Alongshore and temporal variability in chlorophyll *a* concentration in Chilean nearshore waters

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ABSTRACT: Phytoplankton and particulate organic matter constitute the primary food source for adult filter-feeders, as well as for larval stages of many benthic and pelagic organisms. The structure and dynamics of nearshore benthic communities may be associated with variation in nearshore primary production. However, we know little about the scales of variability in phytoplankton in nearshore waters along open coasts, or about their causes. To characterize spatial and temporal patterns of chl *a* concentration, we conducted 2.5 yr of daily, shore-based monitoring at 3 sites separated by 10s of km within an upwelling region in central Chile. We found that: (1) peaks in chl *a* concentration were typically short-lived, persisting no longer than 4 d, (2) blooms occurred in spring to early summer months at all sites, but also during autumn months at 1 site (Las Cruces), and (3) the intensity and frequency of blooms were consistently different among sites; highest concentrations were at Las Cruces, lower at El Quisco, and the lowest at Quintay. Analyses of wind data and surface temperature, and inspection of Advanced Very High Resolution Radiometer (AVHRR) satellite images, suggested that among-site differences were due, at least in part, to alongshore variation in upwelling intensity and the formation of warm-water pockets or upwelling shadows in sections of the coast, such as Las Cruces. In contrast to the spatial pattern described offshore and over larger spatial scales, chl *a* concentrations were significantly lower at the coldest site, Quintay, located at the core of an upwelling center (Pta. Curaumilla), than at the warmer site of Las Cruces, which lies downstream from upwelling. Day-to-day variation in chl *a* levels during spring at Las Cruces seems related to the alongshore intrusion of waters upwelled upstream. Overall, the pattern observed at our 3 sites, together with previous studies at other upwelling systems, suggests that sections of the coast around 15 to 20 km downstream (equatorward) from upwelling centers could exhibit consistently higher phytoplankton concentrations than sites located in front of upwelling centers, generating a source-sink type of geographic pattern of nearshore nutrients and phytoplankton along the coast.

KEY WORDS: Phytoplankton · Chl *a* · Nearshore oceanography · Upwelling · Upwelling shadow

INTRODUCTION

Coastal oceans are among the most productive ecosystems of the world (Lubchenco et al. 1995, Ricciardi & Bourget 1999). A large biomass of filter feeders characterizes most hard- and soft-bottom habitats, and nearshore waters serve as a nursery ground for larvae of many commercially and biologically important species (Roy et al. 1992, Cole & McGlade 1998). Phytoplankton and particulate organic matter (POM) in surface waters constitute the primary food source for both the early life-history phases of many benthic and

pelagic organisms and the adult filter-feeding organisms that often dominate benthic habitats (Walker et al. 1987). Field studies have shown that abundance of phytoplankton and POM can regulate the growth, overall size and distribution of adult filter feeders in soft and hard-bottom habitats (Page & Hubbard 1987, Grebmeier et al. 1988, Duggins et al. 1989, Smaal & Van Stralen 1990, Bertness et al. 1991, Leichter et al. 1998, Sanford & Menge 2000). In addition, higher phytoplankton concentrations can lead to increased development and survival rates of larvae (Barnes 1956, Hentschel & Emlet 2000). However, except for research conducted in estuarine and fjord systems (e.g. Demers et al. 1989, Archambault et al. 1999), we still know little about the spatial and temporal scales of variability in phytoplankton biomass in nearshore waters along the open coast, and even less about the processes causing such variation.

Large and persistent differences in chlorophyll *a* (chl *a*) levels in inshore waters along the open coast have been documented over regional and continental scales, like those occurring along the east and west coasts of Africa (Brown 1992, Bustamante et al. 1995) and America (Longhurst 1998, Thomas et al. 2001). These differences are attributed to geographic-scale differences in nutrient influx, largely caused by differences in coastal upwelling (Small & Menzies 1981, Huyer 1983), with significantly higher nutrient and chl *a* levels along the west coasts of the continents (Longhurst 1998). Patterns of chlorophyll variability over spatial scales smaller than entire continents or oceanic regions are much less clear, especially in nearshore environments. On the one hand, benthic ecologists have traditionally adhered to the idea of high spatial homogeneity of alongshore phytoplankton biomass over spatial scales smaller than 100s of km and, therefore, the potential of bottom-up effects as important structuring forces in benthic marine communities have largely been ignored (Menge 1992). However, recent studies on the coast of Oregon, USA, have shown at least short-term differences in nearshore phytoplankton among sites 10s of km apart, apparently as a result of meso-scale differences in upwelling intensity, water retention, or both (Menge et al. 1997a,b). On the other hand, the nearshore dynamics of nutrients and phytoplankton biomass at upwelling centers has been described in some detail at only 2 sites, 1 in Oregon and 1 in South Africa (Field et al. 1980, Menge 1997a,b), and for limited periods of time. These studies have shown that at upwelling centers, rates of nutrient advection nearshore can sometimes surpass the rates of phytoplankton assimilation, leading to phytoplankton-poor waters at the center of upwelling. This general pattern is contrary to those described over much larger scales and observed

