^{4-}$  / Variabilidad mensual de la concentración de nutrientes en la columna de agua (0-60 m): A) Nitrato- $\text{NO}_3^-$ , B) Fosfato- $\text{PO}_4^{3-}$  y C) Silicato- $\text{SiO}_4^{4-}$**

## PHYTOPLANKTON

Phytoplankton biomass (Chl-*a*) showed a sub-surface maximum (~5-10 m) especially from October to March (Mdn range ~2.60-4.60 mg m<sup>-3</sup>; Table 4); low Chl-*a* values were registered from April-August period (Mdn ~2-0.5 mg m<sup>-3</sup>). In fact, winter showed low Chl-*a* with biomass barely reaching 1 mg m<sup>-3</sup> in the water column (Table 4); spring and summer had the highest biomass values (Table 4).

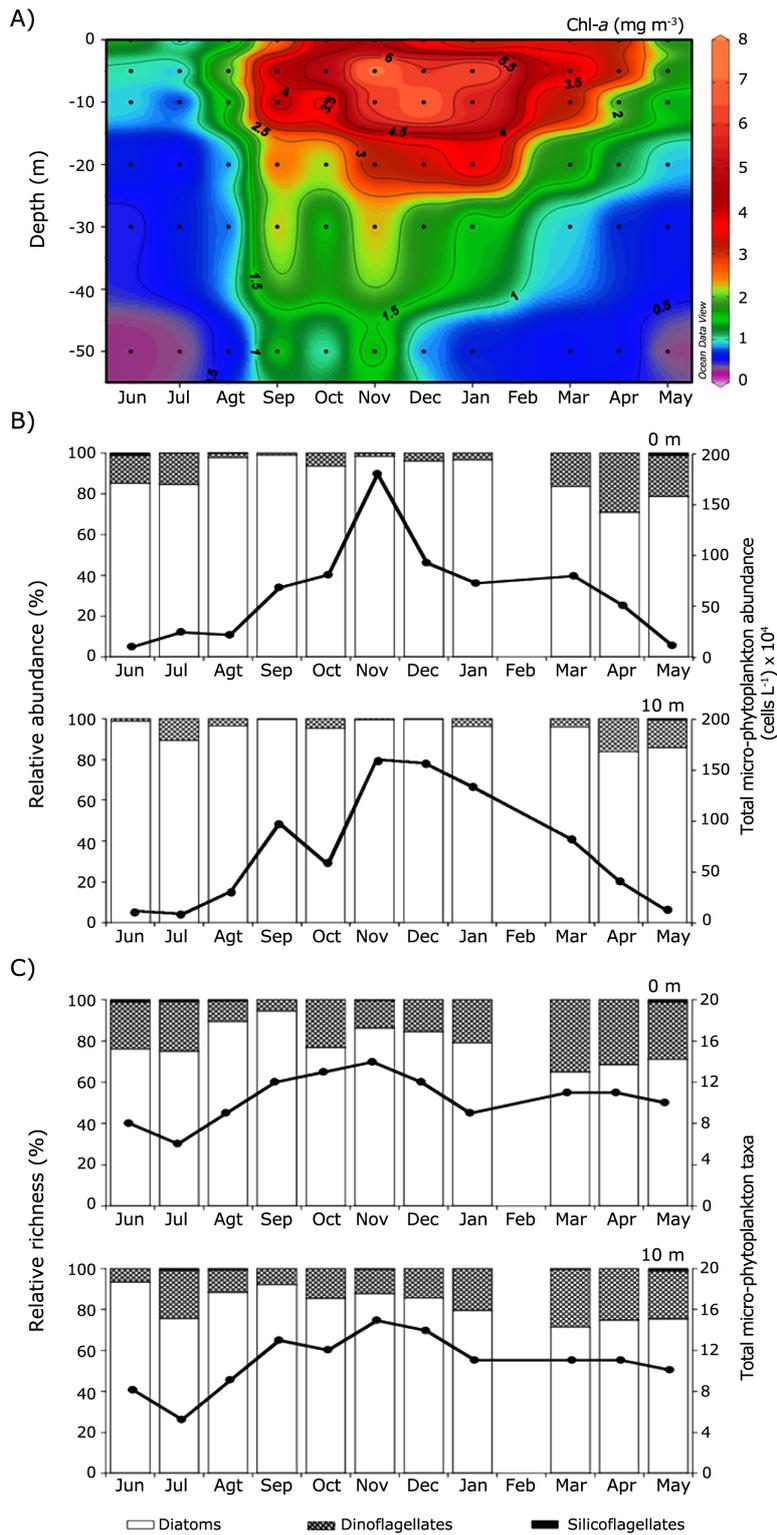
The total micro-phytoplankton abundance was high from September to March with the highest values in November (180.3-159.6 x 10<sup>4</sup> cells L<sup>-1</sup> at 0 and 10 m, respectively) (Fig. 6B, Table 4). The abundance was low from May to August (Fig. 6, Table 4). In relation to the total micro-phytoplankton taxa, similar values of richness were registered along the year with a slight decrease from June to August, in winter, when the lowest abundance and richness were registered (Fig. 6C, Table 4).

