

Revisiting chlorophyll data along the coast in north-central Chile, considering multiscale environmental variability

Reinterpretando datos de clorofila en la costa centro-norte de Chile, considerando
variabilidad ambiental de multiescala

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ABSTRACT

Phytoplankton abundance in the surface mixed layer of the coastal ocean responds to environmental changes at various time scales. Here the “warm”, “cold” and “neutral” phases of “three environmental cycles” have been jointly considered to assess chlorophyll-*a* (Chl-*a*) biomass variability for both the active and relaxed phases of the local, wind-driven coastal upwelling: (i) the interannual ENSO cycle (ii) the annual (seasonal) cycle and (iii) the intraseasonal cycle associated with equatorially-sourced, ocean trapped-waves along the coast in northern Chile. The main goal of this study is to quantitatively assess the variability of the depth-integrated Chl-*a* biomass in the euphotic zone ($\int\text{Chl-}a$) in terms of an overall “environmental condition” over a 50 km upwelling sensitive coastal strip, revisiting published and unpublished Chl-*a* ship ($C_{\text{ship}} = \text{Chl-}a + \text{Phaeopigments}$) data. All possible “environmental conditions” combinations were further ranked into seven “environmental indices” ranging from 0 (“absolutely cold”) to 6 (“absolutely warm”). Out of 332 samples of $\int\text{Chl-}a$, 198/134 were obtained during active/relaxed upwelling conditions from which 24/38 and 30/36 samples were associated with the simultaneous occurrence of at least two “cold”/“warm” phases of the three environmental cycles (“cold”/“warm” environmental conditions), respectively. Lower $\int\text{Chl-}a$ values during “cold” and “warm” environmental conditions relative to the “neutral” ones reached statistical significance for both active and relaxed conditions (144/60 samples respectively). Higher turbulent mixing during “cold” environmental conditions and a deeper nutricline during “warm” ones would explain lower $\int\text{Chl-}a$ -values. Satellite chlorophyll (C_{sat}) data obtained in clear skies (active upwelling only), showed a similar distribution to those of $\int\text{Chl-}a$ when classified into the corresponding “environmental indices”. These results suggest that during “neutral” (transitional) “environmental conditions”, nutrient supply, mean light exposure and mixing thresholds, including biological interactions, could be more effective in producing a higher phytoplankton biomass, in spite of a larger dispersion.

Key words: ENSO, Coastal trapped waves, coastal upwelling, phytoplankton biomass, Antofagasta-Valparaíso, Chile.

RESUMEN

La abundancia de fitoplancton en la capa de mezcla superficial del océano costero responde a cambios ambientales en diferentes escalas de tiempo. Aquí se han considerado conjuntamente las fases “cálida”, “fría” y “neutra” de “tres ciclos ambientales” para estimar la variabilidad de la biomasa de la clorofila (Chl-*a*) para las fases activa y relajada de la surgencia costera inducida por el viento local: (i) el ciclo interanual ENOS (ii) el ciclo anual (estacional) y (iii) el ciclo intraestacional asociado con ondas oceánicas atrapadas a lo largo de la costa en el norte de Chile. El objetivo principal de este estudio es estimar cuantitativamente la variabilidad de la Cl-*a* integrada en la zona eufótica ($\int\text{Chl-}a$) en términos de una “condición ambiental” conjunta, para la banda costera de 50 km sensible a la surgencia, reinterpretando datos in situ de Chl-*a* ($C_{\text{ship}} = \text{Chl-}a + \text{Feo pigmentos}$) publicados y no publicados. Todas las combinaciones posibles de las “condiciones ambientales” se ordenaron en siete “índices ambientales” que van desde 0 (“absolutamente frío”) a 6 (“absolutamente cálido”). Del total de 332 muestras de $\int\text{Chl-}a$, 198/134 se obtuvieron en condiciones de surgencia activa/relajada, de las cuales 24/38 y 30/36 muestras estuvieron asociadas con al menos dos fases frías/cálidas, de los tres ciclos ambientales (condiciones ambientales “fría”/“cálida”) respectivamente. Los menores valores de $\int\text{Chl-}a$ durante las condiciones ambientales “frías” y “cálidas” respecto de las “neutras” alcanzaron

significancia estadística tanto en surgencia activa como relajada (144/60 muestras respectivamente). Una mayor mezcla turbulenta durante condiciones ambientales “frías” y una nutriclina más profunda durante las “cálidas” explicarían los menores valores de $f\text{Chl-}a$. Datos de clorofila satelital (C_{sat}) obtenidos para cielos despejados (sólo surgencia activa), mostraron una distribución similar a los de la $f\text{Chl-}a$ cuando se clasificaron dentro de los correspondientes “índices ambientales”. Estos resultados sugieren que durante las condiciones ambientales “neutrales” (transicionales), el aporte de nutrientes, la exposición promedio a la luz y los umbrales de turbulencia, incluyendo interacciones biológicas, podrían ser más efectivos en producir una mayor biomasa fitoplanctónica, a pesar de una mayor dispersión.

