ARTICLE

# Variability of environmental heterogeneity in northern Patagonia, Chile: effects on the spatial distribution, size structure and abundance of chlorophyll-*a*

Variabilidad de la heterogeneidad ambiental en la Nor-Patagonia, Chile: efectos sobre la distribución espacial, abundancia y estructura de tamaños de la clorofila-*a*

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**Resumen**.- La cadena de islas incluyendo Desertores-Apiao y Quemchi situada en el Mar Interior de Chiloé, en la Patagonia chilena norte (41-44°S), actúa como una barrera natural para el flujo de agua en dirección norte-sur que influye en el intercambio y circulación entre las micro cuencas norte y sur. La micro cuenca norte se caracteriza por el dominio de las aguas estuarinas superficiales mientras que la micro cuenca sur se encuentra afectada por aguas Subantárticas y Ecuatoriales Subsuperficiales desde el océano costero adyacente. Esta situación determina diferencias claves en la distribución espacial, abundancia y composición por tamaño de la biomasa autotrófica (medida como clorofila-*a*). Estas diferencias cuali y cuantitativas de clorofila-*a* se evaluaron en dos épocas contrastantes durante expediciones en 2004 y 2005 (Cruceros de Investigación Marina, CIMAR 10 y 11 Fiordos). En ambas micro cuencas, se analizaron parámetros físicos, químicos y bio-ópticos de la capa de mezcla superficial junto con imágenes satelitales compuestas de 8 días de clorofila-*a* (MODIS-AQUA). La principal diferencia de la heterogeneidad ambiental entre zonas fue determinada por la concentración de nitratos y ácido silícico. En primavera la abundancia de la clorofila-*a* mostró alta variabilidad en ambas micro cuencas y con predominancia del micro-fitoplancton. En el invierno austral el micro-fitoplancton también fue dominante en una amplia gama de condiciones ambientales, pero estrechamente vinculada a zonas con alta concentración de ácido silícico. Las fracciones más pequeñas, sin embargo, dominaron en un entorno más homogéneo caracterizado por una mayor concentración de nitratos. Aunque los nutrientes no se agotan en el área de estudio, la razón nitrato/ácido silícico influencia claramente la abundancia, la composición por tamaño y la estructura espacial de la comunidad autotrófica durante invierno bajo menor disponibilidad de luz y procesos oceanográficos más complejos durante la primavera.

**Palabras clave**: Geoestadística, Mar Interior de Chiloé, nutrientes, fitoplancton

**Abstract**.- The chain of islands including Desertores, Apiao and Quemchi located in the Inner Sea of Chiloé, in northern Chilean Patagonia (41°-44°S), acts as a natural barrier for the flux of water in the north-south direction, influencing exchange and circulation between the northern and southern micro basins. The northern micro basin is mainly characterized by the dominance of surface estuarine waters whereas the southern micro basin is affected by the inflow of Subantarctic Surface and Equatorial Subsurface Waters from the adjacent coastal ocean. This setting determines key differences in the spatial distribution, abundance and size composition of phytoplankton biomass (measured as chlorophyll-*a*). These chlorophyll-*a* qualitative and quantitative differences were evaluated in contrasting seasons twice during 2004 and 2005 surveys (Cruceros de Investigación Marina, CIMAR 10 and 11 Fjords). In both micro basins, physical, chemical and bio-optical data from upper mixed layer water samples were analysed along with 8-days composite satellite images of chlorophyll-*a* (MODIS-AQUA). The largest difference in environmental heterogeneity between zones was in the concentration of nitrate and silicic acid. In spring the abundance of chlorophyll-*a* showed high variability in both sub-basins and predominance of micro-phytoplankton. In austral winter the micro-phytoplankton fraction was also dominant in a wide range of environmental with conditions, but closely linked to regions with high silicic acid concentrations. The smaller fractions, however, dominated in a more homogeneous environment characterized by higher nitrate concentration. Although nutrients are not depleted in the study area, the nitrate/silicic acid ratio clearly influenced the autotrophic community abundance, size composition and spatial structure under lower light availability during winter and more complex oceanographic processes during spring.

**Key words**: Geostatistics, Inner Sea of Chiloé, nutrients, phytoplankton

## INTRODUCTION

The distribution of planktonic organisms as the central focus of this study is due to the importance of the chemical, physical and biological interactions that affect the marine pelagic ecosystems, generating different spatial patterns in the structure of the phytoplankton community at different scales (Stewart *et al.* 2000). One of the largest regions of fjords in the world, the Chilean Patagonia, with a total area of 240,000 km (Pantoja *et al.* 2011), situated on the southwest frontier of the Pacific Ocean at 41.5°S (Reloncaví Fjord) to 55.9°S (Cape Horn), presents a unique opportunity to study temporal and mesoscale phytoplankton patterns given its potential sensitivity to human pressure and climate change.

In northern Patagonia (41°-43°S), in the Inner Sea of Chiloé, the surface salinity level is influenced by the convergence of ocean waters and freshwaters from local rivers especially in the northern sector (Silva *et al.* 1995). Described as a transitional marine system (Iriarte *et al.*