Dinoflagellate abundance was considerably lower than diatoms (10-220 fold lower) (Table 4). Diatoms abundance was highest from September to March; whereas dinoflagellates were highest from March to April (Table 4). The dinoflagellates displayed seasonal highest abundance in autumn, and diatoms peaks in spring/summer (Table 4).

Relative values (%) of richness and abundance were quite similar at 0 and 10 m depth. Diatoms dominated in the bay especially between August and January when high percentages are registered at 0 and 10 m (~71-99.5% of abundance and ~65-94.5 % of richness) (Fig. 6B and C). On the other hand, dinoflagellates had high values from March to July (~15-30% of abundance and ~20-35% of richness) (Fig. 6B and C). Meanwhile, silicoflagellates were only present from May to August with very low values for abundance (~0.05-1.25%) and richness (~0.4-1.4%) (Fig. 6B and C).

**Table 4. Monthly and seasonal variability of phytoplankton biomass (Chl-*a*), total micro-phytoplankton abundance and richness, and diatoms and dinoflagellates abundance / Variabilidad mensual y estacional de la biomasa del fitoplancton (Chl-*a*), abundancia y riqueza total del micro-fitoplancton; y abundancia de diatomeas y dinoflagelados**

	Chl- <i>a</i> (mg m <sup>-3</sup> )	Total abundance (cells L <sup>-1</sup> ) x 10 <sup>4</sup>		Diatoms abundance (cells L <sup>-1</sup> ) x 10 <sup>4</sup>		Dinoflagellates abundance (cells L <sup>-1</sup> ) x 10 <sup>4</sup>		Total richness	
		0 m	10 m	0 m	10 m	0 m	10 m	0 m	10 m
Jan	3.0 ± 1.9	73.0 ± 97.2	132.6 ± 140.5	72.8 ± 97.2	132.3 ± 140.5	0.3 ± 0.5	0.5 ± 1.0	9 ± 5	11 ± 6
Feb	-	-	-	-	-	-	-	-	-
Mar	3.1 ± 1.7	79.9 ± 123.4	82.1 ± 112.2	77.0 ± 124.2	81.3 ± 112.1	6.4 ± 10.8	1.0 ± 2.1	11 ± 6	11 ± 6
Apr	2.1 ± 1.4	50.9 ± 62.3	40.1 ± 77.0	36.2 ± 47.9	37.7 ± 78.8	19.7 ± 53.7	5.5 ± 16.1	11 ± 5	11 ± 5
May	1.2 ± 0.6	11.6 ± 23.1	11.6 ± 16.8	11.7 ± 23.6	12.5 ± 17.2	0.5 ± 0.9	0.2 ± 0.3	10 ± 5	10 ± 5