Palabras clave: ENOS, ondas atrapadas a la costa, surgencia costera, biomasa fitoplanctónica, Antofagasta-Valparaíso, Chile.

INTRODUCTION

Phytoplankton distribution in the central part (16–26° S) of the Humboldt Current System (HCS), has been characterised by low spatial/high temporal variability, as shown through satellite chlorophyll (C_{sat}) data averaged in space over 100 km next to the coast (Thomas et al. 2001, Montecino et al. 2006). These large temporal changes are due to the phytoplankton response to quasi-weekly upwelling favourable wind events, which depends primarily on the mean depth of the nutricline. Here we hypothesise that these nutricline mean depth is the fundamental parameter explaining phytoplankton abundance associated to any particular upwelling wind event, as it changes according to the phase of intraseasonal Coastal Trapped Waves (CTW's); the annual cycle and the interannual El Niño/Southern Oscillation (ENSO) cycle (Rutllant & Montecino 2002).

The local atmospheric forcing seems to be always active along north-central Chile, largely independent of the phase of lower-frequency environmental cycles (e.g., Rutllant et al. 2004). Although environmental variability on interannual (ENSO) scales has been noticed as important, particularly during strong El Niño/La Niña events, weak seasonal variability patterns in the phytoplankton concentration have been reported between 18–30° S through remote sensing of ocean colour, with C_{sat} maxima centred on austral summer coinciding with the season of maximum strength of the upwelling- favourable winds along the coast (Thomas et al. 2001). However seasonal changes seem to be moderate in strength off Perú and stronger at mid- and high latitudes off Chile (Montecino et al. 2006). Intraseasonal variability in the depth of the nutricline is dominated by equatorially-sourced CTWs, as reflected in coherent changes in coastal sea

level (e.g., Shaffer et al. 1997) and sea surface temperature along the west coast of South America, the latter showing a 90° phase lag relative to the sea level (Hormazábal et al. 2001, Rutllant et al. 2004).

Global ocean primary production has been positively linked to cold SSTs as a proxy of nutrient availability (Behrenfeldt & Falkowski. 1997). Temperature, nutrients, light-shade adaptation (Falkowski 1981) and species growth rates (Cloern et al. 1995), change the abundance of phytoplankton Chl-*a* biomass and the chlorophyll:carbon ratio. This variability is not absent in the Chilean coastal region where higher phytoplankton biomass (estimated as Chlorophyll-*a* like pigments from ship measurements, C_{ship}) is mostly restricted to a coastal strip of 50 km (Montecino et al. 1998, Stuart et al. 2004), although high pigment concentrations associated with filaments extending several hundred kilometres from coastal upwelling centres in the HCS have been detected in satellite pigment and SST imagery (Yáñez et al. 1995, Carr 2002, Marín & Delgado 2003).

Revisiting published and unpublished data of C_{ship} (Chl-*a* + Phaeopigments) along the north-central Chilean coast, the present study aims at a quantitative assessment of the column-integrated Chl-*a* biomass variability over a 50 km “upwelling sensitive” coastal strip (Fig. 1). Since concurrent cycles at various time scales are modulating the nutricline depth, the specific phases of intraseasonal, annual and interannual environmental cycles were established for each datum. The effect of multiscale environmental cycles over the Chl-*a* biomass variability (Rutllant & Montecino 2002), leads to the hypothesis that differences should arise when at least two cold, warm or neutral phases of the three environmental cycles are simultaneously considered.

