

Phytoplankton size structure during and after the 1997/98 El Niño in a coastal upwelling area of the northern Humboldt Current System

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ABSTRACT: Primary production (PP) and phytoplankton biomass changes in an intense upwelling area off northern Chile (Antofagasta, 23°S) associated with the strong El Niño of 1997/98 are described over a 5 yr sampling period. The oceanographic anomalies observed during July 1997 and January 1998, associated with the intrusion of warmer oligotrophic waters to the coast, reduced the upwelling of cold, nutrient-rich waters in the upper 100 m. An oligotrophic regime seems to have resulted in a higher dominance (45 to 70 %) of pico- and nanoplankton in inshore areas during summer/winter 1997 and summer 1998, with values of biomass and PP of 5 mg chl *a* m⁻³ and 2.0 g C m⁻² d⁻¹, respectively. After that period, when the frequent upwelling of cold, nutrient rich water was re-established along the coast off Antofagasta, biomass and PP estimates increased up to 80 mg chl *a* m⁻³ (mean = 25.5 mg chl *a* m⁻³) and 12 g C m⁻² d⁻¹ (mean = 6.5 g C m⁻² d⁻¹), respectively. During that period, the microphytoplankton size fraction accounted for >50 % of the biomass and productivity. Sedimentation trap studies showed that the sedimentation rate of diatoms was very low during El Niño conditions (January 1997 and 1998) with values between 0.02 and 0.2 mg C m⁻² d⁻¹, increasing by 2 orders of magnitude during winter and spring 2001 (mean = 28 mg C m⁻² d⁻¹). The data showed that during 1997/98 El Niño event, pico- and nanophytoplankton size classes made a significant contribution to the production and may thus represent an alternative energy-flow pathway within this upwelling area.

KEY WORDS: Primary production · El Niño 1997/98 · Size distribution

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INTRODUCTION

The frequent upwelling of cold, nutrient-rich water along the northern coast of Chile (off Antofagasta) during most of the year (Rodríguez et al. 1991, Marín & Olivares 1999, Thomas et al. 2001, Ulloa et al. 2001) produces a highly productive phytoplankton assemblage, dominated by chain-forming diatoms, which supports a large commercial fishery. During the 1997/98 El Niño event in July 1997, warm equatorial waters moved to the coast, and reduced the upwelling of nutrient-rich waters in the upper 100 m to a narrow

coastal band (<15 km) (González et al. 1998). During this event, the pico- and nanophytoplankton size classes dominated both oceanic and coastal stations off Antofagasta and accounted for 67 % of the primary production (PP) and chl *a* biomass (Iriarte et al. 2000).

Phytoplankton of different size fractions produce different types of organic nutrients which could support different pathways of materials in the food web (Legendre & Rassoulzadegan 1995). In marine ecosystems, the smaller phytoplankton (less than 2.0 µm) fuel the microbial food web within the photic layer, while larger microphytoplankton (greater than 20 µm) are an

important component of the 'classical' food chain, furnishing with energy large pelagic and benthic organisms. Most of the phytoplankton in this area are larger than 20 μm and their detritus is abundant in the sediment (up to 800×10^6 diatom valves g^{-1} , Ortlieb et al. 2000). Ortlieb et al. (2000) pointed out that high microphytoplankton abundances in the sediment record correlate positively with intense/more frequent upwelling events (higher PP) and negatively with El Niño conditions (lower PP). On the other hand, small-sized phytoplankton ($<20 \mu\text{m}$) predominate in oligotrophic and high nutrient, low chlorophyll (HNLC) regions (Chavez 1989), as well as in some coastal waters (Hall & Vincent 1990). In these areas small phytoplankton should also contribute to the flux of particles leaving the euphotic zone via macrozooplankton fecal pellets in coastal environments (Urban et al. 1993), as well as fuelling the microbial loop via protozoan grazing (Rassoulzadegan & Sheldon 1986).

Time-series observations are useful for documenting the consequences of climatic-driven oceanographic

events (e.g. El Niño phenomena) and also for establishing baseline conditions for long-term studies in coastal ecosystems.

The aim of this study was to assess the changes in size-fractionated PP, biomass, and the sedimentation rate of phytoplankton in a coastal area, the Bay of Mejillones (Antofagasta, Chile, 23°S), resulting from the El Niño of 1997/98 and the period following this event. Data were obtained during 8 visits to the area over a 5 yr period that included the El Niño of 1997/98 (Fig. 1). This allowed us to compare the temporal distribution of 3 phytoplankton size classes, to assess the consequences of the El Niño on the size structure of phytoplankton assemblages as well as the contribution of the dominant group to the downward carbon flux.