2010), the Inner Sea of Chiloé has micro basins and geographic barriers such as the Desertores/Apiao/Quemchi island chain (Fig. 1) which hinders the passage of Subantarctic Waters towards the northern zone and stops the Equatorial Subsurface Waters flowing northward of this barrier (Silva *et al.* 1995, Sievers & Silva 2008). These geographic characteristics produce long water residence time (Silva & Palma 2006, Carrasco & Silva 2010) and affect the tide regimes and their resonance in the northern zone (Cáceres *et al.* 2003). Here, semidiurnal internal waves enhance vertical mixing, increasing nutrients at the surface through shear instabilities that favour primary production for more extended periods than in classical seasonal systems (Ross *et al.* 2014). Overall, these estuarine waters are relatively poor in nitrate ($NO_3$) and phosphate ($PO_4$) but rich in silicic acid ($Si(OH)_4$) unlike the southern zone which has more oceanic water influence and therefore more nitrate and phosphate (Silva *et al.* 1997, 1998; Silva & Palma 2006, Vargas *et al.* 2011).
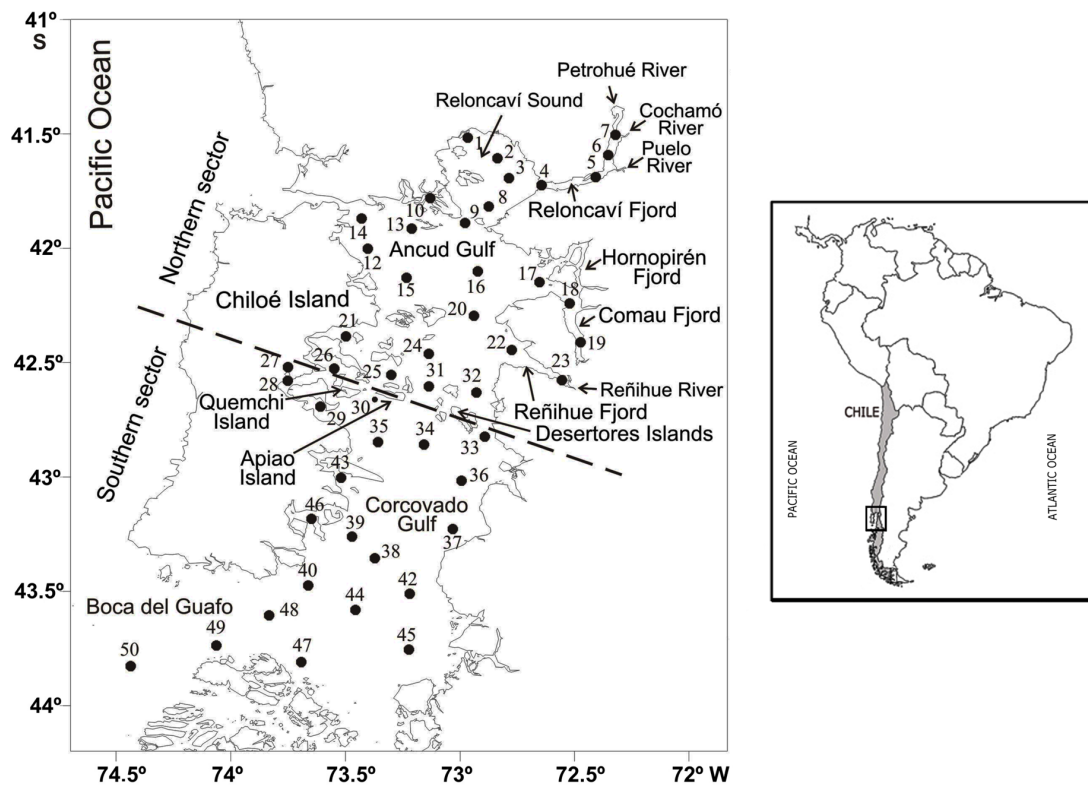


Figure 1. Map of the Inner Sea of Chiloé (ISoCh) and positions of sampling stations during the winter and spring cruises CIMAR 10 and 11 in 2004 and 2005. Dotted line indicates the division between the northern (1-32 stations) and the southern (33-50 stations) sector / Mapa del Mar Interior de Chiloé (ISoCh) y posición de las estaciones de muestreo durante los cruceros de invierno y primavera CIMAR 10 y 11 en 2004 y 2005. Línea punteada indica la división entre el sector norte (estaciones 1-32) y sur (estaciones 33-50)

The concentration of *in situ* chlorophyll-*a* (Chl-*a*) and satellite chlorophyll-*a* (Chl-$a_{Sat}$), as an indirect measurement of the biomass of the phytoplankton community (Brewin *et al.* 2010), has been found to be higher in the northern zone than in the southern part of Northern Patagonia (Pizarro *et al.* 2000, Ramírez & Pizarro 2005, Delgado & Marín 2006, Tello & Rodríguez-Benito 2009, Montecino *et al.* 2009). Using MODIS-AQUA satellite images, Lara *et al.* (2010) observed Chl-$a_{Sat}$ patches with clearly differentiated spatial temporal patterns. In this last mesoscale study, the spatial dimension of Chl-$a_{Sat}$ patch sizes was greater than 50 km, attributed to low environmental variability including reduction in light availability in autumn-winter, while during spring-summer the patches were smaller than 30 km and it was associated with high environmental variability *i.e.* the presence of oceanic fronts and high frequency of South West winds. Spatially, in the northern zone of the Desertores/Apiao/Quemchi island chain, the structure of Chl-$a_{Sat}$ patches are smaller and there is more environmental variability while toward the south through the Boca del Guafo (Fig. 1) the larger Chl-$a_{Sat}$ patches (spatial structures) are associated with higher homogeneity.

The latitudinal changes observed in phytoplankton Chl-*a* concentrations in Chilean Patagonia have been attributed to the availability of nutrients (Aracena *et al.* 2011), seasonal patterns in the light regimes (González *et al.* 2010, Paredes & Montecino 2011), the direction and intensity of winds (Montero *et al.* 2011) and the stratification of the water column (Lara *et al.* 2010). The size composition and structure of this autotrophic community is a result of the environmental conditions and depends on biological factors such as reproduction and growth, morphology and different functional types (Reynolds 1988, Alvés de Souza *et al.* 2008). Spatial and temporal changes in abiotic conditions will have different effects depending on the size of the different thriving phytoplankton components (Marañon *et al.* 2008). Therefore, in oligotrophic environments with more oceanic influence or in those that are far from the coast, small cell sizes are dominant (Kiørboe 1993, Montecino & Quiroz 2000, Sabetta *et al.* 2005, Paredes & Montecino 2011). By contrast, large cell sizes tend to dominate in well-mixed and turbulent waters such as coastal zones where the concentration of nutrients is higher (Margalef 1978, Sabetta *et al.* 2005, Marañon 2008, 2009).

Given the underlying oceanographic and latitudinal features in winter and spring in the Inner Sea of Chiloé, it is expected to find peculiar structural patterns in autotrophic communities in accordance with the hypothesis about dissimilarities between environmental heterogeneity north and south of the natural barrier Desertores/Apiao/Quemchi island group. Recognizing which environmental factor (physical, chemical and bio-optical) is characteristic of each micro basin in contrasting seasons would enable us to reach a better understanding of the distribution and abundance of *in situ* Chl-*a* according to the dominant size fraction, as well as Chl-$a_{Sat}$ as a proxy for the spatial structures, obtaining greater ecological information on the phytoplankton community of northern Chilean Patagonia.

## MATERIALS AND METHODS

### STUDY AREA AND DATA COLLECTION

The study area was surveyed during CIMAR 10 and 11 Fjord cruises which were carried out in the R/V AGOR Vidal Gormáz: CIMAR 10-1 (August 2004; winter), CIMAR 10-2 (November 2004; spring), CIMAR 11-1 (July 2005; winter) and CIMAR 11-2 (November 2005; spring), covering a total of 50 oceanographic stations during each survey (Fig. 1).