Jun	0.7 ± 0.2	10.3 ± 18.7	11.7 ± 19.6	11.4 ± 19.5	11.6 ± 19.6	0.2 ± 0.2	0.1 ± 0.2	8 ± 5	8 ± 6
Jul	0.5 ± 0.3	24.6 ± 111.6	84.5 ± 37.8	27.0 ± 117.0	8.9 ± 38.4	0.2 ± 0.5	0.02 ± 0.02	6 ± 4	5 ± 4
Agt	0.9 ± 0.6	21.8 ± 34.2	30.1 ± 47.7	21.8 ± 34.2	30.1 ± 47.7	0.1 ± 0.2	0.03 ± 0.02	9 ± 5	9 ± 5
Sep	1.5 ± 1.0	68.6 ± 104.7	97.1 ± 132.0	68.6 ± 104.7	97.1 ± 132.0	0.1 ± 0.1	0.2 ± 0.2	12 ± 5	13 ± 6
Oct	2.6 ± 1.7	81.4 ± 117.9	56.6 ± 64.2	84.8 ± 119.3	59.0 ± 64.5	0.2 ± 0.3	0.1 ± 0.1	13 ± 6	12 ± 8
Nov	4.6 ± 2.9	180.3 ± 257.5	159.6 ± 172.3	180.1 ± 257.5	159.5 ± 172.3	0.3 ± 0.4	0.2 ± 0.2	14 ± 5	15 ± 6
Dec	3.7 ± 2.9	93.0 ± 150.3	156.3 ± 188.3	92.8 ± 150.3	156.2 ± 188.4	0.3 ± 0.5	0.2 ± 0.3	12 ± 5	14 ± 6
Spring (Sep/Oct/Nov)	3.1 ± 2.3	116.9 ± 189.3	109.7 ± 140.5	116.8 ± 189.3	111.0 ± 140.9	0.2 ± 0.3	0.1 ± 0.2	13 ± 5	13 ± 7
Summer (Dec/Jan)	3.5 ± 2.4	83.4 ± 126.8	145.8 ± 167.7	83.2 ± 126.8	145.6 ± 167.7	0.3 ± 0.5	0.3 ± 0.7	11 ± 5	13 ± 6
Autumn (Mar/Apr/May)	1.9 ± 1.3	50.3 ± 89.5	47.6 ± 86.6	45.0 ± 87.4	47.9 ± 87.9	8.7 ± 30.7	2.1 ± 8.9	11 ± 6	11 ± 5
Winter (Jun/Jul/Agt)	0.7 ± 0.3	19.4 ± 68.1	17.6 ± 39.0	20.6 ± 70.2	17.9 ± 39.2	0.2 ± 0.4	0.04 ± 0.07	8 ± 5	7 ± 5

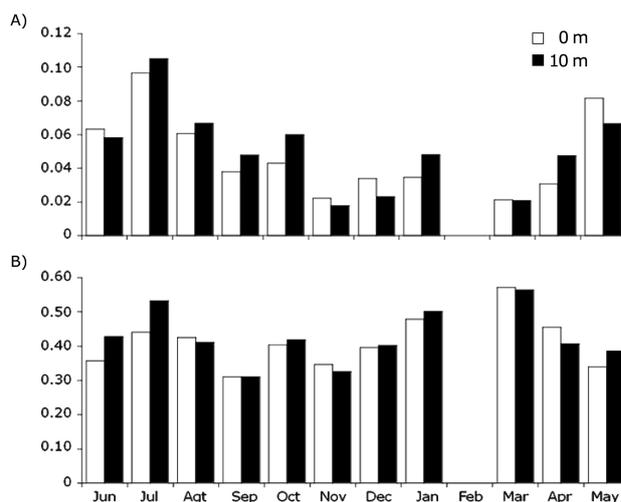


**Figure 6. Monthly variability of: A) phytoplankton biomass (Chl-*a*), B) micro-phytoplankton groups relative (histogram) and total abundance (line) (0 and 10 m depth) and C) micro-phytoplankton groups relative (histogram) and total richness (line) (0 and 10 m depth). Median monthly values (line) are indicated in Table 4 / Variabilidad mensual de: A) biomasa del fitoplancton (Chl-*a*), B) abundancia relativa de los grupos (histograma) y abundancia total (línea) del micro-fitoplancton (0 y 10 m de profundidad) y C) riqueza relativa de los grupos (histograma) y riqueza total (línea) del micro-fitoplancton (0 y 10 m de profundidad). Los valores de la mediana mensual (línea) están indicados en la Tabla 4**