MATERIALS AND METHODS

Chl *a* and PP of 3 size fractions, pico-, nano-, and micro-phytoplankton, were measured in the coastal

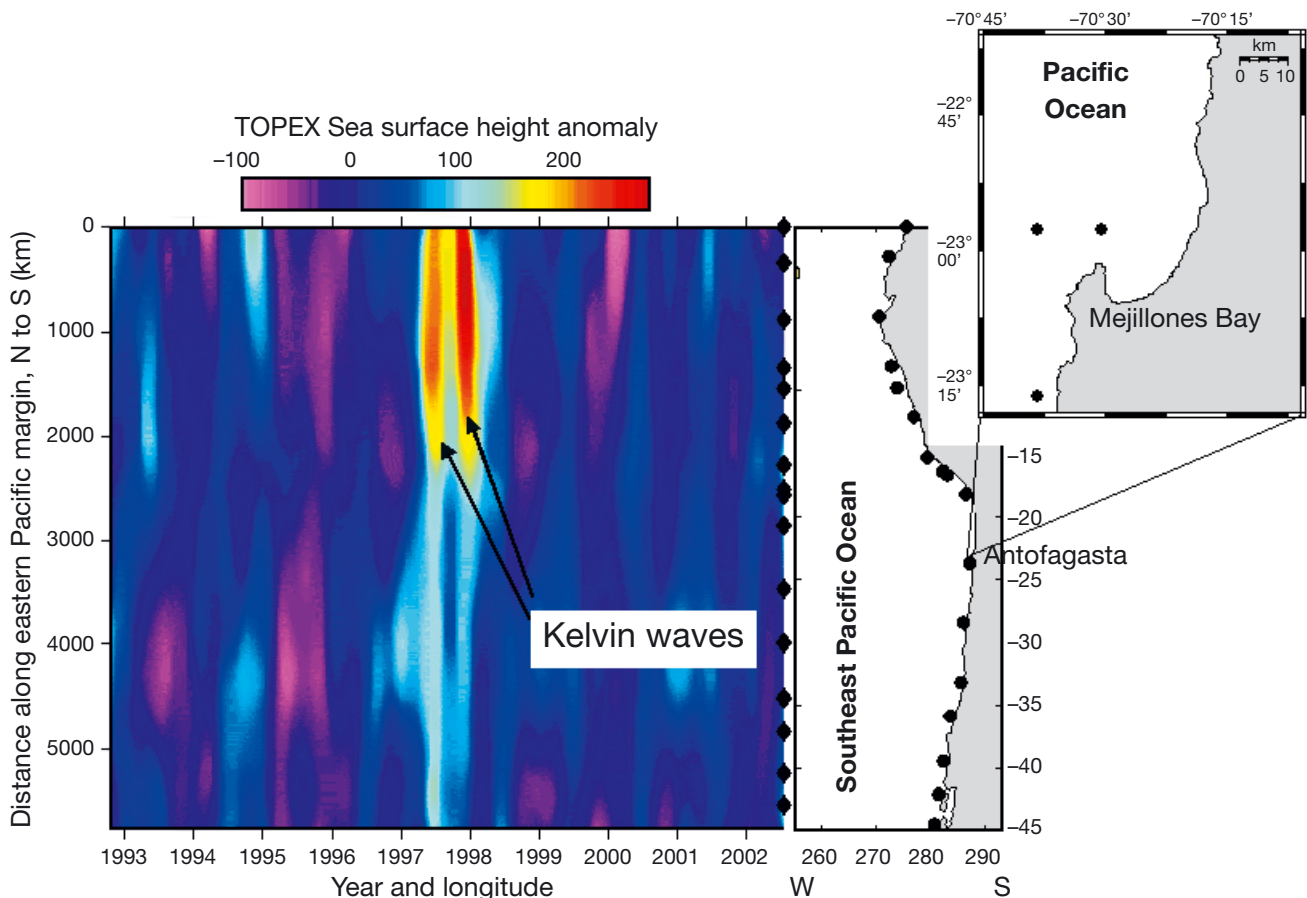


Fig. 1. Time series of sea surface height anomaly (cm) image of the eastern Pacific region. Shown is the site of sampling, Antofagasta (in the upper 200 m depth of continental shelf) and the signal of equatorial Kelvin waves (KW) travelling along the northern coast off Chile during the 1997/98 El Niño Event. Three closed symbols on the insert map represent the sampling stations for the present study. Diamonds and closed symbols along the coastline represent locations from where TOPEX data were extracted

waters off Antofagasta, Bahía de Mejillones (23° S) during 8 research cruises: summer 1997 (1 to 31 January), winter 1997 (1 to 24 July, El Niño event), summer 1998 (15 to 20 January), spring 2000 (19 to 23 October), summer 2001 (2 to 11 February), winter 2001 (1 to 11 August), spring 2001 (20 to 30 October) and summer 2002 (20 to 25 January). The first 3 cruises occurred during El Niño and the remainder followed the event.