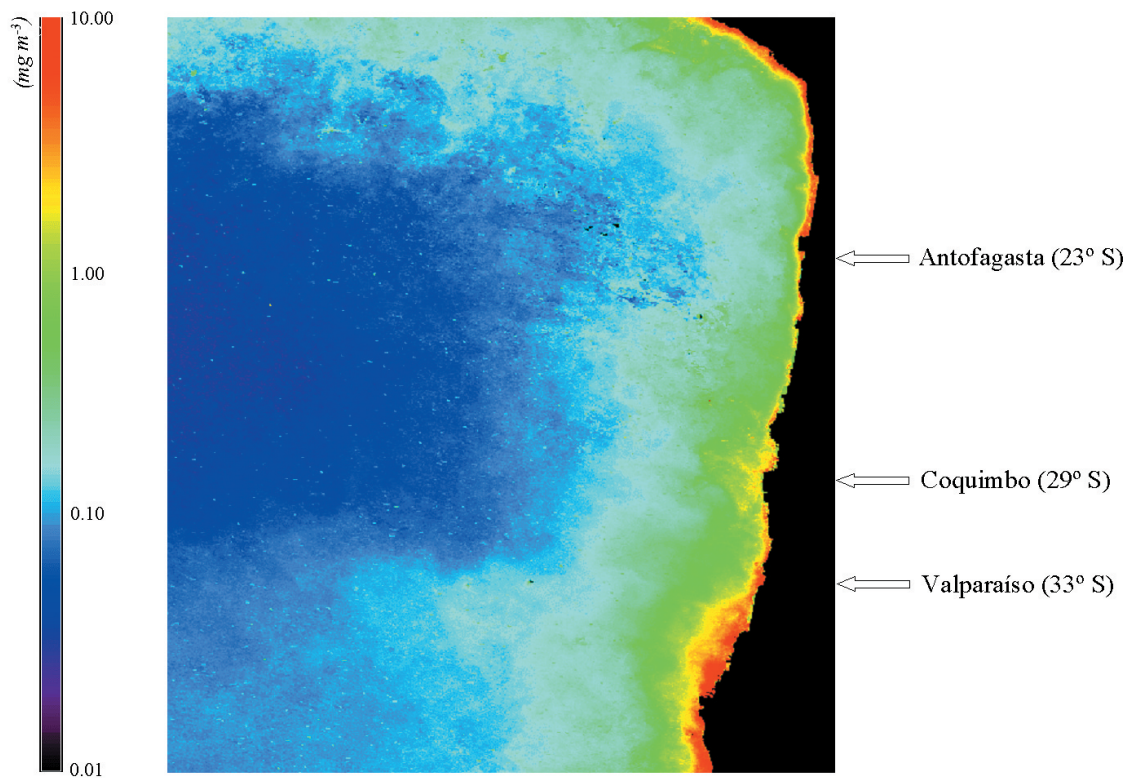


Fig. 1: The location of three coastal upwelling sites in north-central Chile (23°-46° S) where C_{ship} samples were collected. These are indicated over a map of surface chlorophyll concentrations, estimated from the first six years of SeaWiFS ocean colour measurements for the Humboldt Current system off western South America (means for austral summer- from hierarchical data files; courtesy of Andrew Thomas).

Ubicación de los tres lugares de surgencia costera en el centro-norte de Chile (23°-46° S) donde se recolectaron las muestras para C_{ship} . Estos aparecen indicados sobre un mapa de concentraciones superficiales de clorofila, estimados para los primeros seis años de mediciones SeaWiFS del color del mar para el sistema de corrientes de Humboldt frente a Sudamérica occidental (promedios para el verano austral a partir de archivos de datos jerárquicos, cortesía de Andrew Thomas).

MATERIAL AND METHODS

To examine the phytoplankton Chl-*a* biomass distribution during different phases of interannual, seasonal and intraseasonal environmental cycles, that have been labelled as “warm”, “cold” and “neutral” (transitional) phases, the euphotic zone depth-integrated Chl-*a* biomass ($\int\text{Chl-}a$) values were calculated within the upwelling-sensitive coastal strip off north-central Chile. The C_{ship} (Chl-*a* + Phaeopigments) data were selected from coastal stations (< 50 km) of different cruises (Table 1) including spring values off Valparaíso. In order to compare the C_{ship} with the C_{sat} data, the values during the active phase of the upwelling cycle (clear sky conditions),

have been considered separately from those corresponding to the relaxed phase of the upwelling, when overcast skies prevail (e.g., Rutllant et al. 1998, Garreaud et al. 2002).

The phase separation of the intraseasonal and interannual cycles was made following previous work (Rutllant & Montecino 2002), in which “cold”/“warm” phases were considered as proxies for “shallower”/ “deeper” nutriclines, without any association with the potential temperature effect on phytoplankton growth. Other biological effects as grazing during warm conditions (Pizarro et al. 2002) and changes in sedimentation processes (González et al. 1998) or increased primary production during cold conditions (Rutllant & Montecino 2002) were also not considered here. Each $\int\text{Chl-}a$ value was

labelled according to the phase (cold- neutral-warm) of: (a) the ENSO (interannual) cycle using the Multivariate ENSO Index (www.cdc.noaa.gov/~kew/MEI/); (b) the annual cycle, as defined by sea surface temperature (SST) monthly means (SHOA- Chile, 1996) (Table 2), and (c) the intraseasonal cycles associated with coastal trapped waves (CTWs), obtained from daily sea level data for Caldera (27° S), supplied by the Sea Level Centre,

University of Hawaii and band-passed (28-70 days) with a Butterworth filter. Consistent with the reported phase lag between SST and sea-level in those CTWs (Hormazábal et al. 2001), “cold”/”warm” intraseasonal phases were assigned when the sea-level was rising/falling, with transition conditions in between (Rutllant & Montecino 2002, Rutllant et al. 2004). The same protocol was used for the available ocean-colour data (C_{sat}).

TABLE 1

List of nominal sites from north to south (26-33° S) of available C_{ship} data at different periods, locations or cruise name and maximum depth (m) of integration of C_{ship} (Max f depth). To assign C_{ship} values, years and month of sampling were used for ENOS cycles. For the seasonal cycle see Table 2 (authors of the related publications can be found in the references)

Nómina de sitios de norte a sur (26-33° S) con disponibilidad de datos de C_{ship} para diferentes períodos, lugares o nombre de crucero y profundidad máxima (m) de integración de C_{ship} (Max f depth). Para adscribir los valores de C_{ship} a los ciclos ENOS se utilizaron los meses y años de muestreo. Para el ciclo estacional ver Tabla 2 (los autores de las publicaciones correspondientes se encuentran en la bibliografía)

