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Mesoscale primary production and bio-optical variability off Antofagasta (23-24° S) during the transition to El Niño 1997-1998

Variabilidad de la producción primaria y bio-óptica a mesoescala frente a las costas de Antofagasta (23-24° S) durante la transición a El Niño 1997-1998

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ABSTRACT

The spatial variability of primary production (PP), chlorophyll-a (Chl-a) and the photosynthetic parameters were studied off Antofagasta, Chile (23-24° S, 70-72° W) during austral summer and winter. Between cruises (January and July 1997), significant changes occurred in the water column, including higher temperatures in the euphotic zone (Z_{eu}) deepening of thermocline below Z_{eu}, an increase of oxygen concentration and the intrusion of Subtropical Waters with potential limitation of nutrients. These strong physical anomalies due to the transition period of El Niño 1997-1998 appeared in this study area during March 1997. During the July cruise, the El Niño event 1997-1998 was in the middle of its development (IOS–2). The hypothesis that chlorophyll-a concentrations and primary production differ significantly in the coastal areas in the Antofagasta region due to year-round coastal upwelling was tested in this study. Photosynthesis versus irradiance (P-E) experiments were performed daily, using simulated in situ incubations with samples collected within the Z_{eu}. Also in vitro incubations were done at several selected stations. For results analyses, stations were pooled in coastal and oceanic sites according to distance from the narrow shelf and differential influence of local upwelling. Integrated Chl-a values during both cruises were significantly higher at the coastal stations, and since between cruises no differences were found, a mean value of 44 mg Chl-a m^{-2} can be reported for the coastal area. Daily PP values were significantly different in space and time ($P < 0.001$), and at the coast also between cruises ($P < 0.004$) as a result of the high mean coastal value in January, 3,129 mg C m^{-2} d^{-1} in comparison to 942 mg C m^{-2} d^{-1} in July. The attenuation coefficient k_d of photosynthetic active radiation (PAR), determined a significant change in the mean depth of Z_{eu} between coastal and oceanic stations (44 ± 20 and 80 ± 17 m, respectively) during both sampling periods. Notwithstanding the spatial differences in chlorophyll-a concentrations and primary production, the observed weaker upwelling favourable winds during both cruises, the increase in depth of the mixing layer and light limitation in July, and the higher mean values of zooplankton grazing rate during January contributed to the similar abundance of chlorophyll-a in time. Although the El Niño event could negatively affect primary production during July, prevailing space and seasonal variability masked this effect.

Key words: primary production, photosynthetic parameters, attenuation coefficient, euphotic zone, mixing depth, El Niño event 1997-1998.

RESUMEN

Durante el verano e invierno austral, se estudió la variabilidad espacial de la producción primaria (PP), clorofila-a (Cl-a) y los parámetros fotosintéticos en las costas de Antofagasta, Chile (23-24° S, 70-72° O). Entre ambos cruceros (enero y julio 1997) hubo cambios significativos en la columna de agua, los que incluyeron aumento de la temperatura en la zona eufótica (Z_{eu}), profundización de la termoclina por debajo de Z_{eu}, un aumento de la concentración de oxígeno y la intrusión de aguas subtropicales con una limitación potencial de nutrientes para el fitoplancton. Estas fuertes anomalías físicas debidas al período de transición El Niño 1997-1998 aparecieron en el área de estudio a partir de marzo de 1997. Durante el crucero de julio, el evento El Niño 1997-1998 estaba en mitad de su desarrollo (IOS –2). En este estudio se puso a prueba la hipótesis que un incremento en las concentraciones de clorofila-a y producción primaria, debido a la ocurrencia de eventos de surgencia costeras durante todo el año, difieren significativamente entre las áreas costeras y oceánicas de la región de Antofagasta. Diariamente se realizaron experimentos de fotosíntesis versus irradiancia (P-E), usando incubaciones simuladas in situ con muestras recolectadas dentro de $Z_{eu.}$ También se realizaron incubaciones in vitro en varias estaciones seleccionadas. Para el análisis de los resultados, las estaciones de acuerdo con su localización fueron agrupadas en costeras y oceánicas según su distancia a la angosta plataforma y al grado de influencia de la surgencia local. Los valores de Cl-a integrada fueron significativamente más altos en las estaciones costeras y éstas a su vez no presentaron diferencias significativas entre cruceros, de modo que es posible señalar un valor promedio de 44 mg Cl-a m^{-2} para el área costera. Los valores de producción primaria diaria fueron significativamente diferentes (P < 0,001) en el espacio y tiempo, y también entre cruceros en el caso del área costera (P < 0,004) como resultado del alto valor promedio encontrado en enero, 3.129 mg C m^{-2} d^{-1} en comparación a 942 mg C m^{-2} d^{-1} en julio. El coeficiente de atenuación k_d de la radiación fotosintéticamente activa (PAR), determinó un cambio significativo en la profundidad media de Z_{eu} entre las estaciones costeras y oceánicas (44 ± 20 and 80 ± 17 m, respectivamente) durante ambos períodos de muestreo. No obstante las diferencias espaciales en las concentraciones de cl-a y producción primaria, los débiles vientos favorables para las surgencias durante ambos cruceros, el aumento de la profundidad de la capa de mezcla y la limitación de luz sumado a las mayores tasas medias de pastoreo del zooplancton durante enero, contribuyeron a que las concentraciones de cl-a fueran similares en el tiempo. Aunque El Niño pudo afectar negativamente la producción primaria durante julio, la variabilidad espacial y estacional enmascaró este efecto.

Palabras clave: producción primaria, parámetros fotosintéticos, coeficiente de atenuación, zona eufótica, profundidad de mezcla, evento El Niño 1997-1998.

INTRODUCTION

Explaining observed variability in El Niño-Southern Oscillation (ENSO) events and their subsequent effects on near-shore ecosystems remains a difficult challenge for biological oceanographers. During ENSO events along the Pacific Coast of South America, there is typically a deepening of the thermo-nutricline, leading to lower primary productivity and phytoplankton biomass and increased light limitation by deepening of the mixed layer depth (e.g., Cowles et al. 1977, Barber & Chávez 1983, 1986, Barber et al. 1996, Bidigare & Ondrusek 1996). These oceanographic and biological changes cascade through the marine food chain, causing drastic and often long-term changes in the coastal marine system (e.g., Arntz et al. 1985, Glynn 1988). In the Humboldt Current System (HCS) in northern Chile, these kinds of ecological impacts are poorly understood due to the lack of empirical studies. However, information from other upwelling systems allows for testing predictions.