Water samples were collected at 3 coastal stations (Fig. 1) using 5-L PVC Go-Flo water-sampling bottles, at 3 depths within the euphotic zone: surface, subsurface chl *a* maximum, and the 2% light penetration depth. The 3 stations roughly correspond to those defined as coastal stations in Iriarte et al. (2000), where significant differences between stations in integrated total chl *a* were not detected (ANOVA test: $F = 0.148$, $p = 0.706$; Pizarro et al. 2002). The sampling depths were selected to characterize the phytoplankton variability in the upper 25 m depth, defined as the depth of the euphotic zone (Marin & Olivares 1999).

Water samples for primary production determinations were incubated in 100 ml borosilicate glass bottles (2 clear replicate bottles and 1 dark bottle at each depth) and placed in a natural-light incubator for 4 h (mainly between 10:00 and 14:00 h). Temperature was regulated by running surface seawater over the incubation bottles. For the subsurface chl *a* maximum and 2% light penetration depth incubation, light intensity was attenuated using a screen to approximate light at the depth where the water was collected. The extent of light (photosynthetically active radiation; PAR) penetration was determined using submersible sensors (QSP 200-D, Biospherical Instruments). Sodium bicarbonate (40 $\mu\text{Ci NaH}^{14}\text{CO}_3$) was added to each bottle. Following incubation, samples were manipulated under subdued light conditions during pre- and post-incubation periods. The contents were filtered according to the fractionation procedures mentioned below. Filters (0.7 and 2.0 μm) were placed in 20 ml borosilicate scintillation vials and kept at -15°C until readings were taken (15 d later). To remove excess inorganic carbon, filters were treated with HCl fumes for 4 h. A scintillation cocktail (10 ml Ecolite) was added to vials and radioactivity was determined in a scintillation counter (Beckmann). Depth-integrated values of PP ($\text{mg C m}^{-2} \text{h}^{-1}$) were calculated using trapezoidal integration over the euphotic zone (3 depths: surface, subsurface chl *a* maximum, and the 2% of surface irradiance depth). Integrated production rates per hour were multiplied by daily light hours for Antofagasta (Arata 1980). Phytoplankton size fractionation was performed post-incubation in 3 sequential steps: (1) for the nanoplankton fraction (2.0 to 23 μm), seawater (100 ml) was pre-filtered using 23 μm Nitex mesh and collected on a

2.0 μm Nuclepore; (2) for the picoplankton fraction (0.7 to 2.0 μm), seawater (100 ml) was pre-filtered using a 2.0 μm Nuclepore and collected on a 0.7 μm MFS (microfiltration system) glass-fiber filter; (3) for the whole phytoplankton community, 100 ml of seawater was filtered through a 0.7 μm MFS glass-fiber filter. The micro-phytoplankton fraction was obtained by subtracting the production estimated in Steps 1 and 2 from the production estimated in Step 3.

Size-fractionated chl *a* was measured at the same stations and depths where PP experiments were carried out. Seawater samples (150 ml) were filtered and analysed using a digital Turner AU-10 fluorometer as recommended by Parsons et al. (1984). The size-fractionated procedure was the same as for PP (Nuclepore and MFS glass fiber filters). Depth-integrated values of chlorophyll (mg chl m^{-2}) were calculated using trapezoidal integration over the euphotic zone (3 depths: surface, subsurface chl *a* maximum, and the 2% of surface irradiance depth). Measurements of PP ($\text{mg C m}^{-3} \text{h}^{-1}$) and chl *a* (mg m^{-3}) were averaged within the euphotic zone for each station.