Continuous recording of water temperature and salinity was carried out with a CTD Sea-Bird model SBE 25 and discrete samples of water were collected for analysis of their salinity, dissolved oxygen, nutrients and Chl-*a*, using a Rosette with 24 Niskin bottles. Water samples were taken at standard depths and for this study only the results obtained at surface depths (0, 5, and 10 m) were used. The CTD data was processed using the Sea-Bird model SBE 25 standard protocol. The salinity sensor was calibrated with the results of the salinity analysis of the discrete samples carried out in an AUTOSAL inductive salinity-meter. Samples of dissolved oxygen were fixed and analyzed on board according to the Winkler method modified by Carpenter (1965). The dissolved oxygen saturation values were calculated based on the Weiss algorithm (1970).

The samples for nutrient analysis were collected in high-density (50 ml) aseptic polyethylene bottles and stored at -20ºC. The analysis of nutrients (nitrate+nitrite, phosphate and silicic acid) was carried out with a nutrient autoanalyzer according to Atlas *et al.* (1971). Since the nitrite content in the austral channels is generally low (~ 0-0.3 μM); the values of nitrate+nitrite can be considered as only nitrate ($NO_3^-$) and they are presented as such.

Water samples from both Rosette and bucket (0 m) were processed to measure the total Chl-*a* (TChl-*a*) and size-fractionated Chl-*a*. To obtain these measurements, 250 ml to 500 ml samples were vacuum-filtered directly onto fiberglass filters (Advantec® nominal pore size of 0.7 μm, 25 mm). The 3 size fractions of phytoplankton corresponding to microphytoplankton (> 20 μm), large nannoplankton (11-20 μm) and small nannoplankton and picoplankton (<11 μm) were obtained by differential filtration of 250-500 ml of the same sample on fiberglass filters, pre-filtering samples through nylon meshes of 20 and 11 μm (Montecino *et al*. 2009, Paredes & Montecino 2011). The filters were stored in liquid nitrogen until the fluorometric assay, from which the Chl-*a* was extracted with acetone (90% v/v). Its concentration was quantified in a fluorometer TURNER TD-700 model (Jeffrey *et al*. 1997). To determine bio-optical parameters, the 250 ml water samples for the absorption of coloured dissolved organic matter (ag) were filtered using 0.7 μm precombusted filters and stored in the dark at 4°C. For further analysis, in the laboratory 100 ml replicates of these samples were filtered through 0.2 μm polycarbonate filters prewashed with 3 ml MilliQ ultrapure water. The optical density of the filtrate was measured in a 10 cm pathlength cuvette with a Shimadzu UV-Visible spectrophotometer between 300-700 nm (+ 0.005) (Strickland & Parsons 1972) and was recorded using ultrapure MilliQ water as a blank. Expressed absorbance was calculated at 375 nm (ag$_{\lambda 375}$) after correction for the average absorption spectrum obtained between 710-700 nm according to Mitchell *et al*. (2000).

For the same study periods Chl-$a_{\text{Sat}}$ data obtained from satellite images MODIS (Moderate Resolution Imaging Spectroradiometer) aboard the AQUA platform were extracted. Because cloud cover in the study area made satellite images inaccessible on specific days of sampling, the 8- day composite Chl-$a_{\text{Sat}}$ was selected, considering the 3 week duration of the oceanographic cruise for each campaign. The 8-day composite chlorophyll from MODIS for the winter 2004 (August 20 to September 5), spring 2005 (November 8 to 24), winter 2005 (July 12 to 28) and spring 2005 (November 9 to 23), have a spatial resolution of 4 km at nadir and level L3 processing. All satellite images were obtained from the NASA website[1]. The Chl-$a_{\text{Sat}}$ product was obtained using the algorithm OC3 MODIS (O'Reilly *et al*. 2000). Collecting data from the Chl-$a_{\text{Sat}}$ satellite images was performed in the Environment for Visualizing Images, 2005 (ENVI) version 4.5, where the

images were processed by an equidistant cylindrical projection. Subsequently, by dynamic interactive IDL language the Chl-$a_{\text{Sat}}$ values were extracted for all pixels in each of the zones as proposed by the Canty (2006) algorithm. In order to avoid anthropogenic effects, masking substances (detritus, dissolved organic matter, coloured substances), and to reduce the noise and anomalies inherent in coastal ocean color data, the information from MODIS images located within 4 km of the coast were excluded from the analysis.

### DATA ANALYSIS

#### DATA OBTAINED *IN SITU*

To evaluate differences between abiotic factors (temperature, salinity, dissolved oxygen, silicic acid, nitrate, phosphate and coloured organic matter, ag$_{\lambda 375}$, and phytoplankton (TChl-*a* and Chl-*a* fractionated by size) between northern and southern sectors of the Desertores/Apiao/Quemchi island group and both winters and springs, two way Analysis of Variance was used. Beforehand, a normality test (Kolmogorov-Smirnov test) was done and homoscedasticity (Bartlett Docimo) of the response variable (integrated from 0 to 10 m) was evaluated. Data were normalized using log (x +1).

In addition, a multiple regression with continuous variables and the Forward Stepwise method was used after establishing independence and identical distribution of errors by means of the Durbin-Watson statistic, and transformed by Box-Cox, through the STATISTICA 6.0 package.

#### SPATIAL ANALYSIS OF CHL-$a_{\text{Sat}}$

A semivariogram function was used to carry out structural analysis of spatial data of Chl-$a_{\text{Sat}}$ obtained from satellite images (Equation 1).

$$\gamma\left(h\right) = \frac{1}{2}\sum_{i=1}^{n}\left\{Z(x_i) - Z(x_i + h)\right\}^2$$

where $\gamma\left(h\right)$ is the semivariance of *Z* variable distance *h*, *Z* ($x_i$) is the value of the variable examined in the ($x_i$), *Z* ($x_i$ + *h*) is the value of the variable examined in the ($x_i$ + *h*) position, while η is the number of pairs of samples spaced by distance *h* (Burroughs 1996) samples. This analysis characterizes the potential spatial dependence of Chl-$a_{\text{Sat}}$ at different spatial scales (Miranda-Salas & Condal 2003, Lara *et al*. 2010, Gerstmann *et al*. 2010). The spatial

[1]<http://oceancolor.gsfc.nasa.gov/cgi/l3>

dependence between the values of Chl-$a_{Sat}$ analyzed in this study was estimated with variograms at intervals of 5 km for each image and a distance 'h' of 50 km. Variogram analysis was performed with GS+ (Geostatistics for the Environmental Sciences) software, version 7.0[2].