In the area off Antofagasta, Chile (23-24° S) the changes observed during El Niño conditions, include the intrusion of warm oligotrophic waters towards the coast, and during non-El Niño (or La Niña) conditions an increase in the local fertilisation by coastal upwelling (Silva 1988, Strub et al. 1998). Small scale events related to the intensification of mixing, produced by along shore winds greater than 1.6 km h^{-1}, increase nitrate (Marín et al. 1993) as well as nutrient regeneration (Friederich & Codiposti 1981), favouring localised pulses of high primary productivity (PP) and the recurrence of phytoplankton blooms (Avaria & Muñoz 1987, Marín et al. 1993, González et al. 1998). Bottom topography along this coast is characterised by an extremely narrow shelf of 5-11 nm (Morales et al. 1996, Strub et al. 1998). This topography and coastal features are important in understanding the location and persistence of upwelling centers as well as understanding how El Niño alters the oceanographic conditions of this region (Rutllant et al. 1998). The bio-optical characteristics of the water column along the Chilean coast have been briefly described only at 30° S off Coquimbo (Montecino & Pizarro 1995) and in the southern fjords region (Montecino et al. 1998). Changes in bio-optical conditions during El Niño due to changes in productivity, are likely to be more remarkable at lower latitudes (Chávez et al. 1989). Zooplancton grazing is another important factor that influences the Chl-a concentration and González et al. (1998) reported for the Antofagasta area during the same sampling periods in 1997, that these rates were at least twice higher in January than in July.

In the present work, spatial and temporal variability of chlorophyll-a and PP in relation to the depths of the euphotic zone were studied ahead and during the onset of the 1997-1998 ENSO event. The hypothesis that chlorophyll-a concentrations and primary production, due to year-round coastal upwelling, differ significantly in coastal areas in the Antofagasta region was tested using samples from two cruises (January and July 1997). Results showed that there were significant space differences in the integrated biomass during these cruises and with no significant differences between January and July, however significant space and temporal differences in the daily PP were found. These findings suggest that interactions between different oceanographic, optical and ecological processes and the physiological mechanisms of phytoplankton and zooplankton, modulates the potential adverse effects and the response of an upwelling ecosystem to El Niño conditions.

MATERIAL AND METHODS

This study was carried out off Antofagasta, Chile (23-24° S, 70-72° W) during two cruises (B/I Abate Molina) from 11 to 31 January and 1 to 22 July 1997. Primary productivity (PP), concentration of chlorophyll-a (Chl-a), surface and underwater photosynthetic active radiation (PAR) were measured at ten stations within 90 nautical miles (nm) (Fig. 1). In July, three stations were added at 120, 160 and 200 nm from the coast and one station at the upwelling front (station F) in order to follow the coldest upwelled isotherm (18 °C). Several stations (stations 15, 19, 24, F and 200) were sampled during 48 h (Yo-Yo stations) in order to measure the daily variability of PP and Chl-a.

Bio-optical characterisation

An underwater light sensor (QSP 200-D, Biospherical Instruments) was used for determining PAR penetration at each station. During January a underwater quantum meter (1809, Li-Cor) was also used for this purpose. The total diffuse attenuation coefficient for downwelling irradiance (K_d in m^{-1}) was corrected for the shadow of the ship and using on deck irradiance for the atmospheric variability (Smith & Baker 1986).

Chlorophyll-a concentrations

For the determination of chlorophyll-a (Chl-a), discrete water samples were collected at six levels of surface irradiance: 84, 51, 28, 16, 8.5 and 2 % using a CTD-rosette system with 5 l PVC Niskin bottles. Three replicates of 250 ml were filtered through 25 mm glass fibre filters (MFS 75) and extracted using 90 % acetone during 24 h at 4 °C. Concentration of total Chl-a and total phaeophytin were calculated according to the calibration curves of standard chlorophyll (Sigma Co.) obtained in a Turner AU-10 fluorometer.

Primary production (PP)

Primary production was measured according to Steemann-Nielsen (1952) to estimate simulated in situ ^{14}C fixation using two incubators, both thermo-regulated by circulating surface sea water. For simulated in situ measurements the on-deck incubator was equipped with six cylinders with different light levels. Each sampling depth in the euphotic zone (Z_{eu}), was selected according to these light levels expressed in percentages: 84, 51, 28, 16, 8.5 and 2 % of surface irradiance. Water samples collected from six depths of the water column were immediately placed in 100-120 ml borosilicate glass bottles, inoculated with 40 mCi- $NaH^{14}C0_3$) and then incubated on deck. An artificial light based incubator was used for stations sampled during the night and also to obtain the photosynthetic parameters: PB_{max} (maxi-

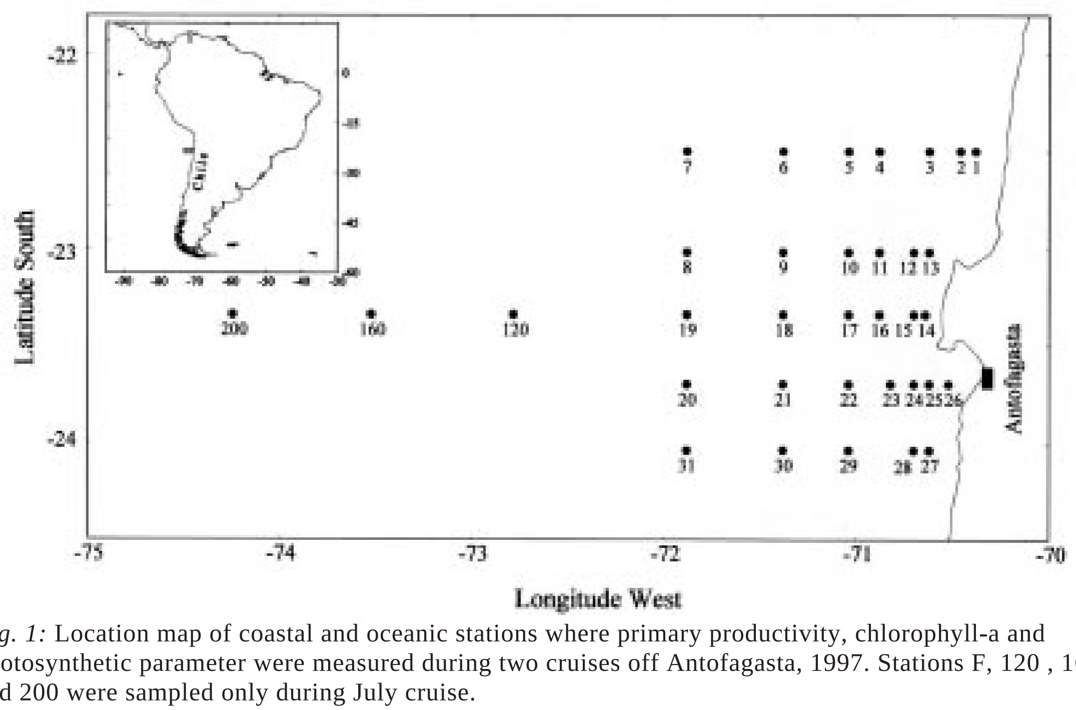

Fig. 1: Location map of coastal and oceanic stations where primary productivity, chlorophyll-a and photosynthetic parameter were measured during two cruises off Antofagasta, 1997. Stations F, 120 , 160 and 200 were sampled only during July cruise.