Samples for phytoplankton cell-counts consisted of 300 ml subsamples, which were stored in clear plastic bottles and fixed and preserved in 1% Lugol iodine solution. From each sample, a 50 ml subsample was placed and left to settle for 30 h in a sedimentation chamber, the bottom of which was observed using an inverted microscope (Hasle 1978). The phytoplankton carbon biomass was estimated from the following nonlinear equations: for athecate dinoflagellates $C = 0.109(\text{Biovolume})^{0.991}$ (Montagnes et al. 1994); for flagellates $C = 0.433(\text{Biovolume})^{0.863}$ (Verity et al. 1992). For diatoms, nonlinear equations for vacuolate and nonvacuolate algae were used, following Smayda's (1978) recommendations.

Vertical flux and phytoplankton carbon. The vertical flux of particulate matter was measured using paired cylindrical sediment traps (modified from Gundersen 1991) with a 122 cm^2 catchment area and a height diameter ratio of 8.3. Traps were deployed in a drifting mode at 50 and 100 m depths for periods ranging between 1 and 2 d. Before deployment, 1 ml of saturated HgCl_2 solution was added per 250 ml of sample solution (GF/F-filtered seawater) to retard bacterial activity in the trap material (Lee et al. 1992).

Subsamples from the traps were taken for estimations of dominant microplankton taxa using standard microscopic methods (Utermöhl 1958). Phytoplankton carbon, based on cell volume, were estimated after counting and sizing the different species according to Edler (1979). A statistical test of non-parametric correlation (Zar 1984) was performed in order to detect tendencies and relationships among variables (biomass, PP).

RESULTS AND DISCUSSION

The 1997/98 El Niño event was one of the strongest recorded over the past century (McPhaden 1999), causing climatic disturbances around the world. Chavez et al. (2002), while discussing the temporal evolution of the El Niño of 1997/98 around the coasts of Ecuador, Peru and northern Chile, suggested that the sea level began to rise in April 1997 and lasted until May 1998, with a maximum in late 1997. Large fluctuations in the depth of the thermocline in Antofagasta (Sobarzo & Figueroa 2001) between July 1997 and January 1998 were associated with the passage of remotely wind-forced equatorial Kelvin waves (Fig. 1). During the El Niño of 1997/98 in northern Chile, oceanographic conditions were characterized by a warm anomaly (1 to 6°C in the upper 100 m), high stratification, low nitrate concentration in the upper 10 m depth (<5 μM), low orthophosphate (<0.5 μM) and silicate (<2 μM), and deepening of the thermocline (up to 200 m depth) and oxycline (below 50 m depth) near the coast (González et al. 2000, Iriarte et al. 2000). Nutrients concentrations from Mejillones Bay, measured during 'normal' oceanographic conditions, showed annual average concentration of PO_4^{3-} and NO_3^- in the euphotic zone of 2.03 and 10 μM (range: 1 – 16 μM), respectively (Rodríguez et al. 1991).

During the El Niño winter 1997 and summer 1998, PP of ca. 1.8 $\text{g C m}^{-2} \text{d}^{-1}$ was only 1/3 of that in summer and winter 2001. After the El Niño event, PP values ranged from 1.1 to 8.1 $\text{g C m}^{-2} \text{d}^{-1}$ (Fig. 2), and were comparable to those recorded in upwelling systems such as Perú (1 to 5 $\text{g C m}^{-2} \text{d}^{-1}$; Calienes et al. 1985) and the Benguela (0.5 to 4.0 $\text{g C m}^{-2} \text{d}^{-1}$; Brown & Field 1986). Primary productivity during spring 2000 increased to a mean of ca. 8.0 $\text{g C m}^{-2} \text{d}^{-1}$, an increase of

400 % over the productivity during the El Niño of winter 1997 (Fig. 2). The time series observations taken during the El Niño of 1992 from warm events along the equatorial Pacific (Barber et al. 1996) and in Central California waters (Chavez et al. 2002) indicated a 50 % decrease in PP and a 70 % reduction in new production, respectively. The satellite-measured chl *a* and temperature figures in Thomas et al. (2001) indicate that the temperature patterns normally associated with upwelling were absent, and chl *a* concentrations were lower during the period from winter 1997 to summer 1998. With the exception of spring 2000, the temporal variation in chl *a* concentration showed a similar pattern compared with PP; values estimated were lowest during summer and winter 1997 (less than 3 mg chl a m^{-3}) and highest during winter 2001 (ranging between 10 and 80 mg chl a m^{-3}) (Fig. 3). Integrated values of chl *a* varied between 19 and 65 mg chl a m^{-2} during El Niño and between 47 and 695 mg chl a m^{-2} after the event with the higher values during February and August 2001 (Table 1). During the upwelling periods (spring 2000 to summer 2002), the increase of PP that occurred in spring 2000 could not be the result of an increase in phytoplankton biomass (Fig. 3), and it would imply that a physiological factor such as light availability, temperature or nutrient supply was modulating the PP.