through satellite images (e.g. Abbott & Zion 1985, Shannon et al. 1985, Thomas et al. 1994, Thomas 1999), but the generality of the upwelling-nutrient-phytoplankton dynamics in nearshore environments is nondescript and, to the best of our knowledge, has not been examined in most major upwelling regions of the world.

Like most coasts of the world, the majority of the knowledge about phytoplankton variability along the coast of Chile comes from low frequency sampling conducted during offshore cruises and from analyses of satellite images. This information has shown that physical forcing by strong, persistent upwelling conditions drives the influx of nutrients to surface waters, which then fuels high phytoplankton productivity (Morales et al. 1996, Strub et al. 1998). Through food-web interactions, this process results in one of the world's most biologically productive fisheries (Alheit & Bernal 1993). Several studies have found elevated phytoplankton concentrations in surface waters 10s to 100s of km offshore associated to localized upwelling centers (Thomas et al. 1994, Morales et al. 1996, 2001, Thomas 1999). Similarly, analyses of SeaWIFS satellite images have shown that seasonal variation in offshore pigment concentration along central Chile is correlated with maximum upwelling activity, with maximal in pigment concentrations and upwelling-favorable winds during summer (Thomas et al. 1994). At the scale of individual upwelling events, the few data available suggest that chl *a* concentration tends to increase nearshore during relaxation events following an initial upwelling pulse (Arcos et al. 1987, Peterson et al. 1988), a pattern similar to that often described off the coast of Oregon (Wroblewski 1977). Whether the spatial and temporal dynamics of phytoplankton biomass in the nearshore waters (<4 km from the shore) are similar to those reported 10s of km offshore is not known.

Here we first describe short- and long-term temporal variation in the nearshore surface chl *a* concentration at 3 sites that differed in their proximity to known centers of upwelling. Second, we explore relationships between physical forcing and phytoplankton dynamics. To the best of our knowledge, this is the first set of data that describes the time-space dynamics in nearshore chl *a* in the Southeastern Pacific, the most productive upwelling ecosystem of the world (Alheit & Bernal 1993, Cury et al. 1998). We answer simple, yet important, questions regarding spatial and temporal patterns in phytoplankton abundance in coastal waters along the central Chilean coast: How long do blooms last? When do blooms occur and are there consistent seasonal differences? Are there persistent differences in concentration and/or synchrony in the timing of blooms among sites 10s of km apart?

MATERIALS AND METHODS

Study sites. The central Chilean coast, where our study sites were located, is characterized by a narrow continental shelf (e.g. 100 m isobath lies ca. 1 to 5 km from shore), which broadens slightly from north to south. Most of the coast is directly exposed to pounding waves, with few protected bays or coves. The region is dominated by seasonal upwelling and much of the alongshore variation in surface water temperature, during typically strong southerly winds and active upwelling, is visible in thermal satellite imagery such as that presented in Fig. 1 (see also Broitman et al. 2001, Poulin et al. 2002b). To characterize spatial variation in phytoplankton biomass within this region, we selected 3 wave-exposed, open-coast, rocky sites: Quintay (33° 11′ S), El Quisco (33° 23′ S) and Las Cruces (33° 30′ S) (Fig. 1). Quintay is located about 15 km to the south of Punta Curaumilla and forms part of this well-known upwelling center (Sievers & Silva 1979, Johnson et al. 1980, Fonseca & Farías 1987, Vergara 1991, 1993). Las Cruces is approximately 40 km to the south

of Quintay, at the northern extreme of Cartagena Bay, and rarely appears to be directly affected by upwelling (Broitman et al. 2001, D. Narváez, S. A. Navarrete & J. C. Castilla unpubl. data). Roughly 20 km south of Las Cruces is another well known center of upwelling, Punta Toro (Arcos & Salamanca 1984, Fonseca & Farías 1987, Bello Mejía 2001). El Quisco is located between Las Cruces and Quintay, approximately 15 to 20 km north of Las Cruces (Fig. 1). Based on initial, informal visual assessment of AVHRR satellite images, we hypothesized that sites that differed markedly in the frequency of occurrence or persistence of cold, upwelled water would likewise differ in phytoplankton abundance and/or the temporal pattern of chl *a* concentration. Other prominent features within the region include the presence of the submarine canyon and the mouth of the Maipo River, which are located about 15 km to the south of Las Cruces and may also play a role in the productivity of coastal waters.