Mapa en que se localizan las estaciones costeras y oceánicas donde se midió productividad primaria, clorofila-a y los parámetros fotosintéticos durante los dos cruceros realizados frente a las costas de Antofagasta, 1997. Las estaciones F, 120, 160 y 200 fueron muestreadas solamente durante el crucero de Julio.

mal photosynthetic rate normalised to Chl-a concentration), I_k (irradiance at which photosynthesis becomes light saturated) and a (initial slope of the P-E curve, or efficiency of photon capture at limiting irradiance of PAR). This incubator (P-E incubator) was provided with a 500 W halogen bulb (Phillips) providing the full spectrum of visible light. For the P-E experiments, the same 100-120 ml bottles were used with samples that were collected at the depth of the chlorophyll fluorescence maximum. After incubation (4 h around midday in the on-deck incubator and 2.5 h in the P-E incubator), the samples were immediately filtered in dim light through 25 mm fibre glass filters (MFS, GF75) and placed in scintillation vials. To remove the inorganic ^{14}C excess,

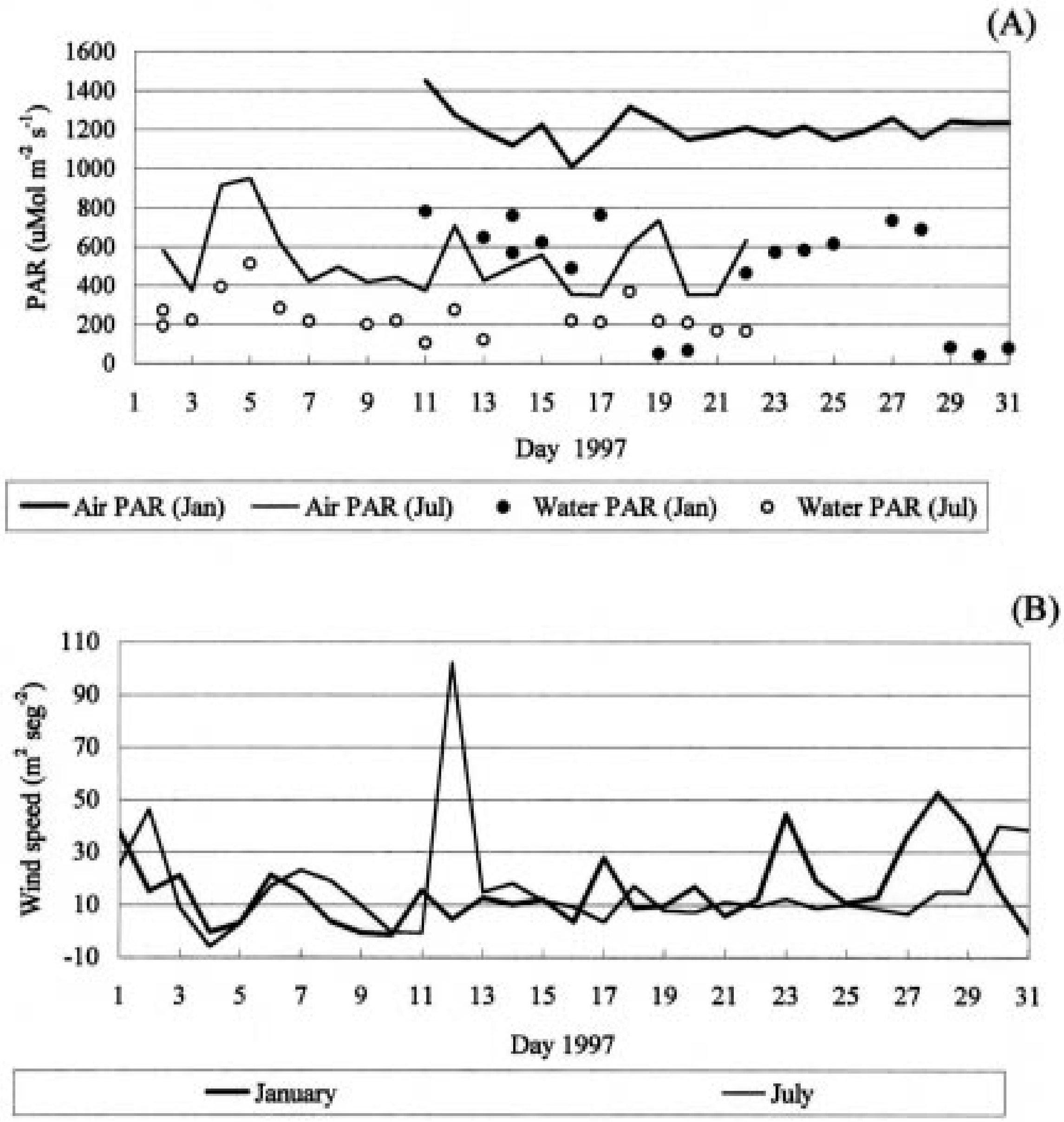

Fig. 2: (A) Photosynthetic active radiation (PAR) (m mol m^{-2} d^{-1}) at the surface and at 10 m depth in the water column measured during the January and July cruises off Antofagasta, 1997; (B) Surface wind stress (m^2 s^{-2}) (upwelling index) calculated for January and July 1997 off Antofagasta.(J. Rutllant personal communication).

(A) Radiación fotosintéticamente activa (PAR) (m mol m^{-2} d^{-1}) medida en la superficie aérea y a 10 m de profundidad durante los cruceros realizados enero y julio frente a las costas de Antofagasta, 1997; (B) tensión superficial del viento (m^2 s^{-2}) (índice de surgencia) calculada para enero y julio de 1997 frente a las costas de Antofagasta (J. Rutllant comunicación personal).

filters were exposed to concentrated hydrochloric acid (HCl) fumes and maintained frozen thereafter. After adding 8 ml of scintillation cocktail (Ecolite+ ICN) the radioactivity was measured in a liquid scintillation counter (Beckmann LS 5000 TD). In order to calculate the fixed carbon, the average value of inorganic carbon present in the water column (mg C m^{-3}) were used (Rodrigo Torres personal communication). Photosynthetic parameters were obtained from the P-E curves, fitted the model of Jassby & Platt (1976) assuming no photoinhibition: $PB = PB_{max} \tanh (a\ I / PB_{max})$. Daily primary production (PP m^{-2} d^{-1}) was calculated by the equation of Baines et al. (1994) using the integrated primary production in the water column per hour, the incubation period (hours) and the daily theoretical light hours for Antofagasta (Arata 1980).

Data analysis

Due to the presence of a narrow shelf and considering that the highest biomass (> 2 mg Chl-a m^{-3}, 50 mg m^{-2}) has been described to be mostly confined within 27 nm along the Chilean coast (Montecino et al. 1998), the stations were grouped as coastal if they were located within 15 nm (stations 1, 3, F, 15, 24 and 27) and considered oceanic if they were > 28 nm from the coast (stations 7, 10, 19, 22, 31, 120, 160 and 200). In order to analyse the spatial and temporal variability of both cruises unbalanced two-way ANOVA of log transformed values, Pearson correlation and non parametric tests were used (Zar 1984).

RESULTS

Light, upwelling favourable winds and bio-optics

Seasonality and overcast conditions determined that the average daily intensity of PAR in July (532 ± 175 m mol m^{-2} s^{-1}) was 56 % less than in January (1,203 ± 85 m mol m^{-2} s^{-1}) (Mann-Whitney U-test, $P < 0.001$). Therefore, PAR at 10 m depth, a depth chosen empirically to compare PAR intensity between both periods, was also different (Mann-Whitney U-test, $P < 0.036$) (Fig. 2A).

Pseudostress of the winds in m^2 s^{-1} during July, reached similar values than in January and were highest at the beginning of the cruise. In January the highest values (Fig. 2B) were found from the 23th throughout the 29th.