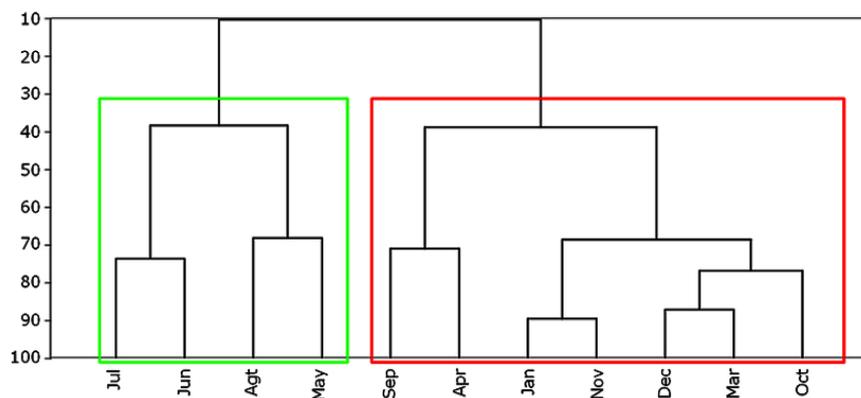
The ecological indexes of the micro-phytoplankton community displayed a generally low diversity at both 0 and 10 m throughout the year ( $\sim 0.02$ - $0.11$ ; Fig. 7A). However, there was some variability with high Menhinick index values in May and July and lower ones in November, December and March (Fig. 7A and B; Supplementary Table 1). Nevertheless, dominance was relatively constant year-round ( $\sim 0.3$ - $0.55$ ; Fig. 7B; Supplementary Table 1).

Finally, cluster analysis studied the relationship among environmental conditions and micro-phytoplankton in the bay at monthly scale considering the oceanographic variables of temperature, salinity, nutrient concentrations ( $\text{NO}_3^-$ ,  $\text{PO}_4^{3-}$ ,  $\text{SiO}_4^{4-}$ ), and UI along with the phytoplankton biomass (Chl-*a*), and the abundance of diatoms and dinoflagellates (Fig. 8).

This cluster analysis showed relatively low similarity percentages, and two monthly periods can be distinguished: September to April and May to August (similarity of  $\sim 40\%$ ; Fig. 8). A one-way PERMANOVA test showed significant differences between these periods (pseudo- $F=12.35$ ,  $P < 0.01$ ).



**Figure 7. Monthly variability of: A) Diversity (Menhinick Index) and B) Dominance (1-Simpson) of micro-phytoplankton at 0 and 10 m depth / Variabilidad mensual de: A) Diversidad (Índice de Menhinick) y B) Dominancia (1-Simpson) del micro-fitoplancton a 0 y 10 m de profundidad**



**Figure 8. Cluster analysis according to micro-phytoplankton (biomass and groups abundance) and oceanographic variables. Two periods grouped: May-August period (green square) and September-April period (red square) / Análisis Cluster del micro-fitoplancton (biomasa y abundancia de los grupos) y las variables oceanográficas. Dos periodos se agruparon: mayo-agosto (cuadrado verde) y septiembre-abril (cuadrado rojo)**

## DISCUSSION

The results showed quasi-permanent S-SW favourable coastal upwelling winds along the year (~40-75%) similar to the wind temporal patterns previously described in Valparaíso Bay (Pizarro 1973, Reyes & Romero 1977). However, a detailed analysis identified two climatological periods with an annual signal in wind regime characterized by maximum in spring-summer and minimum during autumn-winter periods (Fig. 3) in agree with previous studies along central-south Chile (Shaffer *et al.* 1999, Narváez *et al.* 2004, Sobarzo *et al.* 2007). Intense S-SW winds and high wind speeds have been described during spring and summer. This is in contrast to the autumn/winter period when weak easterly winds increase in the bay with a shift from the southwest to the east winds. This temporal pattern in the winds at Valparaíso Bay contrast with the shift from the southwest to the north-northwest described by Sobarzo *et al.* (2007) at Concepcion Bay.