Chl *a* concentration. To characterize temporal variations in phytoplankton biomass in onshore waters, we took, daily or 3 times per week, shore-based water samples at the 3 study sites from January 1998 through June 2000. Chl *a* measurements were obtained following the method described by Menge et al. (1997b). Three water samples were taken each time from 20 to 40 cm depth using 3×250 ml dark bottles that were firmly lodged into a weighted plastic bucket. Immediately after collection, the water sample from each bottle was pre-filtered using a 300 μm mesh to remove large, organic particles. From each sample, 100 ml were filtered through a GF/F Whatman glass fiber filter using a syringe and inline filter holder. Filters (3 d^{-1} $site^{-1}$) were wrapped in aluminum foil and frozen at −20°C for later laboratory analysis. Chl *a* was extracted by soaking filters in 90% acetone for 20 h in darkness at 0°C (Parsons et al. 1984). Fluorescence was measured using a 10-AU Turner Designs Fluorometer and chl *a* concentration was calculated after correcting for phaeopigments (US Environmental Protection Agency method: Arar & Collins 1997).

Daily samples were taken at Las Cruces and Quintay, while samples were taken roughly 3 times per week at El Quisco. Logistic constraints prevented us from sampling regularly at
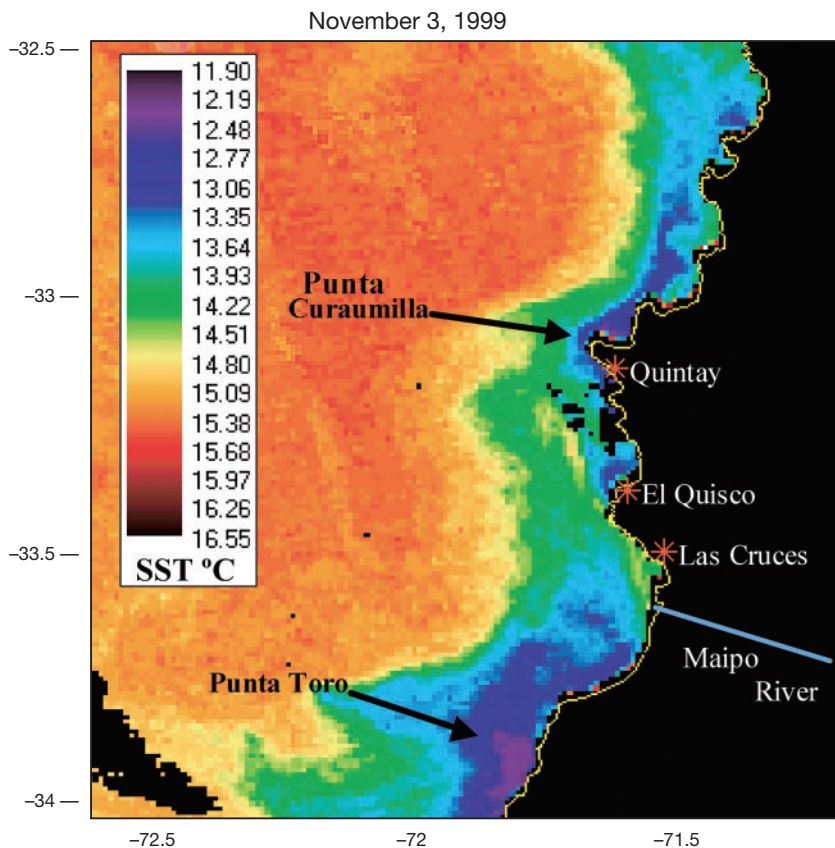

Fig. 1. Location of wave-exposed, rocky intertidal study sites (red stars: Quintay, El Quisco, and Las Cruces), which stretch along approximately 30 km of coastline. Differences in upwelling intensity among sites are visible in AVHRR (Advanced Very High Resolution Radiometer) thermal imagery. SST: sea surface temperature

El Quisco during austral spring and summer 1998-99, and therefore data from this site are not used in all comparisons (see 'Data analysis'). Preliminary data from various days of hourly sampling during different seasons of the year at these same sites showed no consistent pattern of within-day variation in chl *a* concentration (S. A. Navarrete unpubl. data). Therefore, we arbitrarily chose to simultaneously take samples within 2 h before sunset at all sites.