Table 1 shows the k_d values that were used to determine Z_{eu}. The parameter k_d changed significantly in space and time (ANOVA, $P < 0.001$, Table 2). In January, k_d fluctuated between 0.062-0.340 m^{-1} at the coastal region and between 0.039-0.073 m^{-1} in the oceanic region. In July, values were considerably different at coastal stations (0.070-0.134 m^{-1}) but remained similar (0.051-0.078 m^{-1}) in the oceanic stations. Consequently, significant differences in Z_{eu} were found between coastal and oceanic stations within each cruise (ANOVA, $P < 0.001$ Table 2). Mean depths of 44 ± 20 and 80 ± 18 m (k_d 0.104-0.058 m^{-1}, respectively) for the coastal and oceanic stations, respectively, were observed for both study periods.

Chlorophyll concentrations

As expected for upwelling areas, the distribution of Chl-a showed its largest variability in the coastal stations (1, 15, 24, 27) with maximum mean values (6.0 mg m^{-3}) in the upper 20 m of the water column in January (Fig. 3). During July the Chl-a maximum mean values (1.0 mg m^{-3}) were found in the same upper 20 m at coastal stations (1, 3, F, 15, 27). Oceanic stations between 28-100 nm (7, 10, 19, 22, 31) showed mean values less than 0.5 mg Chl-a m^{-3} in January and July with maximum values in the upper 40 m of the water column in both cruises. At the oceanic stations >100 nm (120, 160, 200) the highest mean value was found at the surface (0 m) and declined sharply with depth.

The Z_{eu} integrated Chl-a were significantly different (Table 2) when stations were grouped as coastal and oceanic during both cruises (ANOVA, $P < 0.003$) with the higher values near the coast. A mean value of 43.5 ± 42.0 mg Chl-a m^{-2} was observed for the coastal stations and 19.8 ± 6.1 mg Chl-a m^{-2} for the oceanic stations. Integrated values of Chl-a varied between 11.5-175.0 mg m^{-2} in January and between 15.4-46.0 mg m^{-2} in July (Table 1).

It is worth noting that the Z_{eu} integrated Chl-a concentrations found in the coastal and oceanic area in July (36.0 and 23.0 mg Chl-a m^{-2}, respectively) were similar in January (55.0 and 17.0 mg Chl-a m^{-2} respectively) and even higher in the oceanic area. However, the zooplankton grazing rates estimated during the same cruises (González et al. 1998) were higher in January (coast: 180 and ocean: 341 mg C m^{-2} d^{-1}) than July (coast: 79 and ocean: 42 mg C m^{-2} d^{-1}).

Primary production and photosynthetic parameters

Primary production profiles (Fig. 4) showed higher values throughout the upper 20 m in January and

TABLE 1

Measurements of diffuse attenuation coefficients (K_d), euphotic depth (Z_{eu}), integrated total chlorophyll-a (Chl-a) and daily primary production (PP) in the water column at oceanic and coastal stations during Juanary and July of 1997

Mediciones del coeficiente de extinción difuso (K_d), profundidad de la zona eufótica (Z_{eu}), clorofila-a total integrada (Cl-a) y producción primaria diaria (PP) en la columna de agua en las estaciones costeras y oceánicas durante enero y julio de 1997

Station	Date	k_d (m^{-1})	Z_{eu} (m)	Total Chl-a ($mg\ m^{-2}$)	Daily PP ($mg\ C\ m^{-2}\ d^{-1}$)
Oceanic (28-100 nm)					
7 (PI)	12-Jan	-	-	12.83	-
7	23-Jan	0.072	63.96	21.25	1,368
19	14-Jan*	0.039	118.08	-	-
19	17-Jan	0.041	112.32	17.47	693
19	27-Jan	0.054	85.28	22.65	535
19	28-Jan	0.052	88.56	19.63	767
31	10-Jan*	0.065	70.85	-	-
31	16-Jan*	0.073	63.08	15.93	510
10	13-Jan*	0.061	75.49	11.52	478
22 (PE)	15-Jan	-	-	12.14	624
22	25-Jan	0.063	73.10	16.31	955
Oceanic (>100 nm)					
200	16-Jul	0.048	95.94	15.90	265
200	17-Jul	0.050	92.10	-	469
160	17-Jul	-	-	33.35	-
120	18-Jul	0.050	92.10	31.95	841
Oceanic (28-100 nm)					
7 (PI)	01-Jul	0.070	65.79	15.37	170
7	20-Jul	0.052	88.56	-	308
19	03-Jul	0.051	90.30	17.68	1,313
19	05-Jul	0.062	74.28	26.79	-
19	06-Jul	0.078	59.04	18.57	453
19	07-Jul	0.067	68.73	23.04	262
31	04-Jul	0.077	59.81	16.45	-
10	02-Jul	0.076	60.59	23.14	1,174
22 (PE)	03-Jul	-	-	25.09	211
Coastal (< 15 nm)					
1	22-Jan	0.096	47.97	110.36	6063
3	11-Jan*	0.062	74.28	13.29	-
15	14-Jan*	0.068	67.72	32.93	2,064
15	24-Jan	0.074	62.23	18.67	2,234
15	29-Jan	0.272	16.93	175.42	4,771
15	30-Jan	0.340	13.54	-	3,515
15	31-Jan*	0.275	16.75	-	5,053
24	19-Jan**	0.320	14.39	40.81	1,474
24 (PE)	20-Jan**	0.288	15.99	32.53	2424
27	15-Jan	0.068	67.72	11.66	563
27	04-Jul	0.085	54.18	31.08	2,045
1	21-Jul	0.075	61.40	-	311
3 (PE)	01-Jul	0.080	57.56	16.40	620
F	11-Jul	0.128	35.98	45.80	-
F	12-Jul	0.095	48.48	40.13	1,271
F	13-Jul	0.127	36.26	39.83	-
15 (PE)	02-Jul	0.111	41.49	32.93	370
15	09-Jul	0.074	62.23	-	338
15	10-Jul	0.070	65.79	17.50	-
15	19-Jul	0.122	37.75	-	981
15B	22-Jul	0.134	34.37	36.82	1,595

*Underwater Li-Cor sensor (all other measures with a Biospherical sensor)
**Secchi disk
***Attenuation due to water itself after Anderson (1993)
(PE) measures obtained from P-E experiments

July at the coastal stations. Highest mean values were 33.0 mg C m^{-3} h^{-1} in January and 10.0 mg C m^{-3} h^{-1} during July. Oceanic stations between 28-100 nm (7, 10, 19, 22, 31) showed mean values less than 3.0 mg C m^{-3} h^{-1} during both cruises with maximum values in the upper 40 m. At the oceanic stations > 100 nm, the highest mean value (1.8 mg C m^{-3} h^{-1}) was found at the surface (0 m) decreasing to less than 0.1 mg C m^{-3} h^{-1} at 40 m.