To quantify the spatial structure of chlorophyll-$a$ concentration, we used spherical models since they adapt to the main properties of the experimental variograms (Garrigues *et al.* 2006). The linear behaviour and the origin continuity diminish the noise with the semivariance rising smoothly to a stable and fixed range (Broitman & Kinlan 2006).

### ANALYSIS OF ENVIRONMENTAL FACTORS

For the definition of the northern and southern sectors (defined *a priori*) and for the seasons (winter-spring), multivariate analyses were used. The relationship between fields of study and environmental variables were ordered by Non-Metric Multi-Dimensional Scaling (NMDS) Analysis. The differences between the sectors were evaluated through analysis of similarity ANOSIM (Clarke & Gorley 2006) considering 999 permutations of the similarity matrix. Furthermore, the SIMPER analysis was used to quantify the average distance from the set of abiotic factors and to identify the physical, chemical and optical variables that contributed (in %) to differentiation (dissimilarity) between groups (geographic areas). The techniques described above were carried out with the software PRIMER 6[3].

## RESULTS

### ENVIRONMENTAL FACTORS

The ordination analysis shows that the physical, chemical and bio-optical conditions (*i.e.*, $ag_{\lambda375}$) obtained during CIMAR cruises exhibited good graphic representations according to Clarke & Warwick (2001), with low stress values (no greater than 0.12) found only during winter 2004 (Fig. 2). The average spatial range distances in the northern sector shows a greater spread of abiotic factors (heterogeneity min and max % values from 21.66 to 117.22) compared to the southern sector (15.55 to 28.4) (Table 1), where the distances of the factors were generally significantly lower ($P < 0.05$), and not different between north and south in the winter of 2005 (Table 1 and Fig. 3). The variables with the greatest differences between sectors were mainly nutrients, specifically nitrate and silicic acid (Fig. 3). Nitrate contributed with the highest percentages of dissimilarity between sectors, over 32% of the total during the 4 cruises, except for winter 2005, where the contribution of silicic acid was higher (85%). In general, nitrate and silicic acid together were the variables contributing more than 70% of the dissimilarity for both sectors. Salinity was the smallest contributor (10-20%) and was relevant only during springtime (Fig. 4).

**Table 1. Mean values for the winter and spring in 2004 and 2005 of environmental heterogeneity (%) measured as the average Euclidean distance of the dispersion of the set of abiotic factors and their significance according to the ANOSIM test (*: significant differences exist). N= north; S= south** / Valores de la heterogeneidad ambiental (%) medida como distancia euclidiana promedio de la dispersión del conjunto de factores abióticos y su significancia según la prueba ANOSIM (*: existen diferencias significativas). N= norte; S= sur

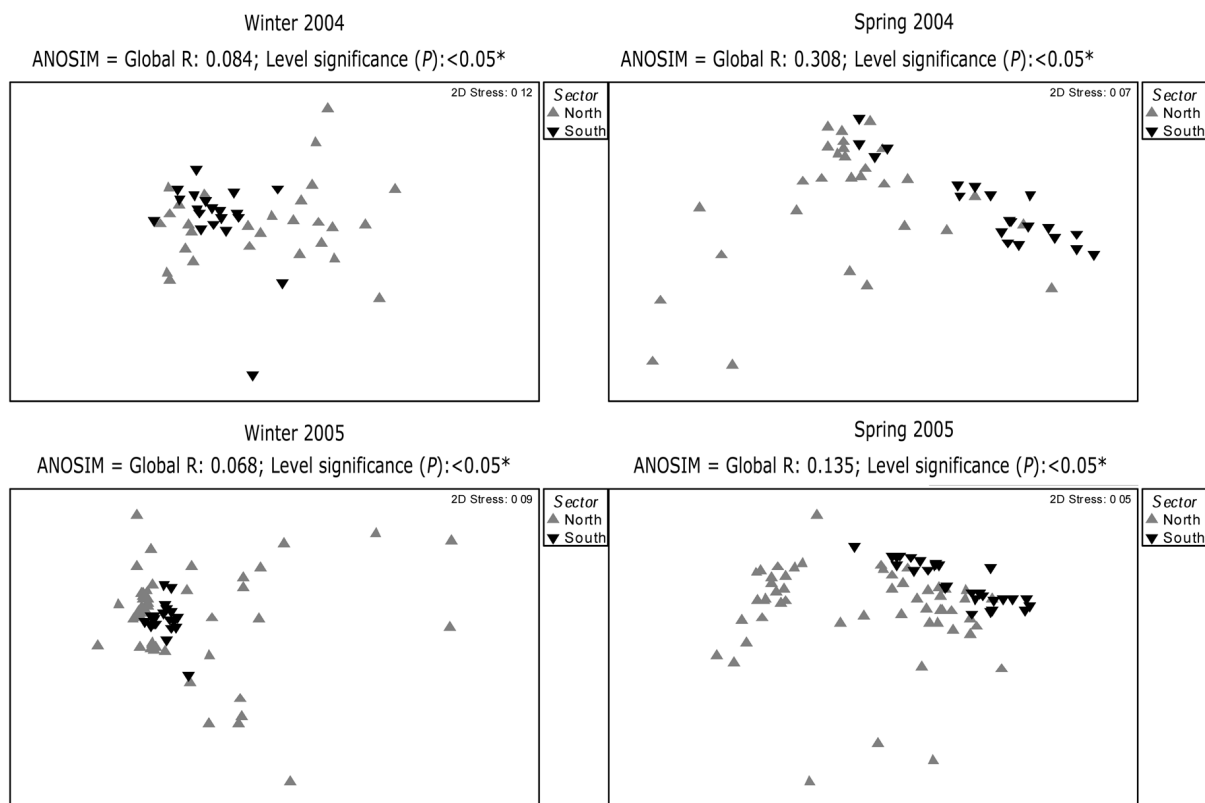| Time | 2004 | | | | 2005 | | | |
|---|---|---|---|---|---|---|---|---|
| | winter | | spring | | winter | | spring | |
| Space | N | S | N | S | N | S | N | S |
| Heterogeneity (%) | 82.19 | 25.6 | 117.22 | 28.4 | 21.66 | 15.55 | 68.19 | 18.55 |
| ANOSIM R + significance level (*P*)* | 0.084 | <0.05* | 0.308 | <0.05* | 0.068 | >0.05 | 0.135 | <0.05* |