Physical variables. In order to characterize the physical environment and shed light onto potential mechanisms driving variation in chl *a* concentration, we recorded several physical variables throughout the study. Surface water temperature was recorded at 20 min intervals with Optic Stowaway® (Onset Computer) submersible temperature dataloggers. Onshore temperature loggers were placed at approximately 1 m depth below the lowest low tide at the 3 sites. An additional onshore temperature logger was deployed at the site of Matanzas, which forms part of the upwelling center of Punta Toro (Fig. 1). To obtain more detailed information on temperature changes and structure in the water column nearshore at Las Cruces, we also deployed a series of temperature loggers suspended from buoyant lines moored approximately 150 m from shore, where bottom depth was approximately 25 m. Moored temperature loggers were placed at 3, 7, 14, and 20 m depth. All data from loggers were downloaded roughly every 2 mo. Wind direction and speed were recorded every 20 min by a Campbell® meteorological station located at the Estación Costera de Investigaciones Marinas (ECIM), Las Cruces. Daily flow rates of the Maipo River were obtained from the Ministry of Public Works' Cabimbao station, located 10 km upstream from the mouth of the river.

Data analysis. Overall chl *a* levels were compared among sites with a 1-way ANOVA on log-transformed data, which exhibited approximately normal distribution and homogeneity of variances, according to inspection of residuals and Cochran's *C*-test, respectively. Tukey's multiple comparison test was used to determine which sites differed significantly from others. Cross-correlation analyses were calculated to determine the degree of temporal synchronicity between sites. These analyses were performed on the raw data and we used only those days for which we had data for both of the sites being compared. Bonferroni adjusted confidence intervals were calculated to adjust for multiple comparisons (see Legendre & Legendre 1998). To characterize seasonal and other 'long-term' trends in chl *a* at Quintay and Las Cruces, for which the most complete databases were available, autocorrelation analyses were performed on time series after smoothing the data with a 7 d running average (see Leichter et al. 1998 for similar procedure).

To examine the relationship between physical variables and chl *a* concentration at Las Cruces, cross-correlation analyses were performed on raw data using: (1) the entire data set, and (2) specific seasons during which we observed peaks in chl *a* concentration. Before these analyses, raw chl *a* and physical data were placed on the same temporal scale. Daily averages of surface water temperature, wind stress, and Maipo river flow were calculated. Confidence intervals on cross-correlation analyses are based on white noise (uncorrelated data).

RESULTS

Temporal and spatial variation in chlorophyll *a*

Overall chl *a* levels were significantly different among sites (Fig. 2), with the lowest levels observed at Quintay (long-term mean [±SE] = 0.358 ± 0.073 µg l^{-1}), higher levels at El Quisco (0.533 ± 0.164 µg l^{-1}) and the highest levels at Las Cruces (0.964 ± 0.096 µg l^{-1}). Chl *a* levels at Las Cruces were significantly higher than at the other 2 sites (ANOVA *F* = 99.4, df = 2, 1250, p < 0.0001). Even after removing all the large chl *a* peaks observed at Las Cruces, the background concentrations were higher overall than at the other 2 sites (Fig. 2c, insert). These long-term average values conceal (smooth over) much of the among-site differences.

Seasonal patterns in phytoplankton bloom events also differed among sites (Fig. 2). At Quintay, peaks in chl *a* concentration occurred during austral spring and summer (September to February) of each year (Fig. 2a). Within this window of time, blooms occurred anywhere between early spring and mid summer, and 2.5 yr of data was not sufficient to show statistically clear seasonality in autocorrelation analysis. At Las Cruces, spring peaks of short duration were also observed, but these were less intense, and their timing more irregular, than the autumn bloom events (Fig. 2c). During March-April (autumn) of each year, chl *a* reached average concentrations of 6 to 8 µg l^{-1}, and occasionally reached up to 70 µg l^{-1} (see Fig. 2c). These fall blooms were observed in 3 consecutive years in Las Cruces, and the regularity of the peaks produced a statistically significant annual signal in the autocorrelation analysis. At El Quisco, an intermediate pattern of seasonality was observed, with chl *a* peaks occurring anytime in spring, summer, and autumn (Fig. 2b). Large gaps in the data set for this site prevented autocorrelation analysis.