The wind regime at Valparaíso Bay (~33°S) was connected to the upwelling activity (UI): The period from September to March (spring/summer) had the highest values followed by a decrease and downwelling events from April to August (autumn/winter). This coastal upwelling activity forced by the seasonally variable wind was also reflected in the oceanographic conditions of the bay. The oceanographic conditions from September to March -under intense upwelling activity- were characterized by the ascent of cold, nutrient-rich salty water in spring (September-November) followed by the development of core thermal stratification conditions in summer (December-March). These temporal temperature patterns have been described at other bays along central Chile including Concepcion (~36.5°S) and Cartagena (~33.5°S) where temperature has been linked to both upwelling activity and solar radiation (Narváez *et al.* 2004, Sobarzo *et al.* 2007, Testa *et al.* 2018). However, the temperature increase in summer under active upwelling has been associated not only with solar radiation but also with local warm-water pockets called upwelling shadows (Narváez *et al.* 2004, Thiel *et al.* 2007). Factors related to the rise of these warm water features include the coastal orientation of the bay (N-NE) and the location of the study area downstream of headlands. These factors correspond well to the study area at Valparaíso Bay. Nevertheless, the definition of an upwelling shadow area cannot be confirmed due to the bay's unknown physical dynamics.

The development of a nutricline has also been observed at Valparaíso Bay in the summer. This pattern is related to both the thermal stratification conditions preventing the arrival of nutrient-rich water to the upper layer (0-15 m) as well as the acquisition of spring upwelled nutrients by phytoplankton. In contrast, the autumn/winter period has homogenous conditions in the first few meters of the water column (temperature, salinity, and nutrients); this homogeneity is associated with weakening of upwelling activity.

This pattern coincided with the typical cycle of upwelling *versus* downwelling conditions (named bi-modal regime) described in coastal systems governed by favourable upwelling winds (Anabalón *et al.* 2007, 2016; Thiel *et al.* 2007). The coastal region of central Chile (~30°-40°S) has an intensification of upwelling-favourable S-SW winds during austral spring/summer period. This is accompanied by a combination of high temperature, salinity, and nutrient concentrations. Meanwhile, a non-upwelling period was seen by colder and less saline water in the surface layer (Montecino *et al.* 2006, Anabalón *et al.* 2007, 2016; Thiel *et al.* 2007).

However, this bi-modal regime is highly heterogeneous due to changes in topography, solar radiation, and freshwater river discharge (Sobarzo *et al.* 2007, Anabalón *et al.* 2016, Testa *et al.* 2018). Therefore, recent studies have suggested changes in the upwelling *versus* non-upwelling cycle at Concepcion Bay (~36.5°S) due to the key role of river discharge in coastal systems (Testa *et al.* 2018). In this bay high nutrient concentrations have been described along the year associated to Itata river input and coastal upwelling activity with peaks in winter and spring, respectively (Léniz *et al.* 2012, Anabalón *et al.* 2016, Masotti *et al.* 2018).

At Valparaíso Bay the Aconcagua river plume arrives as seen via salinity changes. However, the river discharge did not impact nutrient availability. Nutrients concentrations showed a bi-modal regime connected essentially with local wind-driven upwelling. Coastline orientation, distance from river mouth to fixed station (~6 km; Fig. 1), low river flow (~4-32 m<sup>3</sup> s<sup>-1</sup>), and the coincidence in time of maximum river discharge and upwelling activity (spring) could explain the river's weak influence on the seasonal scales in terms of the bay's oceanographic conditions.

Changes (both biomass and cell abundance) in phytoplankton at Valparaíso Bay at the annual scale are related to upwelling activity. These changes are not related to river discharge as seen in other coastal upwelling systems, (*e.g.*, California/Oregon, NW Iberian-Portugal coasts), or even in central-south Humboldt area. In those areas, freshwater input leads to changes in phytoplankton structure, biomass (Chl-*a*) and PP (Warrick *et al.* 2005, Silva *et al.* 2009, Iriarte *et al.* 2012, Léniz *et al.* 2012, Masotti *et al.* 2018, Testa *et al.* 2018, Aparicio-Rizzo & Masotti 2019).