Site	Year	Month	Location or cruise*	Max f depth	Author
Antofagasta	1989	Nov-Dec	Mejillones	11	Marín et al. (1993)
Antofagasta	1990	Jan-Dec	Mejillones	48	Marín et al. (1993)
Antofagasta	1991	Jan-Dec	Mejillones	59	Marín et al. (1993)
Antofagasta	1993	Apr-Dec	Antofagasta bay	45	Rodríguez et al. (1996)
Antofagasta	1993	Nov-Dec	IFOP*	25	Morales et al. (1996)
Antofagasta	1994	Jan-Dec	Antofagasta bay	40	Rodríguez et al. (1996)
Antofagasta	1994	Feb	IFOP*	100	Morales et al. (2001)
Antofagasta	1994	May	IFOP*	100	Morales et al. (2001)
Antofagasta	1995	Jan-May	Antofagasta bay	30	Rodríguez et al. (1996)
Antofagasta	1996	July-Dec	Mejillones	60	Ulloa et al. (2001)
Antofagasta	1997	Jan	Sectorial*	74	Rutllant & Montecino (2002)
Antofagasta	1997	July	Sectorial*	66	Rutllant & Montecino (2002)
Antofagasta	1997	Jan-Dec	Mejillones	60	Ulloa et al. (2001)
Antofagasta	1998	Jan	Mejillones	60	Ulloa et al. (2001)
Coquimbo	1987	Nov	Cruz Grande	47	Rutllant & Montecino (2002)
Coquimbo	1988	Nov	Cruz Grande	47	Rutllant & Montecino (2002)
Coquimbo	1992	Apr	JGOFS*	47	Rutllant & Montecino (2002)
Coquimbo	1992	Jun	JGOFS*	66	Rutllant & Montecino (2002)
Coquimbo	1992	Oct	JGOFS*	60	Rutllant & Montecino (2002)
Coquimbo	1993	Sep	JGOFS*	74	Rutllant & Montecino (2002)
Coquimbo	1994	Jan-Feb	JGOFS*	48	Rutllant & Montecino (2002)
Coquimbo	1995	Jan	JGOFS*	59	Rutllant & Montecino (2002)
Coquimbo	1995	July	JGOFS*	84	Rutllant & Montecino (2002)
Coquimbo	1996	July	JGOFS*	73	Rutllant & Montecino (2002)
Coquimbo	1997	Feb	JGOFS*	70	Rutllant & Montecino (2002)
Coquimbo	1997	Nov	JGOFS*	82	Rutllant & Montecino (2002)
Valparaíso	1996	Nov	Valparaíso bay	19	Sievers & Vega (2000)
Valparaíso	1997	Nov	Valparaíso bay	27	Sievers & Vega (2000)
Valparaíso	2000	Sep-Dec	Valparaíso bay	45	Pablo Muñoz (personal communication)
Valparaíso	2001	Sep-Dec	Valparaíso bay	48	Pablo Muñoz (personal communication)

*IFOP: Instituto de Fomento Pesquero.

*JGOFS: Joint Global Ocean Flux Studies.

As suggested previously (Rutllant & Montecino 2002) the simultaneous occurrence of at least two cold/warm conditions (ww=w; cc=c) in the concurrent three scales of variability defines a resulting “cold”/“warm” Environmental Condition (EC) for the Chl-*a* biomass abundance; otherwise the EC is labelled as “neutral” (Table 3). For all possible EC realisations ($3^3 = 27$) an arbitrary discrete numerical value from zero to six (EI = Environmental Index) ranks them from “absolutely cold” (0 = ccc) to “absolutely warm” (6 = www), passing through “mostly cold”, “weakly cold”, “neutral”, “weakly warm” and “mostly warm” (Table 3). Increasing EIs discrete values (0 to 6) also represent increasing water column stability and decreasing

nutrient availability, both affecting phytoplankton biomass abundance.

The significance of the differences between the integrated C_{ship} values for the warm, cold and transition ECs was assessed separately for the upwelling active and upwelling relaxed data by nonparametric Kruskal-Wallis test by ranks (Sokal & Rohlf 1981). The same procedure was applied to the C_{sat} data, which only correspond to the upwelling active (clear skies) cycle. These comparisons were conducted using standart statistical procedures. The shape of the distribution of $fChl-a$ and C_{sat} data into the EI values was tested for significance through quantile regression analysis with a quadratic fit for the 10-95 percentils using the “quantreg” R library software (<http://www.R-project.org/>) (Cade et al. 1999, Knight & Ackerly 2002)

TABLE 2

Monthly mean sea-surface temperatures (°C) at three different upwelling centers obtained from the first coastal isotherm (Chilean Oceanographic Atlas 1996). Warm (grey and bold), transition (white and italics) and cold (grey and normal) seasonal conditions define the annual thermal cycle

Promedio mensual de temperaturas superficiales (°C) en tres diferentes centros de surgencia obtenido desde la primera isoterma costera (Atlas Oceanográfico de Chile 1996). Las condiciones estacionales cálida (gris y negritas), transición (blanco y cursivas) y fría (gris y normal) definen el ciclo anual termal