The greatest variability in chl *a* levels occurred at the synoptic-scale variability associated with weather time-scales. Phytoplankton bloom events (peaks in
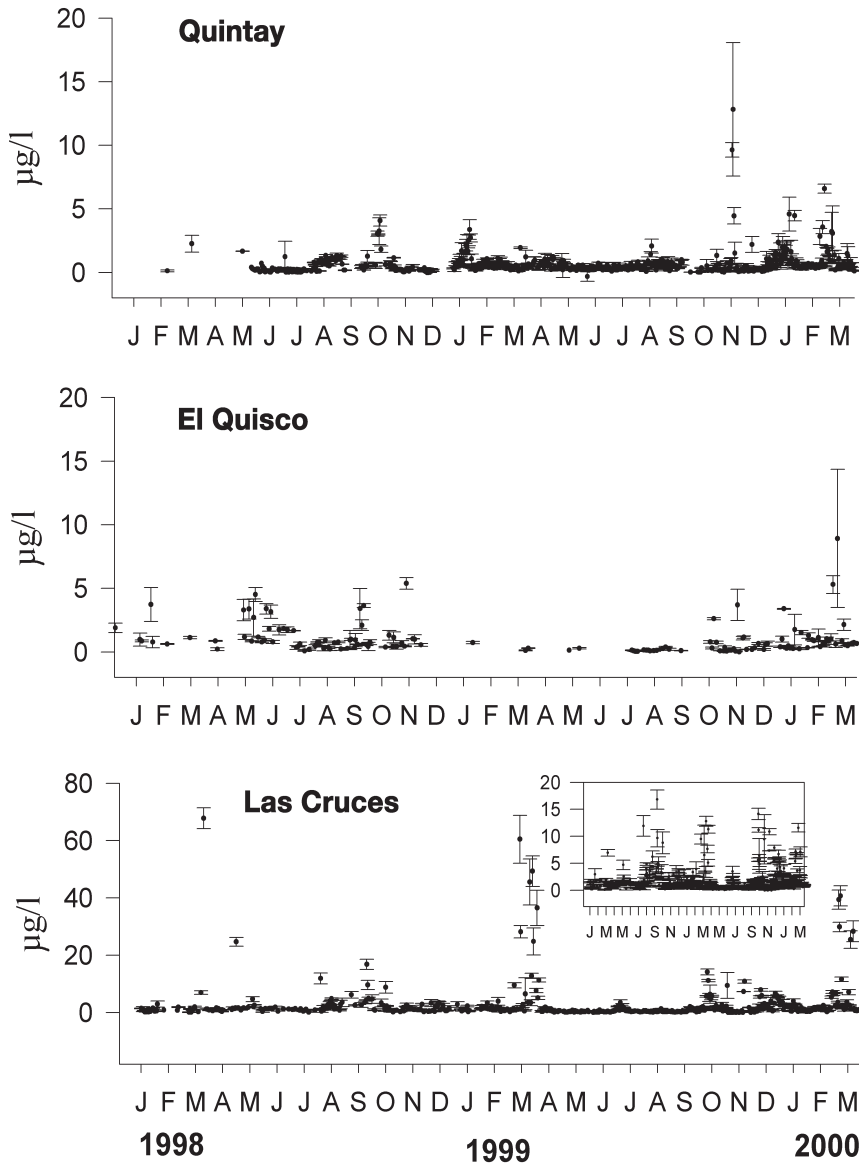
Fig. 2. Daily chl *a* concentration at Quintay, El Quisco, and Las Cruces. Each point is the mean (±SE) of 3 replicate 100 ml water samples taken from the shore

Physical variables

There were consistent differences in onshore daily mean sea surface temperature (SST) among sites (Fig. 4). Onshore SST was consistently warmer at Las Cruces (long-term mean ± SE = 14.3 ± 0.05), while Quintay was consistently colder (long-term mean ± SE = 12.6 ± 0.06). Mean temperatures at El Quisco were intermediate between Quintay and Las Cruces (long-term mean ± SE = 13.2 ± 0.05).

At all sites, a clear seasonal cycle was observed in SST. In general, autumn and winter temperatures (April-August) were low (approx. 12.5°C), homogeneous across sites and presented little high frequency (weekly, daily) variability. Spring and summer temperatures were generally higher (approx. 16°C across sites), but also presented large high frequency variability (weekly, daily, hourly), and clear differences among sites (Fig. 4). The largest among-site differences in SST occurred during spring, when Las Cruces presented marked seasonal warming in contrast to the overall colder temperatures at Quintay and El Quisco (see Fig. 4 inserts).