**Figure 2. Sorting of the abiotic variables in the ISoCh\* during CIMAR 10 and 11 Fjords (winter and spring 2004-2005) between the northern and the southern sector, obtained through nonmetric multivariate multidimensional scaling analysis (NMDS). Details of the data treatment and results of ANOSIM analysis are given, (\*) significant differences exist** / Ordenación de las variables abióticas en el ISoCh\* durante los Cruceros CIMAR 10 y 11 Fiordos (invierno y primavera 2004-2005) entre los sectores norte y sur, obtenidos mediante análisis multivariado de escalamiento no métrico multidimensional (NMDS). Se detallan los tratamiento de los datos y los resultados del análisis ANOSIM, (\*) existen diferencias significativas

### PHYTOPLANKTON SIZE FRACTIONS AND TOTAL CHL-*a* ABUNDANCES

The concentration of TChl-*a* presented a seasonal pattern both in the northern as well as in the southern sectors of the Inner Sea of Chiloé (thereafter referred to as ISoCh\*). During both winter seasons, the northern and southern sectors showed significant differences ($P < 0.05$) in the abundance of TChl-*a*. The phytoplankton concentration of the large fraction ($> 20$ μm) in the northern sector was significantly higher during winter, while in the southern sector the small fraction ($<11$ μm) was significantly higher ($P < 0.05$) during this season. Moreover, higher concentrations of TChl-*a* were recorded during the 2 campaigns in 2004 compared to what was observed during the two campaigns in 2005 (Table 2).

### ASSOCIATION OF PHYSICAL AND CHEMICAL CONDITIONS WITH THE CONCENTRATION OF TCHL-*a*

The concentration of TChl-*a* during the winter cruises presents an inverse relationship ($P < 0.005$) with nitrate in the northern zone (Beta coeff.: -0.69; $r^2$: 0.66) and southern zone (Beta coeff.: -0,45; $r^2$: 0.60) of the ISoCh. In the case of the relationship of TChl-*a* with silicic acid within the same season, this negative relationship was only found for the northern zone (Beta coeff.: -0,25; $r^2$: 0.66). On the other hand during both springs, there is a positive relationship of TChl-*a* with oceanographic factors such as salinity in the northern zone (Beta coeff.: 0.49; $r^2$: 0.20) and with temperature (Beta coeff.: 0.51; $r^2$: 0.68) in the southern zone.
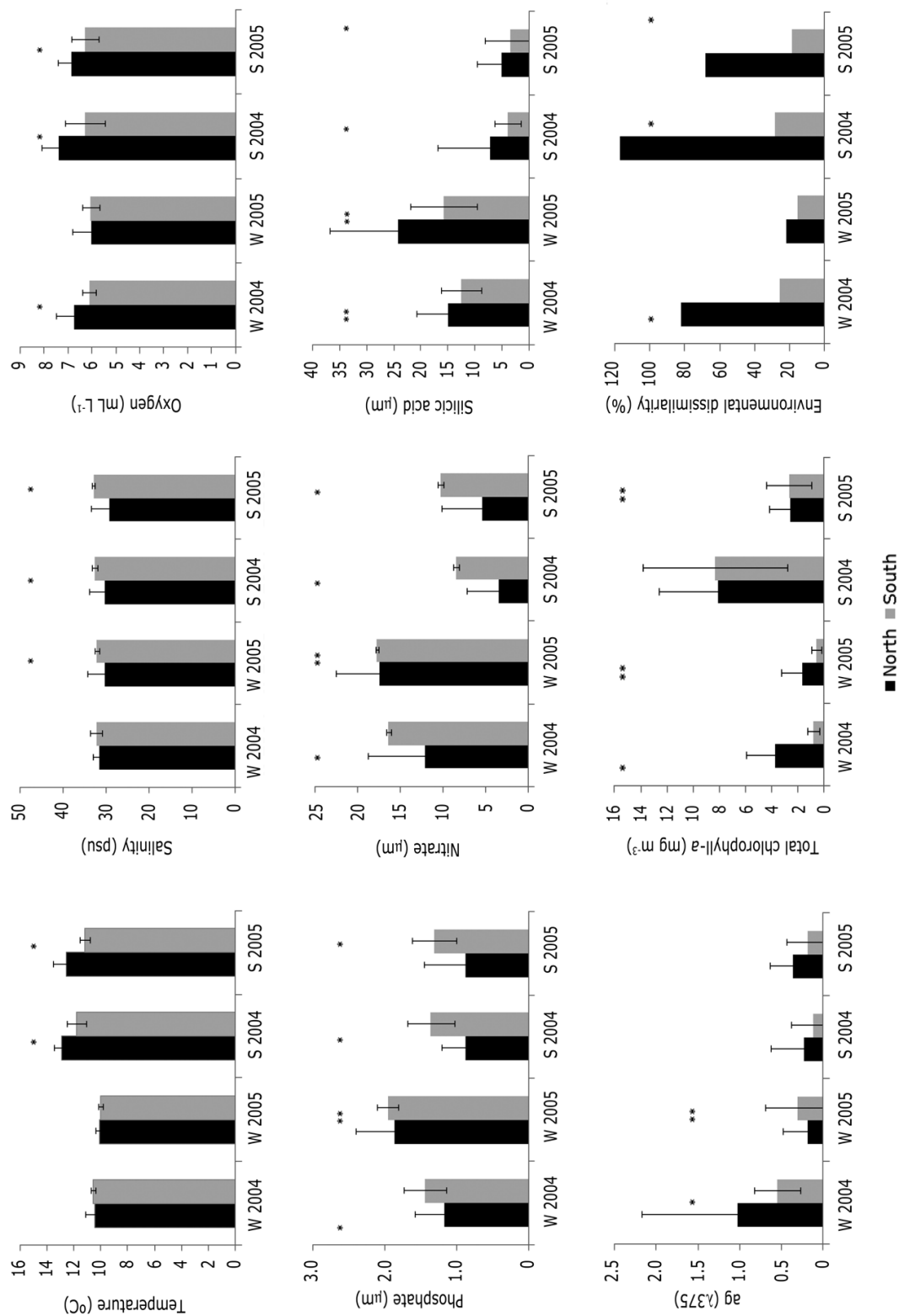
**Figure 3.** Average and standard deviation of abiotic factors for the northern and southern sector of the ISoCh during winter and spring 2004-2005 cruises. ANDEVA (\*) Northern and southern significant differences. (\*\*) Significant differences between winters (2004-2005) or between springs (2004-2005). Bottom right: Environmental dissimilarity values (%) (dispersion of combined abiotic factors) measured as Euclidean distance ANOSIM (\*: significant differences exist) / Promedio y desviación estándar de los factores abióticos para los sectores norte y sur del ISoCh durante los cruceros de invierno y primavera 2004-2005. ANDEVA (\*) Diferencias significativas entre sectores norte y sur. (\*\*) Diferencias significativas entre inviernos (2004-2005) ó entre primaveras (2004-2005). Gráfico abajo a la derecha: Valores de la disimilaridad ambiental (%) (dispersión del conjunto de factores abióticos) medida como distancia euclidiana ANOSIM (\*: existen diferencias significativas)
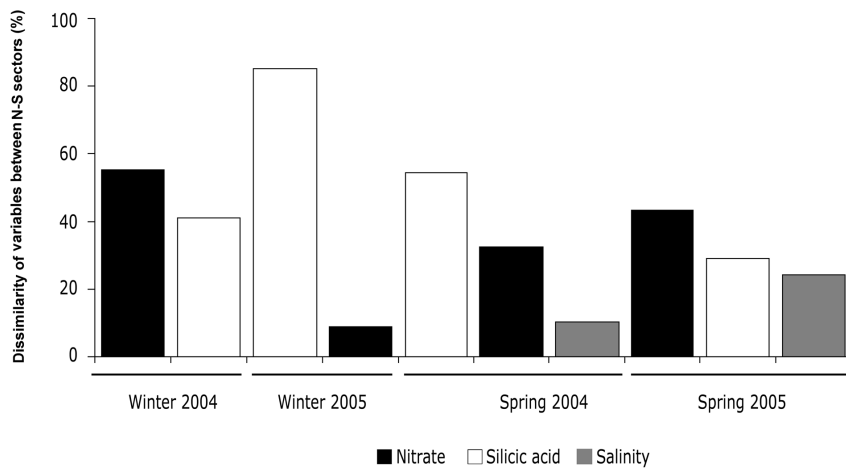
**Figure 4. Contribution in percentage (%) of dissimilar variables between the northern and southern sectors of the four cruises analyzed (winter and spring 2004-2005) according to SIMPER analysis results /** Contribución en porcentaje (%) de las variables disimiles entre los sectores norte y sur de los cuatro cruceros analizados (invierno y primavera 2004-2005), de acuerdo con los resultados obtenidos de análisis SIMPER