Zone	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Antofagasta	20	21	20	<i>19</i>	<i>18</i>	<i>16</i>	16	16	15	<i>17</i>	<i>18</i>	<i>18</i>
Coquimbo	18	16	17	<i>15</i>	<i>15</i>	<i>14</i>	13	13	13	<i>14</i>	<i>15</i>	16
Valparaíso	17	15	15	<i>14</i>	<i>14</i>	<i>14</i>	13	13	13	<i>13</i>	<i>14</i>	15

TABLE 3

Environmental Conditions (EC), and the Environmental Index (EI). Conditions with at least two “cold/warm” components are shaded. The EI values (0-6) result from the sum of cold (0), transition (1) and warm (2) conditions from the three environmental cycles considered here

Condiciones ambientales (EC) e índice ambiental (EI). Condiciones con al menos dos componentes “fría/cálida” están sombreadas. Los valores EI (0-6) resultan de la suma de las condiciones fría (0), transición (1) y cálida (2) a partir de los tres ciclos ambientales aquí considerados

EC	Absolutely cold	Mostly cold	Weakly cold	Neutral	Weakly warm	Mostly warm	Absolutely warm
EI	0	1	2	3	4	5	6
	ccc	ccn	ccw	wnc	wwc	wwn	www
		cnc	cwc	wcn	wcw	wnw	
		ncc	wcc	nwc	cww	nww	
			cnn	nnn	wnn		
			ncn	ncw	nwn		
			nnc	cwn	nwn		
				cnw			

C_{sat} data were extracted from SeaWiFs images obtained from the Distribution Active Archive Center (DAAC), Goddard Space Flight Center (GSFC), NASA, and selected according to cloud coverage criteria. For image processing SeaDAS V4.3 software for Linux and OC4 algorithm were used. In northern Chile, C_{sat} data were obtained from seven sampling points slightly south of Mejillones peninsula, (station 15 in Pizarro et al. 2002) within the 70.67-70.79° W and 23.31-23.36° S rectangle, and seven sampling points from Punta Coloso (Station 25, in Pizarro et al. 2002) within 70.60-70.68° W and 23.75-23.83° S rectangle for 1997, 1998, 1999 and 2000 ($n = 27, 15, 33, 85$ images respectively). C_{sat} values for each EI were plotted in the same way as it was done with $\int\text{Chl-}a$. From a total of 242 C_{sat} , 120/34 samples were associated with “cold”/“warm” environmental conditions.

RESULTS

C_{ship} data concentrated off Antofagasta (23° S) and Coquimbo (30° S) with some sparse information off Caldera (27° S) and Valparaíso (33° S). Altogether, about 72 % of the samples correspond to distances within 10 km from the coast and 20 % of the samples were either between 10-20 or 40-50 km.

Warm, cold and neutral seasons along the coast of north-central Chile, based on the SST monthly means (Table 2), indicate that the annual amplitude of SST changes from 6 °C (northern Chile) to 4 °C (central Chile). The cold season (July to October) in central Chile (Valparaíso) lags by about one month the northern one (Antofagasta to Coquimbo).

From a total of 332 $\int\text{Chl-}a$ samples, 198/134 were obtained during active/relaxed upwelling conditions. For the active/relaxed upwelling subsets, 24/38 and 30/36 samples were associated with cold/warm ECs, respectively, in contrast with 144/60 samples taken during neutral ECs, in which the largest variability was found (Fig. 2).

The highest $\int\text{Chl-}a$ biomass was found during “neutral” ECs, representing transitions from “cold” to “warm” or “warm” to “cold”. In fact, a unimodal distribution with lower maximum values during “absolutely cold” (EI = 0), “mostly cold” (EI = 1), “mostly warm”

(EI = 5) and “absolutely warm” (EI = 6) EC conditions was found (Fig. 3A). Mean values of $\int\text{Chl-}a$ ranged from 29.55 to 47.52 mg Chl- a + Php m^{-2} . The corresponding average figures for the transition groups ranged from 31.32 to 102.76 mg Chl- a + Php m^{-2} .

$\int\text{Chl-}a$ differences between three categories of EI’s (“absolutely”, “mostly” and “weakly-cold”, “neutral” and the “absolutely”, “mostly” and “weakly-warm”) were significant (Kruskal-Wallis test, $H_{2,198} = 8.13$, $P = 0.0172$) for the active upwelling samples (Fig. 2A) as they were for the relaxed upwelling ones (Fig. 2B) (Kruskal-Wallis test, $H_{2,134} = 10.02$, $P = 0.0067$).

To overcome deficiencies in the spatial and temporal coverage, $\int\text{Chl-}a$ data were complemented with ocean colour satellite (C_{sat}) data obtained in clear skies, conditions that prevail during active upwelling only. Since most of the satellite data were obtained for year 2000, they were biased towards cold interannual conditions (La Niña). Although C_{sat} data arranged into EI bins indicate a similar pattern as with $\int\text{Chl-}a$ (Fig. 3B), significance in the differences between cold, warm and neutral C_{sat} values was not attained (Kruskal-Wallis test, $H_{2,122} = 1.63$, $P = 0.4422$).