The mean primary production estimates of different size fractions in each cruise are presented in Table 1. The >23 μm -fraction production ranged from 0.29 to 26 $\text{mg C m}^{-3} \text{h}^{-1}$. The <2 μm and 2 to 23 μm -fractions productions varied from 0.99 to 3.26 $\text{mg C m}^{-3} \text{h}^{-1}$ and from 0.21 to 12 $\text{mg C m}^{-3} \text{h}^{-1}$, respectively. Microphytoplankton biomass and PP are usually high in the study area (Marín & Olivares 1999). However, during El Niño, the pico- and nanophytoplankton (<23 μm)

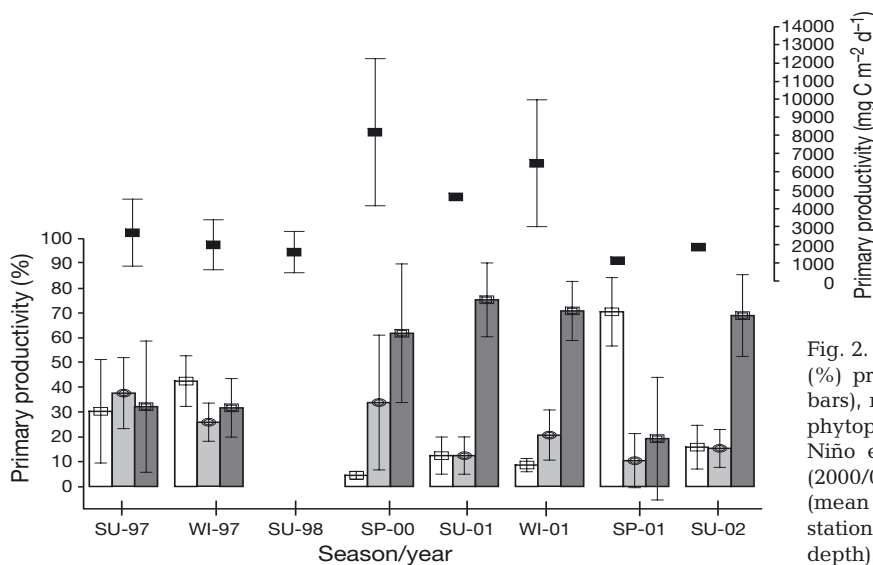


Fig. 2. Total ($\text{mg C m}^{-2} \text{d}^{-1}$) and size-fractionated (%) primary production of picoplankton (white bars), nanoplankton (light gray bars) and microphytoplankton (dark gray bars) during the El Niño event (1997/98) and non-El Niño period (2000/02) in coastal waters of Bahía Mejillones (mean \pm 1 SD). Values were taken from 3 coastal stations on the upper continental shelf (<200 m depth). x-axis: SU, summer; SP, spring; WI, winter

Table 1. Mean values of primary productivity and chl *a* estimates from the photic layer of each size fraction from coastal waters off Antofagasta (± 1 SD; n = number of samples)

Cruise	Primary (mg C m ⁻³ h ⁻¹) <2.0 μ m	Productivity		Chl <i>a</i> (mg chl <i>a</i> m ⁻³)			Chl <i>a</i> (mg chl <i>a</i> m ⁻²)
		2–23 μ m	>23 μ m	<2.0 μ m	2–23 μ m	>23 μ m	
January 1997	1.99 (1.17; n = 30)	5.32 (7.16)	7.67 (10.27)	0.66 (0.70)	0.59 (0.61)	1.35 (3.18)	65
July 1997	1.99 (1.28; n = 18)	1.30 (1.04)	1.52 (1.35)	0.32 (0.19)	0.15 (0.12)	0.26 (0.19)	19
October 2000	1.61 (0.81; n = 6)	12.29 (10.18)	20.39 (7.57)	0.50 (0.24)	6.92 (4.51)	1.48 (1.36)	115
February 2001	1.28 (0.84; n = 6)	1.27 (0.88)	15.30 (17.93)	1.82 (1.80)	1.30 (1.52)	14.36 (15.46)	585
August 2001	3.26 (2.43; n = 14)	8.65 (8.48)	26.26 (15.37)	4.40 (3.93)	5.60 (3.72)	35.74 (29.80)	695
October 2001	1.29 (0.54; n = 4)	0.21 (0.24)	0.29 (0.36)	0.56 (0.35)	0.42 (0.26)	1.46 (1.35)	47
January 2002	0.99 (1.33; n = 6)	0.96 (1.26)	3.43 (2.69)	0.92 (0.36)	0.99 (0.59)	3.38 (1.88)	65

were the dominant size classes, and accounted for more than 50% of chl *a* and PP in coastal waters (Figs. 2 & 3). After re-establishment of cold nutrient-rich upwelled water, microphytoplankton (>23 μ m) productivity and biomass was enhanced. Phytoplankton species composition was constant and living carbon biomass remained low during the El Niño (0.03 to