**Table 2. Summary of descriptive statistics (one-way ANOVA, F and *P* values) in right columns of the abundance of phytoplankton total chlorophyll-*a* and of the three size fractions between the northern and southern sector of the ISoCh during winter and spring cruises in 2004-2005. Percent (%) fraction sizes according to north-south sectors and time of year are also indicated. * Indicate statistically significant differences /** Resumen de estadística descriptiva (ANDEVA de una vía, valores F y *P*) de la abundancia fitoplanctónica de la clorofila-*a* total y por tres fracciones de tamaño entre los sectores norte y sur del ISoCh durante los cruceros de invierno y primavera 2004-2005. (%) Porcentaje de la fracción de tamaños de acuerdo a sector y época del año. * Indica diferencias estadísticamente significativas

| | North | Percentage of TChl-*a* | South | Percentage of TChl-*a* | F | *P* |
|---|---|---|---|---|---|---|
| | mg m$^{-3}$ | % | mg m$^{-3}$ | % | | |
| Total chlorophyll-a (TChl-*a*) | | | | | | |
| Winter 2004 | $3.70 \pm 2.27$ | | $0.77 \pm 0.47$ | | 13.87 | <0.05* |
| Spring 2004 | $8.05 \pm 4.60$ | | $8.31 \pm 5.51$ | | 0.02 | 0.87 |
| Winter 2005 | $1.67 \pm 1.57$ | | $0.55 \pm 0.40$ | | 4.41 | <0.05* |
| Spring 2005 | $2.55 \pm 1.63$ | | $2.66 \pm 1.72$ | | 0.08 | 0.78 |
| Large fraction (microphytoplankton) | | | | | | |
| Winter 2004 | $2.67 \pm 2.30$ | 72.1 | $0.32 \pm 0.30$ | 42.6 | 14.27 | <0.05* |
| Spring 2004 | $6.34 \pm 2.40$ | 78.7 | $6.46 \pm 2.00$ | 77.8 | 0.42 | >0.05 |
| Winter 2005 | $0.81 \pm 0.90$ | 48.4 | $0.03 \pm 0.03$ | 5.3 | 5.93 | <0.05* |
| Spring 2005 | $1.44 \pm 1.10$ | 56.3 | $1.79 \pm 1.70$ | 67.4 | 0.57 | >0.05 |
| Medium fraction (large nannophytoplankton) | | | | | | |
| Winter 2004 | $0.25 \pm 0.47$ | 6.6 | $0.05 \pm 0.06$ | 6.9 | 2.28 | >0.05 |
| Spring 2004 | $0.05 \pm 0.04$ | 0.6 | $0.24 \pm 0.31$ | 2.8 | 0.98 | >0.05 |
| Winter 2005 | $0.33 \pm 0.38$ | 19.5 | $0.09 \pm 0.19$ | 15.7 | 3.15 | >0.05 |
| Spring 2005 | $0.42 \pm 0.58$ | 16.5 | $0.37 \pm 0.24$ | 13.9 | 0.04 | >0.05 |
| Small fraction (small nannophytoplankton and picophytoplankton) | | | | | | |
| Winter 2004 | $0.78 \pm 0.93$ | 21.2 | $0.39 \pm 0.20$ | 50.4 | 2.43 | >0.05 |
| Spring 2004 | $1.66 \pm 0.43$ | 20.6 | $1.61 \pm 0.45$ | 19.4 | 1.19 | >0.05 |
| Winter 2005 | $0.54 \pm 0.43$ | 32.2 | $0.43 \pm 0.24$ | 78.9 | 0.44 | >0.05 |
| Spring 2005 | $0.69 \pm 0.51$ | 27.2 | $0.49 \pm 0.22$ | 18.6 | 1.33 | >0.05 |

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## Spatial analysis of Chl-$a_{Sat}$

Chl-$a_{Sat}$ abundance results show a different spatial and temporal pattern in both ISoCh zones (Table 3). In the northern zone during the two spring periods the maximum Chl-$a_{Sat}$ mean values were recorded (7.99 ± 2.29 mg m$^{-3}$; 7.24 ± 2.23 mg m$^{-3}$ respectively) and higher than those during winter periods (1.99 ± 2.7 mg m$^{-3}$; 2.59 ± 2.29 mg m$^{-3}$, respectively). In the southern zone the pattern was similar, reaching maximum values of 6.60 ± 1.99 mg m$^{-3}$; 6.91 ± 2.13 mg m$^{-3}$ during spring periods, significantly higher than those during winter periods (0.81 ± 1.28 mg m$^{-3}$; 0.87 ± 1.25 mg m$^{-3}$). The greatest spatial Chl-$a_{Sat}$ variability (Table 3) was observed in the northern zone during spring season (nugget: 3.60 and 4.56) associated with smaller size spatial structures or patch sizes (39.2 ± 4.0 km and 20.1 ± 4.0 km), while less heterogeneity (nugget 0.17 and 0.75) was associated during both winter periods to larger spatial structures (48.2 ± 8.0 km and 52.7 ± 5.0 km).