DISCUSSION

The period of re-examination of C_{ship} data (Table 1) started with a warm phase (El Niño) of the ENSO cycle in 1987, followed by a cold one (La Niña) in 1988. A long and moderate warm event occurred between 1991 and 1995. During this 12-13 year period, measurements off the Mejillones peninsula area and at the outer section of the Valparaíso bay, allowed $\int\text{Chl-}a$ comparisons in different phases of intraseasonal, annual and ENSO cycles. Since available data for northern Chile were scarce, Valparaíso data had to be included although Valparaíso lies at the poleward edge of the seasonally-persistent strong upwelling zone (Mackas et al. 2006).

Based on Moraga et al. (1994) and Escribano et al. (2004), seasonal-intraseasonal and interannual variability in the mean depth of the thermocline base for Coquimbo (30° S) and Antofagasta (23° S) can be described to oscillate between 85 ± 35 m and 42 ± 32.5 (EI

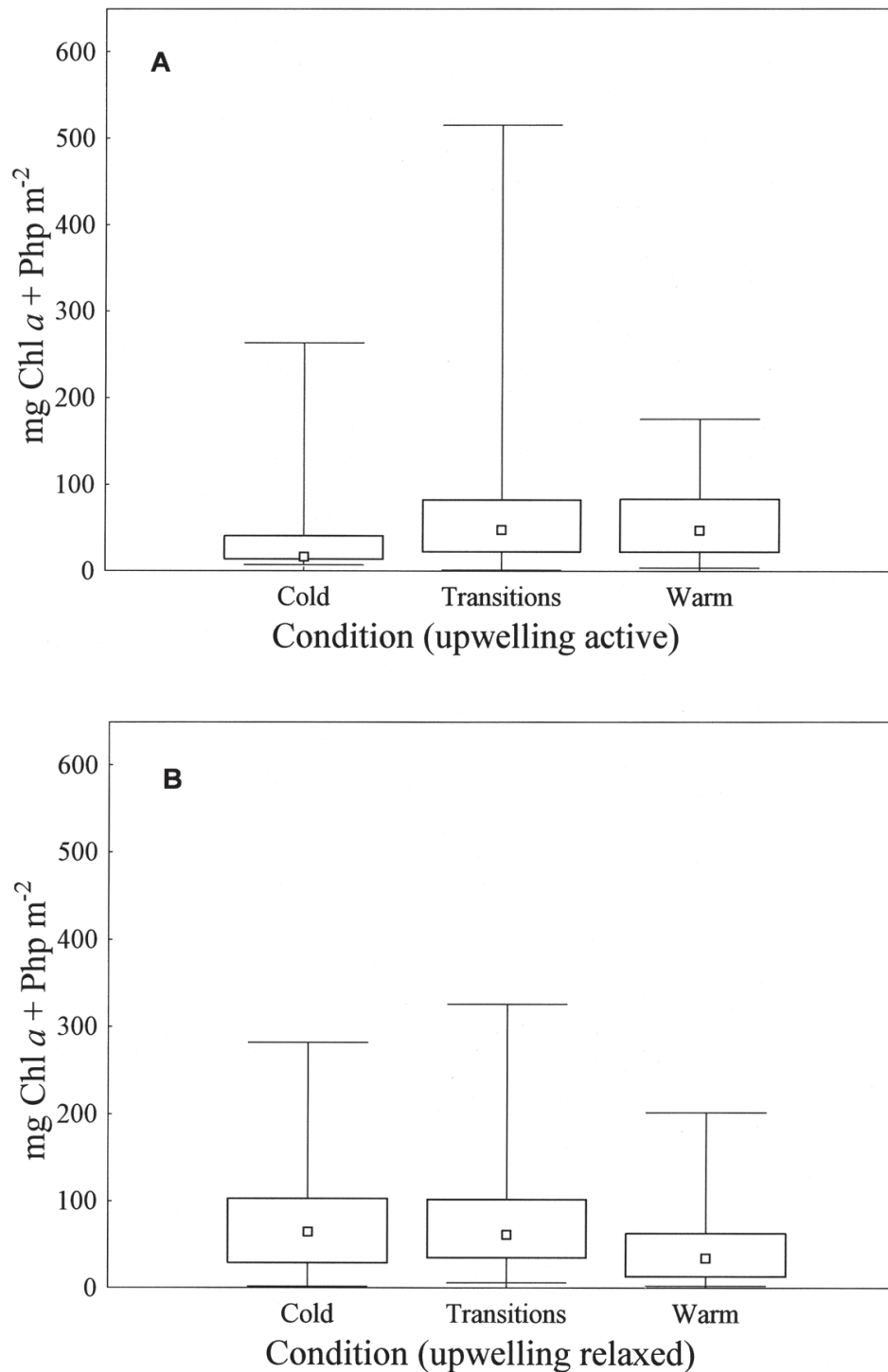


Fig. 2: Minima, maxima and medians of integrated chlorophyll-a + Phaeopigments (Chl-a + Php) for “cold”, “neutral” (transition) and “warm” environmental conditions (ECs), for active (A) and relaxed upwelling conditions (B). The results of the statistical analysis are indicated in the text.