0.65 μ g C l⁻¹). Stepped diatom colonies (*Pseudonitzschia* cf. *delicatissima*) and small naked dinoflagellates (*Gymnodinium* spp., size: 5 to 25 μ m) and autotrophic flagellates dominated the phytoplankton assemblages. After El Niño, large living carbon biomass pulses are due to large microphytoplanktonic species (500 to 900 μ g C l⁻¹) of long chain-forming diatoms (>20 μ m). *Chaetoceros* spp., *Guinardia delicatula*, *Rhizozolenia* spp. *Detonula pumila*, *Eucampia cornuta*, formed more than 70% of the total phytoplankton abundance.

The sedimentation rate of diatoms was very low before (January 1997) and during (July 1998) the El Niño conditions, with values between 0.02 and 0.2 mg C m⁻² d⁻¹, increasing 2 orders of magnitude during the La Niña in winter and spring 2001 (mean = 28 mg C m⁻² d⁻¹) (Fig. 4). On average, the phytoplankton sedimentation rate was 0.01% of the PP of coastal waters during the 1997/98 El Niño event, compared with 0.1% of PP estimated after that period. This data suggests that, although small-sized phytoplankton (<23 μ m) dominated during the 1997/98 El Niño period, they did not contribute significantly to the flux of carbon biomass leaving the euphotic zone, probably because they are effectively grazed by protozoans (Rassoulzadegan & Sheldon 1986), and they have low sinking rates (Takahashi & Bienfang 1983). In the same area, González et al. (2000) showed vertical flux of total particulate organic carbon (POC; as % PP) before (8%) and during (9%) El Niño 1997/98, suggesting that the decrease

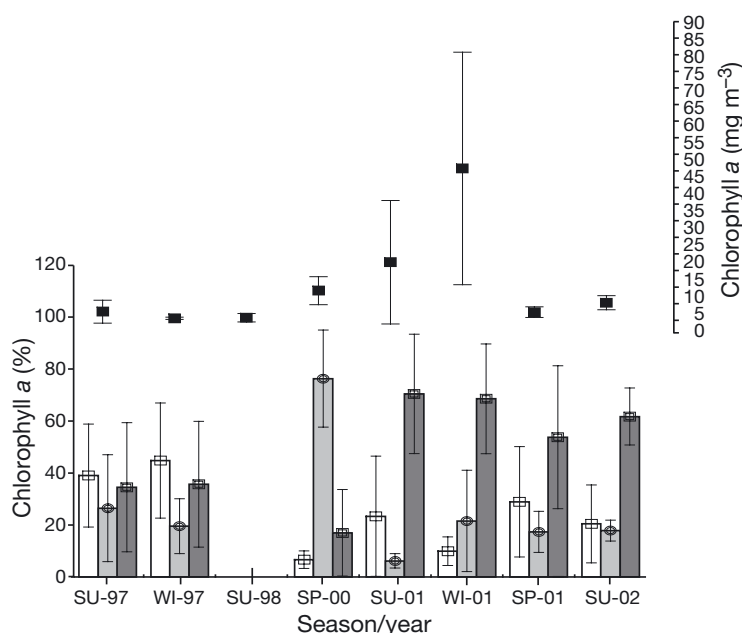


Fig. 3. Total (mg chl *a* m⁻³) and size-fractionated (%) chl *a* of picoplankton (white bars), nanoplankton (light gray bars) and microphytoplankton (dark gray bars) during the El Niño event (1997/98) and non-El Niño period (2000/02) at coastal waters of Bahía Mejillones (mean \pm 1SD). Mean values were taken at 3 coastal stations within the euphotic zone (surface: 0 m; chlorophyll maximum depth: 5–10 m; 2% of surface irradiance: 20–25 m). x-axis: SU, summer; SP, spring; WI, winter