In the southern zone, smaller Chl-$a_{Sat}$ spatial structures (34.0 ± 4.0 km; 37.8 ± 6.15 km) associated with greater spatial heterogeneity (nugget: 3.40 and 2.65) were obtained during spring seasons (2004-2005). During both winters lower spatial heterogeneity was associated with larger spatial structures (56.2 ± 12.0 km; 43.0 ± 9.0 km) (Table 3).

Despite similar temporal patterns in *in situ* Chl-$a$ and Chl-$a_{Sat}$, when comparing average values shown in Tables 2 and 3, there were some differences between the 8-day composite satellite data and those obtained in predetermined oceanographic stations during 2004-2005

(*i.e.*, in spring: 7.99-7.24 m$^{-3}$ Chl-$a_{Sat}$ in the northern zone, 6.60 -6.91 mg m$^{-3}$ Chl-$a_{Sat}$ in the southern zone compared with 8.05-2.55 mg m$^{-3}$ TChl-$a$ in the northern zone, 8.31-2.66 mg m$^{-3}$ TChl-$a$ in the southern zone).

## DISCUSSION

The phytoplankton communities in the ISoCh are characterized by a highly seasonal temperate zone pattern (Parsons *et al.* 1977, Ramirez & Pizarro 2005, Iriarte *et al.* 2007, Montecino *et al.* 2009, Aracena *et al.* 2011, Montero *et al.* 2011, Rebolledo *et al.* 2011). The temporal variations in both Chl-$a_{Sat}$ and TChl-$a$, showed the same seasonal trends, although average monthly values of Chl-$a_{Sat}$ were relatively higher than those TChl-$a$ recorded *in situ*. Nevertheless, maximal temporal variability for Chl-$a_{Sat}$ is within the range of values described by SeaWiFS and MODIS satellite images for the Inner Sea of Chiloé (Delgado & Marín 2006, Iriarte *et al.* 2007, Tello & Rodríguez-Benito 2009, Lara *et al.* 2010). The difference between the average Chl-$a_{Sat}$ and *in situ* TChl-$a$ (Table 2 and 3) that was observed in the northern zone could be related to the greater dissimilarity (heterogeneity) of the physical, chemical and optical factors measured in this zone (Fig. 2). The northern zone has a greater continental contribution compared to the southern zone, which has more homogeneous abiotic environmental conditions (Fig. 3). Moreover, the higher spatial resolution of satellite images (4 km) coupled with the L3 adjustments derived from MODIS based in case I water optical properties

**Table 3. Summary of the spatial statistical results of heterogeneity measured as initial variance, nugget, patch size and average Chl-$a_{sat}$ for the northern (N) and southern (S) sectors of the ISoCh during the winter and spring cruises (2004-2005) /** Resumen de los resultados del análisis de estadística espacial de la heterogeneidad medida como variación inicial, pepita, tamaño del parche y el promedio de Chl- $a_{Sat}$ para los sectores norte (N) y sur (S) del ISoCh durante los cruceros de invierno y primavera (2004-2005)

| | Chl-$a_{Sat}$ (mg m$^{-3}$) | | Heterogeneity | | | | Patch Size (km) | |
|---|---|---|---|---|---|---|---|---|
| | | | initial variance | | nugget | | | |
| | N | S | N | S | N | S | N | S |
| | Mean ± σ | | Mean ± σ | | | | Mean ± σ | |
| **2004** | | | | | | | | |
| winter | 1.99 ± 2.70 | 0.81 ± 1.28 | 1.99 ± 2.70 | 0.81 ± 1.28 | 0.17 | 0.12 | 48.2 ± 8.0 | 56.2 ± 12.0 |
| spring | 7.99 ± 2.29 | 6.60 ± 1.99 | 7.99 ± 2.29 | 6.60 ± 1.99 | 3.60 | 3.40 | 39.2 ± 4.0 | 34.0 ± .0 |
| **2005** | | | | | | | | |
| winter | 2.59 ± 2.29 | 0.87 ± 1.25 | 2.59 ± 2.29 | 0.87 ± 1.25 | 0.75 | 1.20 | 52.7 ± 5.0 | 43.0 ± 9.0 |
| spring | 7.24 ± 2.23 | 6.91 ± 2.13 | 7.24 ± 2.23 | 6.91 ± 2.13 | 4.56 | 2.65 | 20.1 ± 4.0 | 37.8 ± 6.1 |

(Moses *et al.* 2009), and also the 8 days average values could help to explain the differences that were found between Chl-$a_{Sat}$ data and those obtained in one day in predetermined oceanographic stations (n= 50).

In addition, it should be noted that the ISoCh is no exception in terms of strong inter-annual changes in seasonal weather conditions (*i.e.*, solar radiation, wind and precipitation; Pickard 1970, Castillo *et al.* 2012) that were reflected in the intra-seasonal variability concentration of Chl-*a* presented in the winter and spring seasons in 2004-2005.

The differences in the concentration of Chl-*a* between the north and south zones in the ISoCh separated by the Desertores/Apiao/Quemchi island group reported by Pizarro *et al.* (2000), Ramírez & Pizarro (2005), Delgado & Marín (2006), Tello & Rodríguez-Benito (2009) and Montecino *et al.* (2009) were consistent with the patterns identified in this study, where, during the winter period, higher concentrations of TChl-*a* were observed in the northern zone (Reloncaví Sound-Gulf of Ancud) compared with the southern zone (Corcovado Gulf-Boca del Guafo). The largest fraction of the phytoplankton dominated in the northern zone, while the southern zone was dominated by the smallest fraction, coinciding with the results of Paredes & Montecino (2011), who point out that TChl-*a* depends on the size of the dominant fraction, fully dominating the small fraction of phytoplankton in low values of TChl-*a* (winter 2004-2005, 50-79%, Table 2). Iriarte *et al.* (2014) include spatial variability in nutrient concentrations, which together with the strong light attenuation induced by glacier-derived freshwater may further explain carbon fluxes and the spatial patterns in primary productivity and phytoplankton biomass.