Most temporal variability in SST was associated with the synoptic event time-scale of 3 to 10 d. Some of the strong, short-term temperature fluctuations were due to wind-driven coastal upwelling events and subsequent drops in SST, as evidenced by the significant, negative correlations between wind stress and SST observed at Las Cruces and Quintay (Fig. 5). Poulin et al. (2002b) and (D. Narváez, S. A. Navarrete & J. C. Castilla unpubl. data) have shown similar patterns for El Quisco. However, the strength of the correlation was markedly higher at Quintay than at Las Cruces, and the speed of response of SST to upwelling-favorable wind stress varied across sites. Almost immediate changes were observed at Quintay (maximum correlation observed at lags of 1 to 5 d) and significantly more sluggish responses in SST at Las Cruces (maximum correlation observed at lags of 2 to 7 d). Differences in the strength and speed of the response to upwelling-favorable winds led to apparent differences in the frequency of temperature drops among sites, as shown in Fig. 4. Abrupt drops in

chl *a* concentration) lasted no more than a few days (see Fig. 2). Short-term daily variability in chl *a* levels did not occur simultaneously at all sites (Fig. 3, nonsignificant correlation with zero lag). Instead, the strength of the correlation and synchrony in timing varied between sites (Fig. 3). Daily fluctuations in chl *a* levels at Las Cruces and El Quisco were correlated with changes in Quintay with similarly long time lags of 7–9 and 11 d, respectively. The correlation was stronger between Quintay and El Quisco ($r^2 = 0.77$) than between Las Cruces and Quintay ($r^2 = 0.3$). Chl *a* levels were more synchronous between Las Cruces and El Quisco ($r^2 = 0.62$), with Las Cruces leading El Quisco by 1 d.
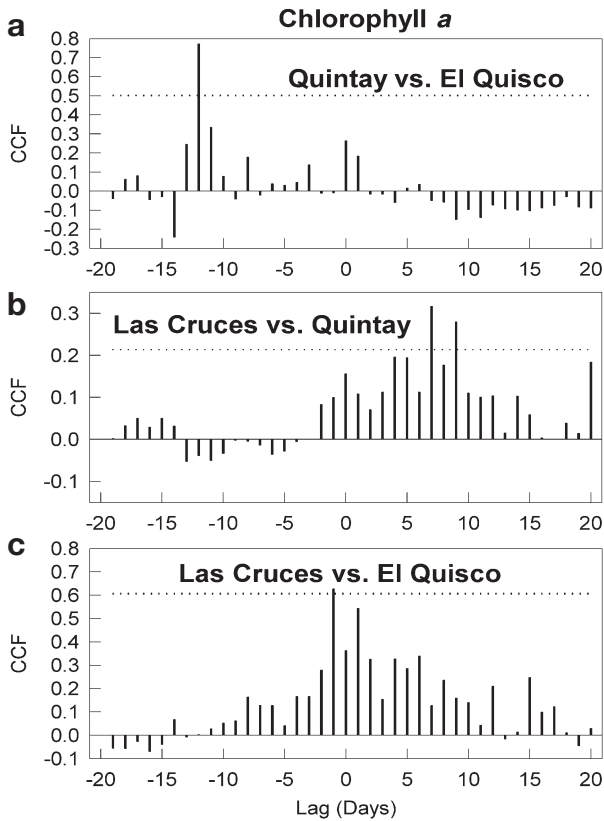
Fig. 3. Cross-correlation function (CCF) of chl *a* concentrations between (a) Quintay and El Quisco, (b) Las Cruces and Quintay, and (c) Las Cruces and El Quisco. Dotted lines are Bonferroni adjusted confidence intervals

lagged slightly behind the temperature drops first observed at Matanzas (Fig. 6b).

Chlorophyll *a* and physical variables at Las Cruces

The spring-summer phytoplankton blooms observed at Las Cruces were linked to major upwelling-relaxation events. During the upwelling season, all major peaks in chl *a* occurred concurrent with 2 conditions: the water column presented a strong vertical gradient in temperature; and surface waters at Las Cruces had begun to warm after a rapid drop in SST (see vertical lines in Fig. 6b,c). The initial forcing role played by southerly winds in the occurrence of these blooms was evidenced by a positive, significant (albeit weak) correlation between chl *a* peaks and wind stress (maximum correlation of 0.18, significant at lags between 7 and 9 d). However, more detailed observations of the immediate physical conditions leading to individual events revealed that each peak in chl *a* concentration occurred when upwelling conditions were followed by periods of relaxation or reversal of strong alongshore (N to S) winds (Fig. 6a), thus accounting for the thermal conditions described above. Note, however, that not all periods presenting these physical characteristics lead to a bloom, which underscores the

surface temperature at Quintay and secondarily at El Quisco were not always accompanied by similar rapid cooling events at Las Cruces.