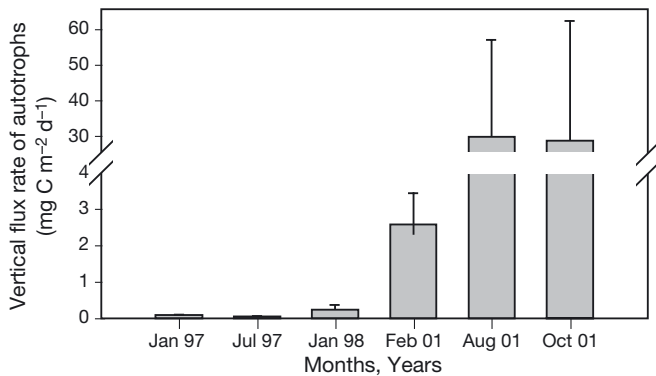


Fig. 4. Phytoplankton sedimentation rates ($\text{mg C m}^{-2} \text{d}^{-1}$) estimated from 6 cruises during the El Niño event (1997/98) and non-El Niño period (2000/01) in coastal waters of Bahía Mejillones (mean \pm 1 SD)

in the vertical flux of diatoms (mainly chain-forming diatoms) during El Niño might be compensated by the increase in vertical flux of other type of particulates, such as faecal material. Increased grazing-impact and vertical fluxes of appendicularian faecal pellets (González et al. 2000) and diminished diatom flux by 75% during El Niño 1997/98 (Romero et al. 2001) give support to this statement.

We suggest that the relatively low export/production rates (0.01 to 0.1%) found in the study area during all sampling periods were a consequence of at least 2 factors: (1) the El Niño of 1997/98 favoured the shift to a microbial loop-based food web over the classical diatom-to-zooplankton food chain and, (2) the strong onshore-offshore variability (e.g. filaments; Sobarzo & Figueroa 2001) of the upwelling area off the Peninsula of Mejillones.

In the northern Humboldt Current System during El Niño, the vertical flux rate of POC plus mesozooplankton grazing (copepods, euphausiids, and pelagic tunicates) removed a small proportion of the photosynthetically produced POC (from 20 to 30%) (González et al. 2000). If less than 1% of PP is sinking, then an important part of the locally generated POC (70 to 80%) might be exported seaward in filaments and eddies. Similar mechanisms were invoked by Olivieri & Chavez (2000) to explain that a large fraction of the PP was unused within the mixed layer and exported horizontally as ungrazed phytoplankton in the coastal upwelling system of Monterey Bay.

There was a significant positive relationship between pico-, nano-, and microphytoplankton biomass and total chl *a* ($r_{\text{pico}} = 0.92$; $r_{\text{nano}} = 0.68$; $r_{\text{micro}} = 0.99$; $n = 60$, $p < 0.05$), indicating that absolute biomass in all 3 phytoplankton size classes increased with the return from El Niño (oligotrophic) to more 'normal' (eutrophic) conditions. During El Niño, water with low chl *a* and

low PP tended to have a high proportion of picophytoplankton compared with conditions of high PP ($r = -0.76$, $n = 42$, $p < 0.05$) and biomass ($r = -0.73$, $n = 54$, $p < 0.05$). A size-spectrum analysis (Fig. 5) ($\log_2 \% \text{ normalized PP} = \log_2 a + b \log_2 \text{ mean size class}$) revealed a more negative slope during El Niño 1997/98 ($b = -0.93$, $p < 0.05$) than a normal phase ($b = -0.44$, $p < 0.05$), suggesting that an oceanographic shift from cold and nutrient-rich waters to oligotrophic conditions may facilitate the dominance of small size classes, and a significant proportion of PP is fuelling through the microbial food web. Results reported in the upwelling area off Coquimbo (30°S, Montecino & Quiroz 2000) suggested that when resources, such as nutrients or light, are limiting, the phytoplanktonic size structure should be displaced toward a smaller size, which is more efficient in using resources than microphytoplankton (Chisholm 1992).

The observed pattern in the changing phytoplankton-community variables associated with El Niño and non-El Niño periods could be explained by the following conceptual model (Fig. 6): (1) During coastal upwelling, the 15 to 16°C isotherm reaches the surface, maximizing PP and biomass (up to $12 \text{ g m}^{-2} \text{d}^{-1}$) and leading to a community dominated by chain-forming diatoms. This phytoplankton is grazed by medium- (copepods) and large- (euphausiids) sized zooplankton groups. A significant fraction of the PP may be exported laterally offshore by physical forcing. (2) During