Although the northern zone has the influence of the major rivers of the area *i.e.*, Petrohué (278 m$^3$ s$^{-1}$), Puelo (670 m$^3$ s$^{-1}$) (Dávila *et al.* 2002, Calvete & Sobarzo 2011, Pantoja *et al.* 2011, Silva & Vargas 2014), the salinity values during the winter 2004 were the same as those of the southern sector (Corcovado Gulf-Boca del Guafo) (Fig. 3). The major differences between the 2 geographic zones during the contrasting seasons are seen in nitrate and silicic acid, while salinity contributes to this differentiation only during spring (Fig. 3). In these results, the narrow passages formed by the presence of the Desertores/ Apiao/Quemchi island group, are highlighted as an important bathymetric barrier to the water flow that favours the generation of different abiotic characteristics located north and south of this barrier. Thus the southern

zone is characterized by its connection with the Boca del Guafo, a strong influence of the oceanic region in which the chemical properties of Subantarctic Waters are maintained with the high concentration of nitrate and phosphate and low silicic acid, while the northern zone is rich in silicic acid from inland waters (Silva *et al.* 1997, 1998; Silva & Guzmán 2006, Silva & Palma 2006, Carrasco & Silva 2010, Vargas *et al.* 2011, Iriarte *et al.* 2014). These environmental heterogeneity differences generate mesoscale changes in the autotrophic community between the two sectors during the winter season, showing a TChl-*a* dominance of the small fraction of phytoplankton in the southern sector and TChl-*a* dominance of the microphytoplankton in the northern sector. Although the chemical and physical properties differ during the contrasting seasons analyzed in this study, in both spring (2004-2005) seasons, the phytoplankton community, expressed as TChl-*a* and fractionated by size, showed a similar feature in the north and south of Desertores/Apiao/Quemchi Passages. This is a dominant contribution of the microphytoplankton fraction (> 20 μm) (Table 2) in both sectors. Furthermore, the approaches used by Paredes *et al.* (2014) explain these patterns of microphytoplankton groups and their composition either at regional or at smaller spatial scales.

Several authors have reported on the dominance of diatom r-strategists in the Chilean fjords region in early spring (Avaria *et al.* 1997, Alvés de Souza *et al.* 2008, Valenzuela & Avaria 2009), which according to Margalef (1958) is characteristic of a productive community that is maintained in the early stages of population succession. In conjunction, this larger size fraction was dominant in the northern sector during both seasons (winter and spring) that were analysed and is similar to those patterns found by other studies in the Patagonian fjords, where the largest fraction of phytoplankton dominates in transitional zones (estuarine-ocean) (Uribe 1992, Iriarte *et al.* 1993, 2001, 2007; Torres *et al.* 2011). Moreover, it has been reported that the phytoplankton community of Reloncaví Sound (Fig. 1) is theoretically more likely to restart production processes in the short term (Ramirez & Pizarro 2005).

Field studies and laboratory microcosms indicate that the limiting diatom growth factor (considering them to be the dominant component of microphytoplankton) is the silicic acid (Egge & Aksnes 1992, Hamm *et al.* 2003, Sánchez *et al.* 2003, González *et al.* 2010, Torres *et al.* 2011) where 2 μM is the minimum concentration required for the development of their populations (Egge & Aksnes 1992). By increasing the concentration of silicic acid, the diatoms

displace other species, increasing their rate of growth and reproduction and decreasing this resource (Egge & Aksnes 1992). Moreover, it has been reported that diatoms require lower concentrations of nitrate and that this decrease occurs with increasing phytoplankton body size (Iriarte *et al.* 2005). Additionally they exhibit other advantages such as faster reproduction in regions of high turbulence (Montecino *et al.* 2006) through higher growth efficiency under low light conditions (Pizarro *et al.* 2000, Goldman & Mc-Gillicuddy 2003). Several studies indicate that phytoplankton assemblages in Chilean Patagonian coastal waters are adapted to low light conditions, because of the extensive cloud cover present in the region for most of the year (Barbieri *et al.* 2001, Iriarte *et al.* 2007).

Confirming previous studies, with the results obtained in this study, we proved that changes in the latitudinal patterns obey physical and chemical forces and where limited light during winter is counteracted by high concentrations of silicic acid supplied by inland waters (northern sector) and may be offset with a threshold concentration of this nutrient. Also, with heterogeneous ambient conditions of the surface water layers, the condition for autotrophic growth under light shortage is enhanced. Moreover, the minimum reported concentration of silicic acid during the entire study period of 3.5 µM, as a bottom up factor exceeds the minimum concentration reported by Egge & Aksnes (1992). Therefore, it can be inferred that as the summer approaches, increasing solar radiation, under no nutrient limitation, and changes in wind direction modulate the distribution and abundance of phytoplankton in the north-south zones of the ISoCh. Regardless of the differences in nutrient concentrations that were established between the two zones, Chl-a concentration behave similarly in both sectors, so that the abundance of TChl-*a* responds primarily to favourable spring time processes shown by the higher temperature of the water column (Fig. 3). This study emphasizes that the robustness of the factors that modulate the growth of phytoplankton depend on the season.

Studies in the ISoCh highlight the influence of temperature and nutrients, particularly nitrate and silicate, on phytoplankton composition and abundance (Avaria *et al.* 1997, Pizarro *et al.* 2000, Ramirez & Pizarro 2005, Montecino *et at.* 2006). In our study, the abundance of TChl-*a* exhibited an inverse and seasonal relationship with the concentration of nitrate and silicic acid. This reveals a direct relationship between the consumption of nutrients and phytoplankton abundance, registering

lower availability of these nutrients in the spring compared to the winter season, where concentrations of TChl-*a* were significantly lower ($P < 0.005$) (Table 2). A direct relationship between geographic areas and Chl-*a* patch size was evident and significant responses were obtained among contrasting conditions, due to seasonality: large and more homogenous patch sizes during winter and smaller patch sizes with higher heterogeneity during spring. This could be related to the complex dynamics of non-lineal responses of natural populations (Beckas & Arndt 2013) to physical processes (*i.e.,* lateral stirring and mixing) that drive spatial dynamics at the mesoscale (Martin 2003), also shown by Lara *et al.* (2010) in the ISoCh. Despite north-south interannual nutrient differences during seasons, the phytoplankton community abundance patterns do respond to seasonality factors, underscoring the relevance of nutrients under lower light availability during winter and more complex oceanographic processes during spring. We suggest that future validation of satellite products in optically complex coastal waters can increase spatial and temporal analysis of phytoplankton communities change especially under the influence of long-term anthropogenic effects.

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