Onshore SST at Matanzas, south of Las Cruces and part of the Punta Toro upwelling center, closely followed the temperature pattern observed at Quintay. Similar, significantly negative correlation between wind stress and SST ($r^2 = -0.35$) characterized the temperature time series at Matanzas (lag 0 to 2 d). This pattern of alongshore variability in upwelling frequency and intensity was also apparent when examining AVHRR satellite images (see our Fig. 1, Broitman et al. 2001, Poulin et al. 2002b, D. Narváez, S. A. Navarrete & J. C. Castilla unpubl. data). Following periods of strong southerly winds (i.e. winds from the south), like those occurring on 3 November 1999 (Fig. 1), cold water was observed at Quintay, near Punta Curaumilla, and at Matanzas, 20 km south of Las Cruces near Punta Toro. A small plume of cold water was also observed at El Quisco. Between such cold water regions, persistent warm water pockets, particularly at Las Cruces, were visible. In addition, cooling events at Las Cruces were generally smaller in magnitude and
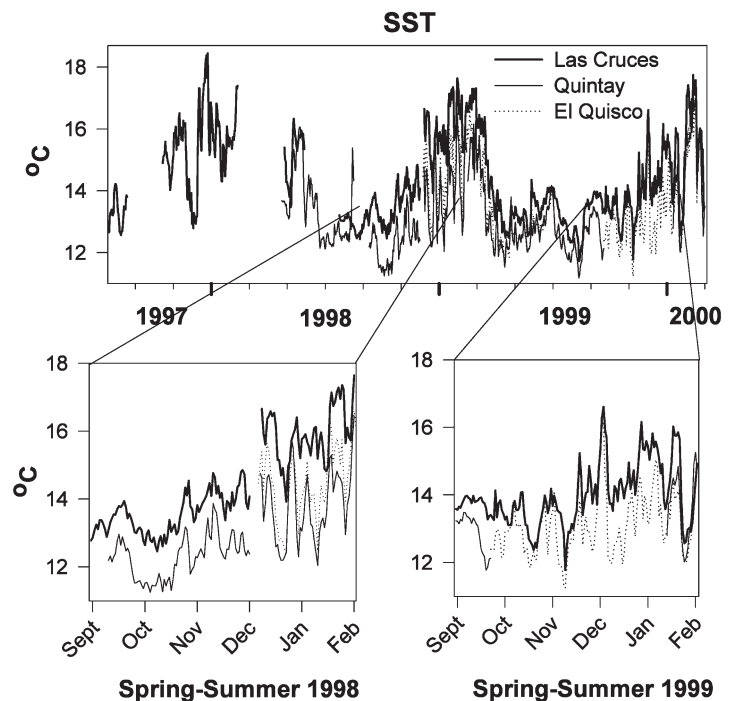