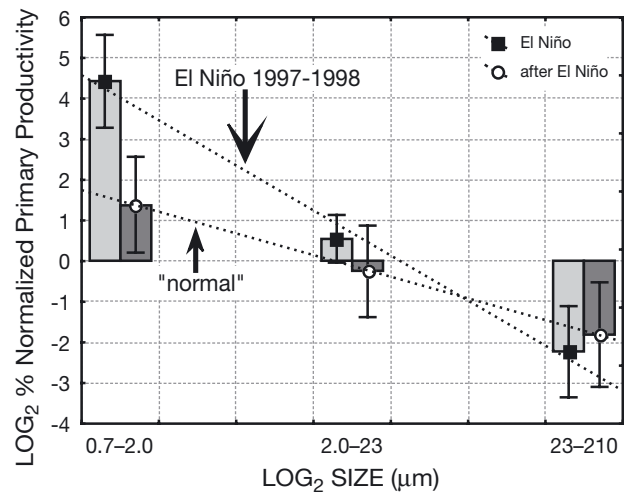


Fig. 5. Relationship between normalized primary productivity estimates ($\log_2\%$) and 3 size classes ($\log_2 \mu\text{m}$) during the El Niño event (light grey bars) and non El Niño period (dark grey bars) in coastal waters of Bahía Mejillones (mean \pm 1 SD). Mean values of primary productivity ($\text{mg C m}^{-3} \text{h}^{-1}$) were taken at 3 coastal stations within the euphotic zone (surface: 0 m; chlorophyll maximum depth: 5–10 m; 2% of surface irradiance: 20–25 m). Phytoplankton size classes (on x-axis): picoplankton = 0.7–2.0; nanoplankton = 2.0–23.0; microplankton = 23–210 μm

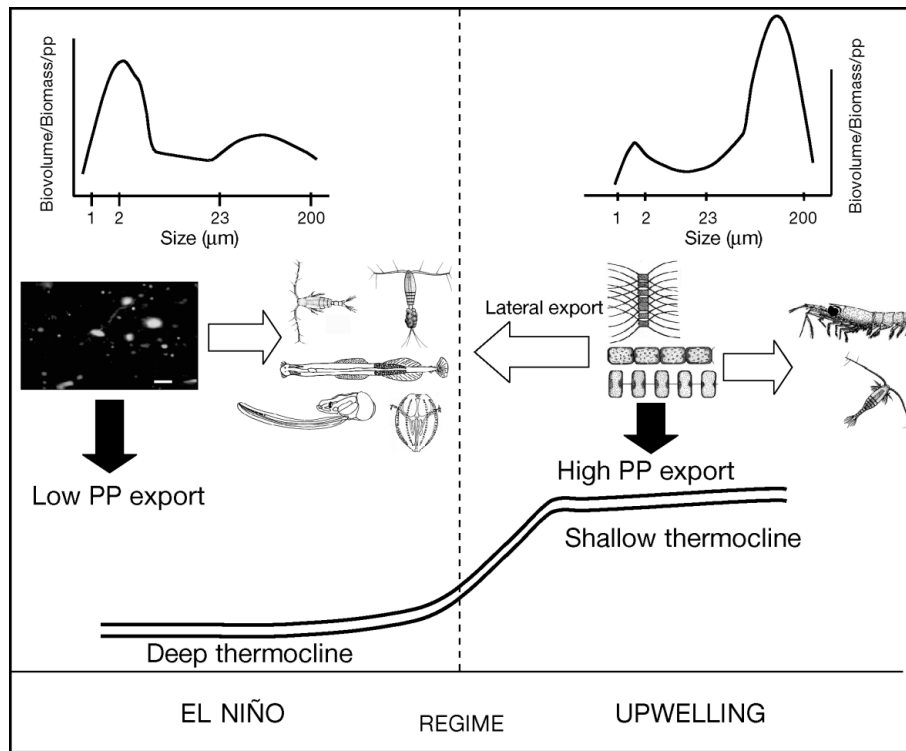


Fig. 6. Schematic model of changes of export/production rates, phytoplankton biomass size-spectrum and phytozooplankton assemblage structure associated with El Niño and normal upwelling events in coastal waters off Antofagasta. PP: primary productivity

warm periods, the 15 to 16°C isotherms deepen, resulting in a suppression of coastal upwelling, low biomass and PP, and domination by pico- and nanophytoplankton size classes in inshore waters. In summary, during El Niño in the northern Humboldt Current System, the dominance of smaller phytoplankton size-fractions, and their larger contribution to both PP and biomass, leads us to believe that biological and physiological shifts occur in phytoplankton assemblages in order to counteract the change in prevailing physical and chemical conditions.

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