Considering the distribution of the daily PP in space, differences were found between coastal (2,099 ± 1,770 mg m^{-2} d^{-1}) and oceanic stations (633 ± 371 mg m^{-2} d^{-1}) as well as between January and July (2,005 ± 1,797 versus 722 ± 553 mg m^{-2} d^{-1}) (ANOVA, $P < 0.001$). Values ranged from 311 to 6,063 mg m^{-2} d^{-1} at the coastal stations and between 170 and 1,368 mg m^{-2} d^{-1} at the oceanic stations (Table 1). Mean daily PP was calculated

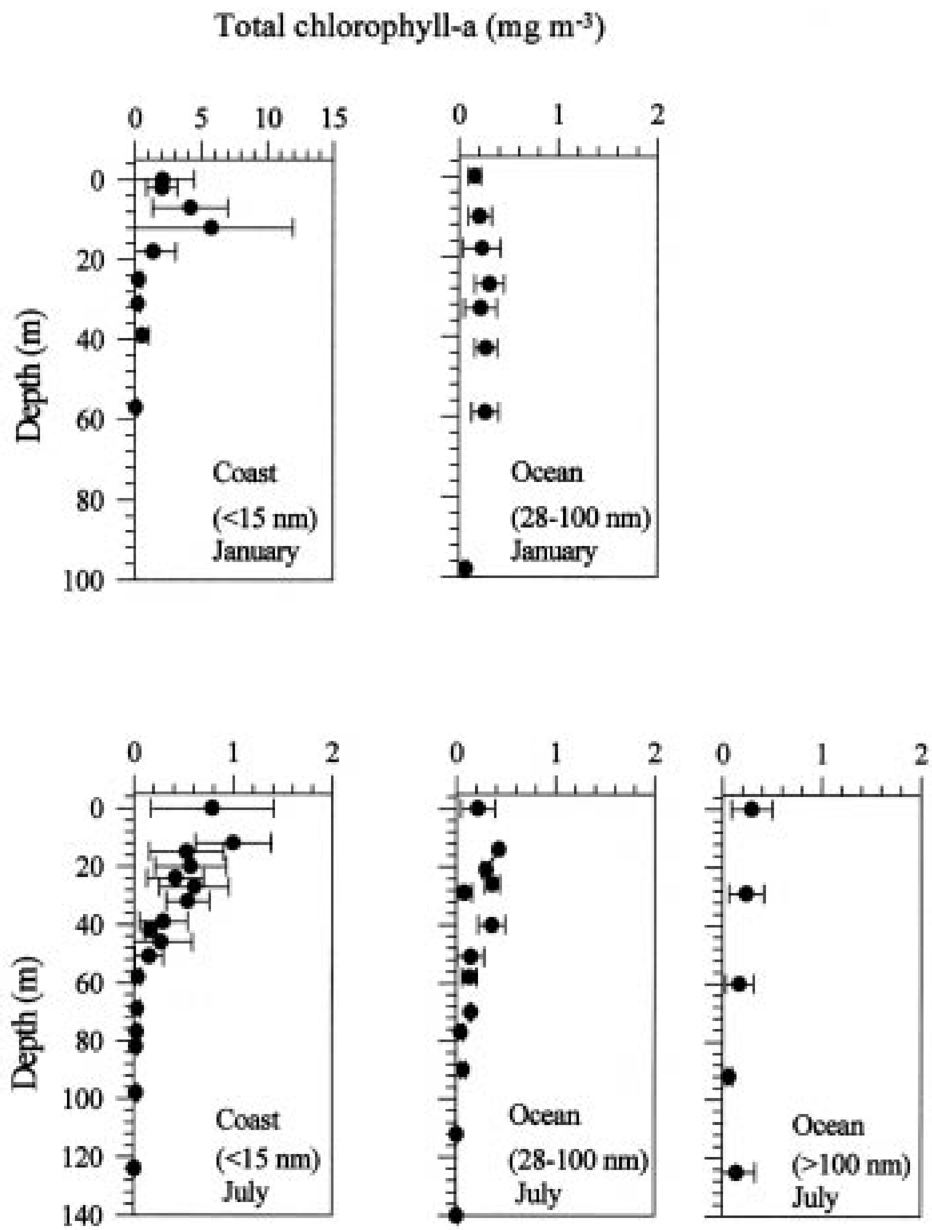

Fig. 3: Depth profiles of mean values of total chlorophyll-a in mg m^{-3} from different stations off Antofagasta: coastal stations (1, 3, F, 15, 27), oceanic stations between 28-100 nm (7, 10, 19, 22, 31) and oceanic stations > 100 nm (120, 160, 200) during January and July 1997.

Perfiles de profundidad de los valores promedios de clorofila-a total en mg m^{-3} medidos en las diferentes estaciones frente a las costas de Antofagasta. Estaciones costeras situadas a < 15mn (1, 3, F, 15, 27), estaciones oceánicas situadas entre los 28-100 mn (7, 10, 19, 22, 31) y estaciones oceánicas situadas a > 100 mn (120, 160, 200) durante enero y julio de 1997.

according to its significance applying a one way a posteriori ANOVA that showed no differences between both cruises for the oceanic stations (Table 2). For both periods, mean daily PP for all the oceanic stations was similar with a mean value of 633 ± 371 mg C m^{-2} d^{-1}. This value is slightly lower than the mean daily PP obtained in July for the whole area. When El Niño was fully developed (July), (IOS -2 Boletín Alerta Climático, 1998) the PP range was between 170 – 2,045 mg C m^{-2} d^{-1} compared with 478-6,063 mg C m^{-2} d^{-1} measured in January (Table 1).

Photosynthetic parameters PB_{max}, I_k, and α (Table 3) were similar between the coastal and oceanic samples (ANOVA, P > 0.359, 0.970, and 0.350, respectively, Table 4) both in January and July (ANOVA, P > 0.418, 0.341, and 0.802, respectively). In January, a increased slightly with depth and PB_{max} did not change (Table 3).

Relationship between the depth of Z_{eu} and chlorophyll-a concentrations

In these waters, the depth of Z_{eu} generally depends mainly on the absorption of PAR by Chl-a. However, the depth variability of Z_{eu} for both cruises and the whole area was significantly re-

TABLE 2

Unbalanced two- and one-way ANOVA analysis comparison of spatial (coast-ocean) and temporal (January-July) measurements of mean extinction coefficient expressed like euphotic depth, daily primary production and integrated total chlorophyll-a. The statistical partial differences for each case are also indicated. The statistical partial differences for each case are also indicated

Comparación espacial (costa-océano) y temporal (enero-julio) (ANOVA desbalanceado de dos vías) de la tasa de fotosíntesis máxima normalizada por la concentración de clorofila-a (PB_{max}), irradiancia de saturación de PB_{max} (I_k) y eficiencia fotosintética (α). También se indican las diferencias estadísticas parciales para cada caso