Mínimos, máximos y medianas de los valores integrados de clorofila-a + Feopigmentos (Chl-a + Php) para condiciones ambientales (ECs) “fría”, “neutra” (transición) y “cálida”, para condiciones de surgencia activa (A) y relajada (B). Los resultados del análisis estadístico se indican en el texto.

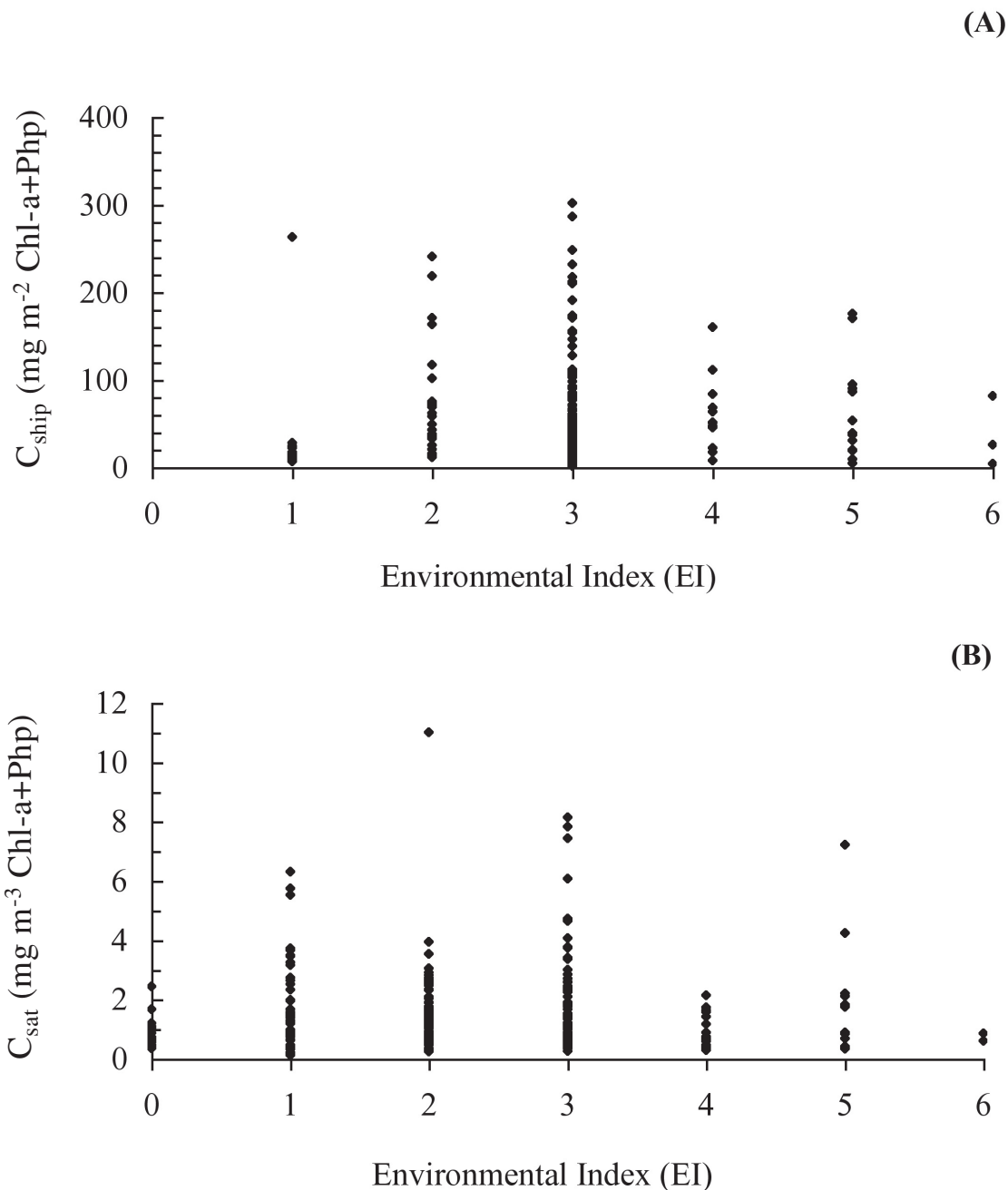


Fig. 3: (A) Distribution of integrated chlorophyll-a + Phaeopigments (Chl-a + Php) values, as a function of the Environmental Index (EI), from *in situ* measurements during upwelling active conditions in Antofagasta, Coquimbo and Valparaíso. The analysis of the resulting unimodal relationship, showed significant quadratic regression ($P = 0.04$) throughout percentils 10 to 85. (B) Distribution of C_{sat} values as a function of the Environmental Index (EI) at two sites off the Mejillones Peninsula during upwelling active conditions. The analysis of the resulting unimodal relationship showed significant quadratic regression ($P < 0.001$) throughout percentils 10 to 75.