The intensification of wind-driven upwelling in spring/summer (September/February) at Valparaíso Bay is a key factor for phytoplankton temporal variability. Here, 10 years of data processing characterized the annual cycle of phytoplankton biomass (Chl-*a*) with a sub-surface maximum (5-10 m) from October to March (spring/summer). This agrees with the highest micro-phytoplankton total abundance values which are triggered by the upwelled nutrient-rich water into the upper layer. The May-August period has the lowest micro-phytoplankton total abundance

and biomass. This relationship between coastal upwelling activity and increased phytoplankton biomass (Chl-*a*) and abundance in the spring/summer period has been described previously along central Chile (Avaria *et al.* 1989, Thiel *et al.* 2007, Correa-Ramirez *et al.* 2012).

Differences in micro-phytoplankton are also detected between upwelling and non-upwelling periods. The micro-phytoplankton community in Valparaíso Bay is largely constituted of diatoms and dinoflagellates with very scarce abundance of silicoflagellates. Although diatoms clearly dominate year-round, (Avaria 1971, 1975; Avaria & Orellana 1975, Avaria *et al.* 1989), maximum abundance is detected during the upwelling-active period in coincidence with highest biomass and richness values. An opposite pattern in terms of low biomass, total abundance, and richness has been described during the non-upwelling period (autumn/winter). Here, increases in diversity were observed in relation to an increment in dinoflagellates and silicoflagellates. These results confirmed a bi-modal regime of phytoplankton in the bay as postulated previously (Yáñez 1948, Avaria 1971, 1975; Avaria & Orellana 1975, Pizarro 1973, 1976). Changes in phytoplankton from diatoms to dinoflagellates are related to upwelling activity and stability conditions in the water column. This is similar to other studies along coastal upwelling systems in California, N-NW Africa, and even in Humboldt (Margalef 1978, Avaria *et al.* 1989, Smayda 1998, González *et al.* 2007, Ochoa *et al.* 2010).

In summary, this study provides evidence supporting the plausible causal relationship between meteorological (wind) and oceanographic variability in Valparaíso Bay. The local wind-forced upwelling regulates oceanographic conditions that trigger micro-phytoplankton response in the bay. In this sense the results suggest that a bi-modal regime of upwelling *versus* non-upwelling conditions regulates micro-phytoplankton in Valparaíso Bay.

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## SUPPLEMENTARY TABLE

**Table 1. Monthly variability of ecological diversity analysis at 0 and 10 m / Variación mensual del análisis de diversidad ecológica a 0 y 10 m**

	Shannon (H)		Menhinick		Margalef		Simpson (1-D)		Dominance (D)	
	0 m	10 m	0 m	10 m	0 m	10 m	0 m	10 m	0 m	10 m
Jan	1.153	1.144	0.035	0.048	0.675	0.823	0.522	0.499	0.478	0.501
Feb	1.037	-	0.027	-	0.849	-	0.471	-	0.529	-
Mar	0.916	0.941	0.021	0.021	0.792	0.779	0.429	0.436	0.571	0.564
Apr	1.185	1.335	0.031	0.048	0.835	0.879	0.545	0.592	0.455	0.408
May	1.455	1.399	0.082	0.067	0.860	0.849	0.661	0.614	0.339	0.386
Jun	1.376	1.214	0.063	0.058	0.658	0.603	0.643	0.572	0.357	0.428
Jul	1.106	0.974	0.097	0.105	0.526	0.513	0.559	0.467	0.441	0.533
Agt	1.259	1.268	0.061	0.067	0.718	0.744	0.574	0.589	0.426	0.411
Sep	1.608	1.628	0.038	0.048	0.895	0.928	0.689	0.690	0.311	0.310
Oct	1.392	1.340	0.043	0.060	0.965	0.884	0.596	0.581	0.404	0.418
Nov	1.485	1.558	0.022	0.018	0.962	1.012	0.654	0.675	0.346	0.325
Dec	1.333	1.347	0.034	0.023	0.853	0.960	0.603	0.597	0.397	0.403