Source of variation	Degree of freedom (effect)	Mean square (effect)	Mean square square (error)	F-value	P-level
Euphotic depth (Z_{eu})					
Coast-ocean (A)	1	0.977	0.033	29.307	0.001
January-July (B)	1	0.056	0.033	1.669	0.204
A x B interaction	1	0.114	0.033	3.419	0.724
Partial differences					
Coast: January-July	1	0.169	0.057	2.968	0.101
Ocean: January-July	1	0.005	0.008	0.603	0.447
January: coast-ocean	1	0.818	0.061	13.337	0.002
July: coast-ocean	1	0.229	0.009	24.014	0.001
Daily primary production (PP)					
Coast-ocean (A)	1	1.409	0.084	16.796	0.001*
January-July (B)	1	1.208	0.084	14.394	0.001*
A x B interaction	1	0.226	0.084	2.700	0.115
Partial differences					
Coast: January-July	1	1.211	0.104	11.700	0.004*
Ocean: January-July	1	0.199	0.065	3.035	0.101
January: coast-ocean	1	1.350	0.066	20.475	0.001*
July: coast-ocean	1	0.259	0.101	2.572	0.128
Integrated total chlorophyll-a (Chl-a)					
Coast-ocean (A)	1	0.531	0.051	10.249	0.003*
January-July (B)	1	0.096	0.051	0.184	0.670
A x B interaction	1	0.078	0.051	1.515	0.227
Parcial differences					
Coast: January-July	1	0.015	0.102	0.148	0.706
Ocean: January-July	1	0.080	0.013	6.101	0.024*
January: coast-ocean	1	0.487	0.088	5.553	0.032*
July: coast-ocean	1	0.105	0.020	5.232	0.035*

*Statistically significant

TABLE 3

Photosynthetic parameters, PB_{max} (maximun photosynthetic rate normalized by total Chl-a), and α (phtosynthetic efficiency), measured during January and July of 1997

Parámetros fotosintéticos PB_{max} (tasa de fotosíntesis máxima normalizada por la concentración de clorofila-a) y α (eficiencia fotosintética), medidos durante enero y julio de 1997

Date 1997	Station	Sample depth (m)	PB_{max} [mg C (total mg Chl a)$^{-1}$ h^{-1}]	α [mg C (total mg Chl-a)$^{-1}$ h^{-1} (mmol m^{-2} s^{-1})$^{-1}$]
12-Jan	7	40	3.8 ± 0.3	0.128 ± 0.053
15-Jan	22	0	9.8 ± 0.5	0.030 ± 0.008
20-Jan	22	0	5.0 ± 0.5	0.001 ± 0.012
01-Jul	3	24	9.8 ± 0.5	0.034 ± 0.003
01-Jul	7	22	2.6 ± 0.0	0.018 ± 0.002
02-Jul	15	0	2.2 ± 0.3	0.024 ± 0.004
03-Jul	22	0	4.6 ± 1.6	0.010 ± 0.002

lated with both, the surface Chl-a and the integrated Chl-a (between 100-1 % of surface irradiance). Integrated Chl-a explained 42 % of $Z_{eu.}$ variability ($r = 0.65$, $P < 0.001$) (Fig. 5A). Surface Chl-a showed a highest correlation coefficient with Z_{eu} ($r = 0.85$; $P < 0.001$) than the integrated Chl-a for the whole area (Fig. 5B).

DISCUSSION

The results of this study support the hypothesis that the larger differences occur in coastal-oceanic gradients in biological and bio-optical properties even considering the physical anomalies associated with the development of El Niño. Taking into account the whole of the area, the total integrated chlorophyll-a (Chl-a) and photosynthetic parameters during January 1997 were similar to July when the El Niño event of 1997-1998 was in the middle of its development (IOS –2). Nevertheless, significant differences were found in the integrated daily PP between both sampling periods.

Most of the January 1997 period was characterised by weak upwelling of Subantartic Surface Waters (SSAW, characterised by the salinity minimum) in contrast to what occurs during intense upwelling (Chávez et al 1998) with an entrainment of Equatorial Subsurface Water (ESSW, characterised by high concentrations of inorganic nutrients). The physical anomalies of strong westerly winds, deeper thermocline and increased sea surface temperature appeared during March 1997 in this study area (Rutllant et al. 1998). Between cruises (January and July 1997), significant changes occurred in the water column, including higher temperatures in the euphotic zone (Z_{eu}), deepening of thermocline below Z_{eu} and increase of oxygen concentration as a result of the deeper thermocline (Morales et al 1999). Moreover, the deepening of the thermocline below the depth of the euphotic zone produces light limitation and a limitation of nutrients due to the intrusion of Subtropical Water (González et al. 1998).

Chlorophyll-a and primary production

The effects of El Niño on the phytoplankton population off Antofagasta in 1997 can be described as a decrease in daily PP at the coastal stations during July with no significant changes in biomass (Chl-a) between January and July cruises. At the coast, PP was 4.0 and 1.4 times higher than offshore in January and July, respectively, and Chl-a was similarly 3.1 and 1.8 times higher. Higher mean values of zooplankton grazing rate during January (González et al. 1998) could be one of the important controlling factors responsible for the similarity of total integrated Chl-a between sampling periods. Surface concentrations of Chl-a during January (Fig. 5B) were within the range of those reported in the spring and also with non El Niño values reported by Morales et al. (1996) for pelagic and inshore waters (0.5-13.8 mg Chl-a m^{-3}) of a wide region off northern Chile, between Arica and Antofagasta (18-24° S), during November-December 1993.

Chlorophyll-a and bio-optical conditions

The change in the physical structure between January and July increased four fold the mixing layer (González et al. 1998) i.e., deepening of the thermocline from 50 to 200 m. As a result of increased mixing, phytoplankton that remained within the euphotic zone during January, reached 1.5 and 3.1 times below Z_{eu} in the oceanic and coastal area respectively during July, taking into account that the mean depth of Z_{eu} oscillated between 40-49 m at coastal stations and 83-77 m at the oceanic stations in January and July, respectively. The amount of irradiance (PAR) in the 10 m water column was significantly larger during January compared with July. Therefore on the coast during January more PAR was available notwithstanding the higher concentration of chlorophyll found in this area. A decrease in the depth of Z_{eu} < 68 m (Fig. 5A) occurred when Chl-a reached more than 30 mg m^{-2} in January. In July, 40-46 mg Chl-a m^{-2} were found with a warm