(A) Distribución de los valores integrados de clorofila-a + Feopigmentos (Chl-a +Php) en función del Índice Ambiental (EI), de mediciones *in situ* en Antofagasta, Coquimbo y Valparaíso durante condiciones de surgencia activa. El análisis de la relación unimodal resultante, mostró regresiones cuadráticas significativas ($P < 0,05$) en los percentiles 10 al 85. (B) Distribución de valores de C_{sat} en función del Índice Ambiental (EI) en dos sitios frente a Península Mejillones durante condiciones de surgencia activa. El análisis de la relación unimodal resultante, mostró regresiones cuadráticas significativas ($P < 0,0001$) en los percentiles 10 al 75.

Niño) and between 35 ± 15 m and 20 ± 10 m (La Niña), respectively. Since geographic differences appear smaller than seasonal or interannual variability, the results reported here should be valid for the merged data from northern and central Chile. Moreover, the lower mean depth of the thermocline base at Coquimbo is compensated by stronger mean southerly winds there (e.g., Hormazábal et al. 2001). Also during El Niño years, the combined seasonal- intraseasonal variability represented by the departures from the mean depth is largest due to stronger intraseasonal oscillations during austral summer just before the onset of El Niño (e.g., Shaffer et al. 1997).

Above the thermocline base low salinity and oxygen- rich subantarctic waters prevail, except during El Niño's when they might become mixed with higher salinity and temperature subtropical waters. Below the thermocline high salinity, nutrient and dissolved carbon dioxide (equatorial subsurface waters) prevail, with very low oxygen content (Blanco et al. 2002, Montecino et al. 2006).

Besides the multiscale environmental cycles influencing the nutrient availability through oscillations in the mean thermo-nutricline depth, the significant differences in $\int\text{Chl-}a$ median values found between cold, warm and neutral ECs can be also attributed to biological changes as increase/decrease of new/regenerated production, size structure of phytoplankton assemblages and low Chl-*a* abundance during cold conditions along the Chilean northern coast (Montecino & Quiroz 2000, Pizarro et al. 2002, Iriarte & González 2004). The dominance of microphytoplankton cells and biological shifts in size composition of phytoplankton assemblages when $\int\text{Chl-}a$ increases (Iriarte & González 2004), explain both the presence of outlayers and the large variability in the observed values during neutral (transition) ECs (Fig. 3). Therefore, higher $\int\text{Chl-}a$ stocks found during neutral ECs can be understood as coupling of the classic template of nutrient supply and mean light exposure of Margalef's diagram, for both small and large phytoplankton fractions (Cullen et al. 2002).

Here we have expanded on the results found by Rutllant & Montecino (2002) while interpreting changes in Chl-*a* biomass and primary production between the active and relaxed phases of the local wind-driven

upwelling. In fact the expected high turbulent mixing/low stability in the upper water column during active upwelling in "cold" conditions, results in lower Chl-*a* abundance in spite of the shallower nutricline (larger nutrient supply). With maximum stratification of the upper water column during "warm" conditions and relaxed upwelling, light availability is larger (except for self-shading) but the nutrient supply in the euphotic zone is less. Therefore increasing EIs also represent decreasing mean nutrient availability (deeper nutricline). These results are consistent with the effects of the upper ocean physical processes on pelagic communities and the biological system, specifically the competing influences of water column stability on the light and nutrient requirements for phytoplankton production, suggested to be maximized when both substrates are adequate (Gargett & Marra 2002).

Mackas et al. (2006) comparing different upwelling areas report temporal and spatial variability of the forcing and response, including seasonal and interannual variability. In this overview, the typical phytoplankton abundances are referred to the differences in the extension of the high pigment region between winter and summer with a temporal mismatch between wind-forcing and phytoplankton response on annual scales off Perú. At a larger scale, C_{sat} in Pacific and Atlantic mid latitude eastern boundary currents share common seasonal patterns in the extensions of the upwelling sensitive strip.

The altered hydrographical conditions during the 1997-1998 El Niño (Blanco et al. 2002) were not reflected in phytoplankton biomass abundance in northern Chile, although temperature and oxygen increased (Ulloa et al. 2001). This was probably due to the narrowing of the region with colder upwelled water off northern Chile (Blanco et al. 2002, Torres et al. 2002), in which the majority of the samples were obtained (10 km from the coast). Biological consequences of interannual variability in non-coastal upwelling areas (Chávez 2006), relate to different phenomena than those reported here.

Contrasting with the results for the $\int\text{Chl-}a$ values, the lack of significance in the differences between C_{sat} values from cold to neutral ECs can be in the first place attributed

to the generally cold interannual conditions during the period in which data were available. Since only near-surface Chl-*a* can be estimated with ocean-colour data, the coexistence within the euphotic zone of more species that thrive at intermediate levels of turbulent mixing and light availability with a characteristic larger dispersion could influence this result. In summary, these results would indicate that it is the whole water column that is more sensitive to the multiscale ECs in stimulating higher \int Chl-*a* stocks during transitional stages.

Finally, since neutral conditions are much more frequent than the absolutely cold/warm ones, as they include transitions for each one of the three environmental cycles considered here, care should be taken when comparing in-situ and time-averaged satellite-derived data off north-central Chile.

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