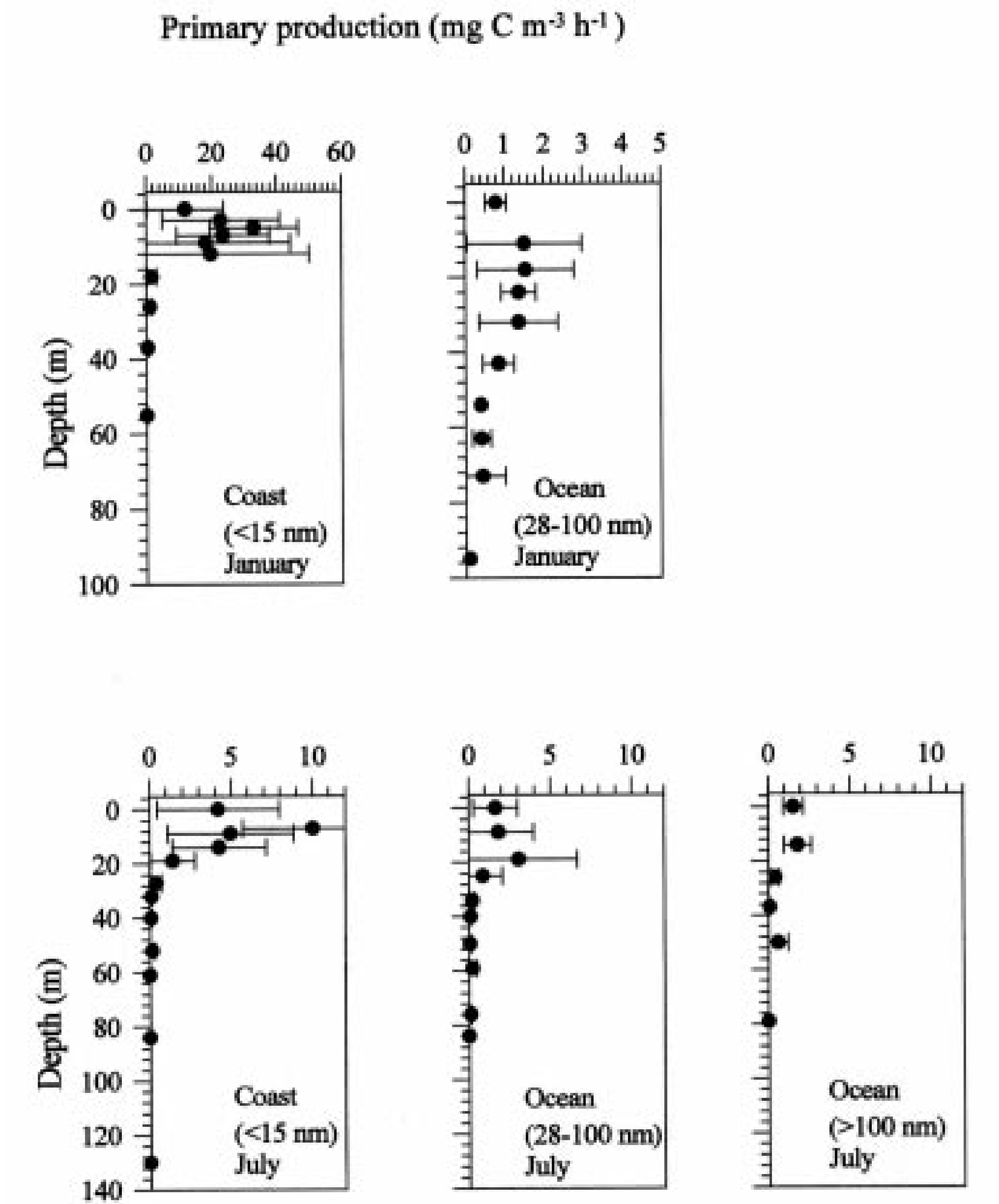

Fig. 4: Depth profiles of mean values of 1997 of total primary production in mg C m^{-3} h^{-1} from different stations off Antofagasta: coastal stations located to < 15 nm (1, 3, F, 15, 27), oceanic stations located between 28-100 nm (7, 10, 19, 22, 31) and oceanic stations >100 nm (120, 160, 200) during January and July 1997.

Perfiles de profundidad de los valores promedios de la producción primaria total en mg C m^{-3} h^{-1} medidos en las diferentes estaciones frente a las costas de Antofagasta. Estaciones costeras situadas a < 15 mn (1, 3, F, 15, 27), estaciones oceánicas situadas entre los 28-100 mn (7, 10, 19, 22, 31) y estaciones oceánicas a > 100 mn (120, 160, 200) durante enero y julio de 1997.

TABLE 4

Unbalanced two way ANOVA analysis comparison of spatial (coast-ocean) and time (January-July) the measurements of maximun photosynthetic rate normalized by total Chl-a (PB_{max}), saturing irradiance of PB_{max} (I_k) and phtosynthetic efficiency (α)

Comparación espacial (costa-océano) y temporal (enero-julio) (ANOVA desbalanceado de dos vías) de la tasa de fotosíntesis máxima normalizada por la concentración de clorofila-a (PB_{max}), irradiancia de saturación de PB_{max} (I_k) y eficiencia fotosintética (α)

Source of variation	Degree of freedom	Mean square (effect)	Mean square (error)	F-value	P-level
Maximun photosynthetic rate					
Normalized by total Chl-a (PBmax)	1	0.094	0.081	1.166	0.359
Coast-ocean (A)	1	0.071	0.081	0.877	0.418
January-July (B)	1	0.018	0.081	0.226	0.667
Saturating irradiance of PBmax (Ik)					
Coast-ocean (A)	1	0.003	0.184	0.001	0.970
January-July (B)	1	0.234	0.184	1.274	0.341
A x B interaction	1	0.054	0.184	0.295	0.625
Photosynthetic efficiency (α)					
Coast-ocean (A)	1	0.000	0.007	0.228	0.744
January-July (B)	1	0.008	0.007	1.278	0.341
A x B interaction	1	0.000	0.007	0.006	0.942

isotherm of 18 °C at 50 m depth while diminishing Z_{eu} between 36-49 m depth. Coastal-oceanic gradients were also found related to water transparency during both cruises. Correlation analysis indicated that the total integrated Chl-a and total surface Chl-a explains a 41-68 % of the variability of Z_{eu} ($P < 0.001$) of coastal and oceanic stations off Antofagasta, respectively.

The extreme low k_d values, found in Antofagasta during El Niño conditions (Table 1), have been reported for other areas with the highest water transparency (Berman et al. 1984, Morel 1988, Ignatiades 1998). The lowest k_d values in the oceanic region during July 1997, are only slightly higher than those of 0.031 to 0.046 m^{-1} reported in the Eastern Mediterranean for the Israeli Coast (Berman et al. 1984). Irradiance transmittance is not constant with depth, and in the Sargasso Sea, Smith et al. (1989) found that the total diffuse attenuation coefficient is relatively large near the surface but at great depths it approaches the value for the attenuation of the wavelength of maximum penetration (450 nm = 0.017 m^{-1}). This suggests that measuring Z_{eu} spectrally it is possible to find a potential limit for Z_{eu} greater than those measured with total PAR sensors. Similarly, Ignatiades (1998) reports that blue light penetrates to 177 m in the Aegean Sea, with an average in k_d of 0.026 m^{-1}. The same author refers to spectral measurements (between 440 and 480 nm) of k_d in autumn, below 0.020 m^{-1}, and Smith & Baker (1981) showed k_d values < 0.021 m^{-1} for clear waters and in the wavelengths of 410 to 480 nm ranging from 0.0168 y 0.0196 m^{-1}. Lowest PAR k_d values measured off Antofagasta were 0.039 to 0.049 m^{-1}.

Blue light enhances cellular Chl-a concentrations (Kirk 1994) and this, together with the dominance of small dinoflagellates, such as *Gymnodinium* sp. (Iriarte et al 2000), whose nitrogen requirements are less than those of microphytoplankton (Chisholm 1992), could explain why integrated Chl-a between January and July were similar. Nevertheless, the results indicate strongly that the zooplancton grazing rate in January, could temporally determine this situation for over the previous mechanism.

Primary production and upwelling process

The frequency of upwelling off the Antofagasta coast have been reported to be higher in spring and summer during non-El Niño conditions (Rodríguez et al. 1991). Therefore, higher integrated Chl-a and daily PP mean values in coastal stations in January could be predicted. In effect, they exceeded those integrated Chl-a and daily PP mean values found at the oceanic stations in summer and were higher to those found at all stations in the winter. However, the larger variability in integrated Chl-a and daily PP at

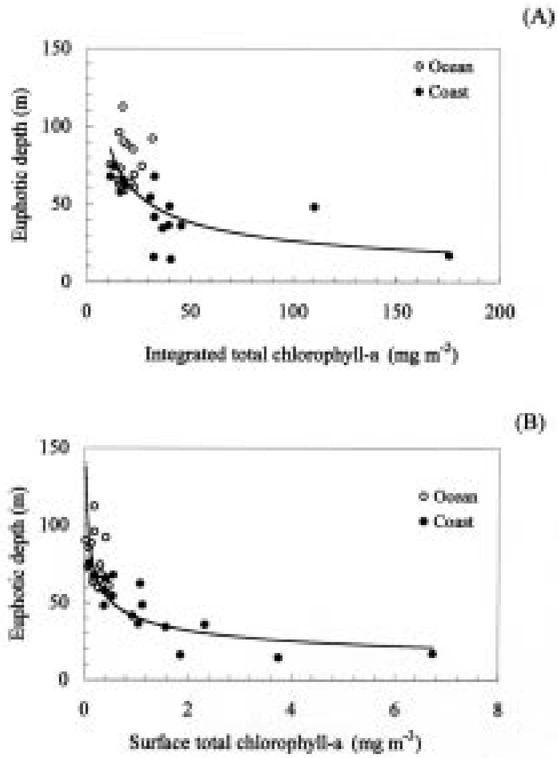

Fig. 5: (A) Power correlation between the euphotic depth and integrated total chlorophyll-a ($y = 324*Z_{eu}^{-0.546}$, $r^2 = 0.42$, $P < 0.001$) from the two cruises of coastal and oceanic stations; (B) depth of the euphotic layer versus surface chlorophyll-a concentration ($y = 41*Z_{eu}^{-3424}$, $r^2 = 0.68$, $P < 0.001$) of coastal and oceanic stations.

(A) Correlación potencial entre la profundidad de la zona eufótica y la clorofila-a total integrada ($y = 324*Z_{eu}^{-0.546}$, $r^2 = 0,42$, $P < 0,001$) registrada durante los dos cruceros en las estaciones costeras y oceánicas; (B) profundidad de la zona eufótica versus la concentración de clorofila-a superficial ($y = 41*Z_{eu}^{-3424}$, $r^2 = 0,68$, $P < 0,001$) en las estaciones costeras y oceánicas.

coastal stations during January 1997 reflected a low frequency of the favourable upwelling conditions (Fig. 2B). Overall, the levels of daily PP were comparable to the values reported from the Peruvian coast (2-18° S) for non El Niño conditions by Calienes et al. (1985) (Table 5). Antofagasta maximum values are higher than maximum values reported for Coquimbo (Montecino et al. 1996) for the coastal and oceanic area. Integrated Chl-a had a lower variability in both the oceanic and coastal region in Coquimbo compared to Antofagasta. In the area of Antofagasta and closer to the coast, 25.0-35.0 mg Chl-a m^{-2} were reported previously for January in the bays of Antofagasta and Mejillones (Rodríguez et al. 1996). These values are in the same range as our results in stations 24-27, (12.0 - 41.0 mg Chl-a m^{-2}). In July, differences are larger 100.0 mg Chl-a m^{-2} reported by Rodríguez et al. (1996) versus 31.1 mg Chl-a m^{-2} registered in this study in station 27. The highest surface values were 6.7 mg Chl-a m^{-3} in January but only 2.3 mg Chl-a m^{-3} in July. During January, a *Mesodinium* bloom had also developed at 5 nm in the upper 2 m and reached a concentration of 108.0 mg Chl-a m^{-3}. These occasional blooms have been observed previously in this region in summer (Avaria & Muñoz 1987) and also in Bahía Mejillones (Marín et al. 1993).

Primary productivity and photosynthetic parameters

The light harvesting system efficiency of different algae classes varies inversely with cell size (Malone & Neale 1981, Pierson et al. 1992). In the upwelling area of Antofagasta, pico and nano-phytoplankton were predominant in January as

TABLE 5

Comparison of minimum, maximum and mean values of Chl-a and PP between Coquimbo (Chile) and Perú, during a period of no El Niño

Comparación entre valores mínimos, máximos y medios de Cl-a y PP entre Coquimbo (Chile) y Perú, durante un período de no El Niño

Variable	Área	Perú (Calienes et al. 1985)	Coquimbo (Montecino et al. 1996)	Antofagasta (this study)
Daily PP (mg C m^{-2} d^{-1})	Coast	2,000-5,000 summer 100-1,000 winter	2,955	6,063
	Ocean	100-1000 Summer and winter	1,323	1,368
Integrated Chl-a	Coast		38 ± 24 (range 8-92)	38 ± 35 (range 9-175)
(mg m^{-2})	Ocean		19 ± 5 (range 12-27)	16 ± 7 (range 3-28)

well as in July (Iriarte et al. 2000), similar to results reported off Central Chile (Montecino & Quiroz 2000). These authors reported for Coquimbo a significant relationship between the photosynthetic parameter α and the proportion of small cells (< 8 mm), suggesting that a cell size dependence of a could be occurring in Antofagasta. Nevertheless, the α values in this study (0.001-0.128 mg C mg Chl-a^{-1} h^{-1} m mol m^{2} s) were lower (Mann-Whitney U-test, $P < 0.007$) than those reported off Coquimbo (Montecino et al. 1996) as was the case for the photosynthetic parameter PB_{max} (Mann-Whitney U-test, $P < 0.04$). PB_{max} in Antofagasta did not change between both cruises and these values fluctuated between 2.3-9.8 mg C mg Chl-a^{-1} h^{-1}. The photosynthetic parameters, PB_{max} and α did not explain the measured differences in daily PP between January and July.

Temperature affects the PB_{max} in micro-phytoplankton and not in smaller size phytoplankton cells (Reynolds 1997). This was also reported by the inverse relationship between PB_{max} and phytoplankton cell size <10mm independent of the temperature (Taguchi 1976). Consistent with this, temperature through its effects on enzymatic systems did not cause an increase of carbon fixation as could have been expected. This is supported by the results of phytoplankton cell size structure reported for Antofagasta (Iriarte et al. 2000). Moreover, PB_{max} of the pico and nano-phytoplankton were higher than the micro-phytoplankton fraction in the upwelling area off Coquimbo (Quiroz 1997).

For this area it has been suggested that when resources, such as nutrients or light are limiting (Montecino & Quiroz 2000), the phytoplanktonic size structure should be displaced toward the smaller cells (< 8 mm) which are more efficient in using resources than micro-phytoplankton (Chisholm 1992, Kirk 1994). The dominance in the present study of smaller phytoplankton size fractions and their (65 %) larger contribution to both PP and total Chl-a, holds that during July biological and physiological shifts occurred in phytoplankton assemblages in order to counteract the change in prevailing physical and chemical conditions between January and July.

In summary, variations in primary production before and during the onset of El Niño can be attributed to weaker upwelling which was especially low during January, in addition to the dominance of smaller phytoplankton size in the whole area in both periods. The weaker upwelling and higher mean values of zooplankton grazing rate during January contributed to the non significant differences in the abundance of chlorophyll-a in time. The effect of upwelling favourable winds during July was masked due to seasonal light limitation and the increase in depth of the mixing layer. Although the El Niño event could negatively affect the primary production during July, the results suggest that this effect was hidden prevailing the space and seasonal variability.

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