Fig. 4. Time series of mean daily surface water temperature measured *in situ* at the Quintay, El Quisco, and Las Cruces. Inserts show sea surface temperature (SST) during upwelling seasons
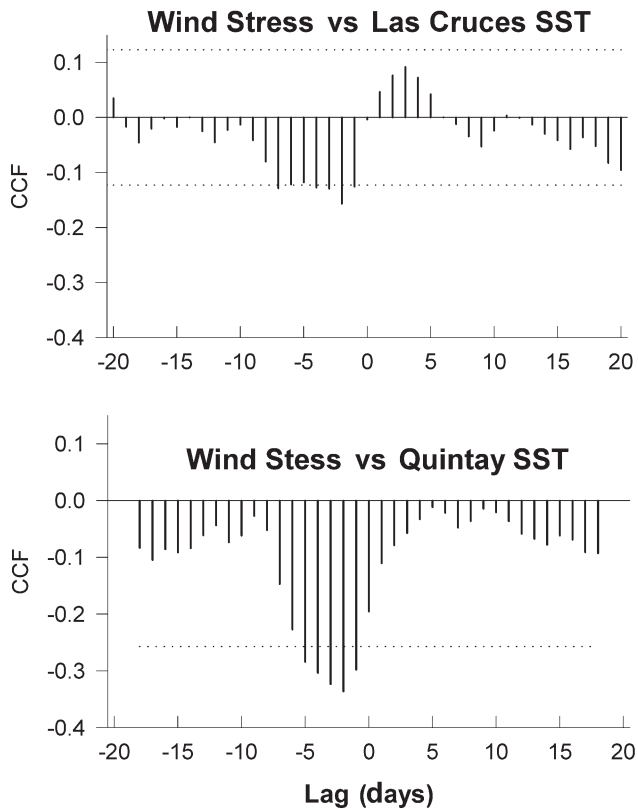
Fig. 5. Cross-correlation function (CCF) of wind and sea surface temperature (SST) at Quintay and Las Cruces. Dotted lines are 95% confidence intervals
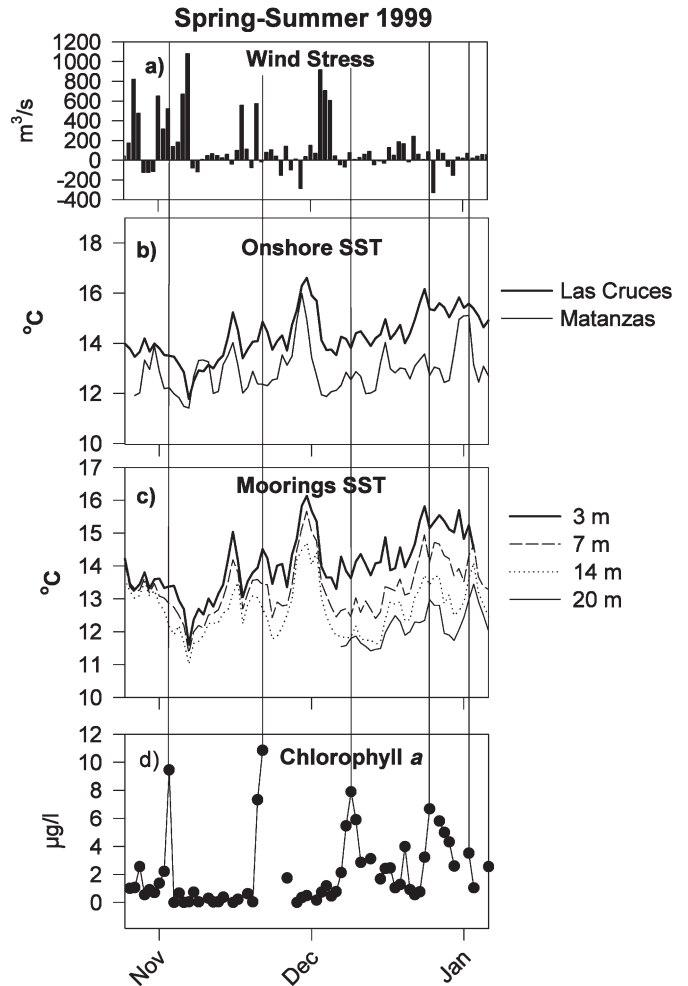

Fig. 6. (a) Wind stress values, (b) mean daily onshore sea surface temperature (SST) for Matanzas and Las Cruces, (c) mean daily SST at 3, 7, 14, and 20 m from moored temperature loggers, and (d) mean daily chl *a* concentration at Las Cruces over the extent of upwelling season (spring-summer) of 1999. Positive wind velocity values indicate upwelling-favorable conditions. Note that temperatures at Las Cruces seem to 'follow' Matanzas. Vertical lines indicate peaks in chl *a* at Las Cruces

complexity of the system and suggests that biological responses to upwelling may vary from one event to another.

Many of the intense autumn blooms also followed the pattern of wind and temperature conditions for the upwelling-relaxation events described above, but the pattern was less consistent than during spring (Fig. 7). Nevertheless, there was still a clear relationship between chl *a* peaks and reversals in local, alongshore wind direction (Fig. 7c).

Due to the particularly high concentration of chl *a* during some of these autumn blooms, we suspect that other factors besides upwelling-relaxation, such as nutrient input from 'external' sources, may also be important in enhancing chl *a* levels. To examine the potential nutrient subsidy contributed by the nearby Maipo River, we looked at the correlation between river flow and chl *a* concentration. While it is known that the Maipo is often nutrient-rich (report by Medio Ambiente, Ecología y Salud Publica: Cabrera 2003), there are no daily data over the period of our study. In contrast to the repeatability of the autumn chl *a* peaks, the seasonal pattern of flow rate of the Maipo River varied considerably between years (Fig. 7a). During

1998, flow rates remained high throughout the summer, with maximum values reaching 300 m³ s⁻¹ during January. In contrast, flow rates were among the lowest recorded during the same months in the summer of 1999. These differences between summer flows probably reflect the unusually strong rains during the 1997-98 El Niño year. During the non-El Niño 'dry' year (1999), autumn chl *a* peaks were observed at Las Cruces, 8 to 9 d after peaks in river flow ($r^2 = 0.55$, significant at 95%), see Fig. 7b. However, these same peaks in chl *a* also closely followed the trend of rapid wind reversals and warming waters following an abrupt drop in SST, as described above for the spring-
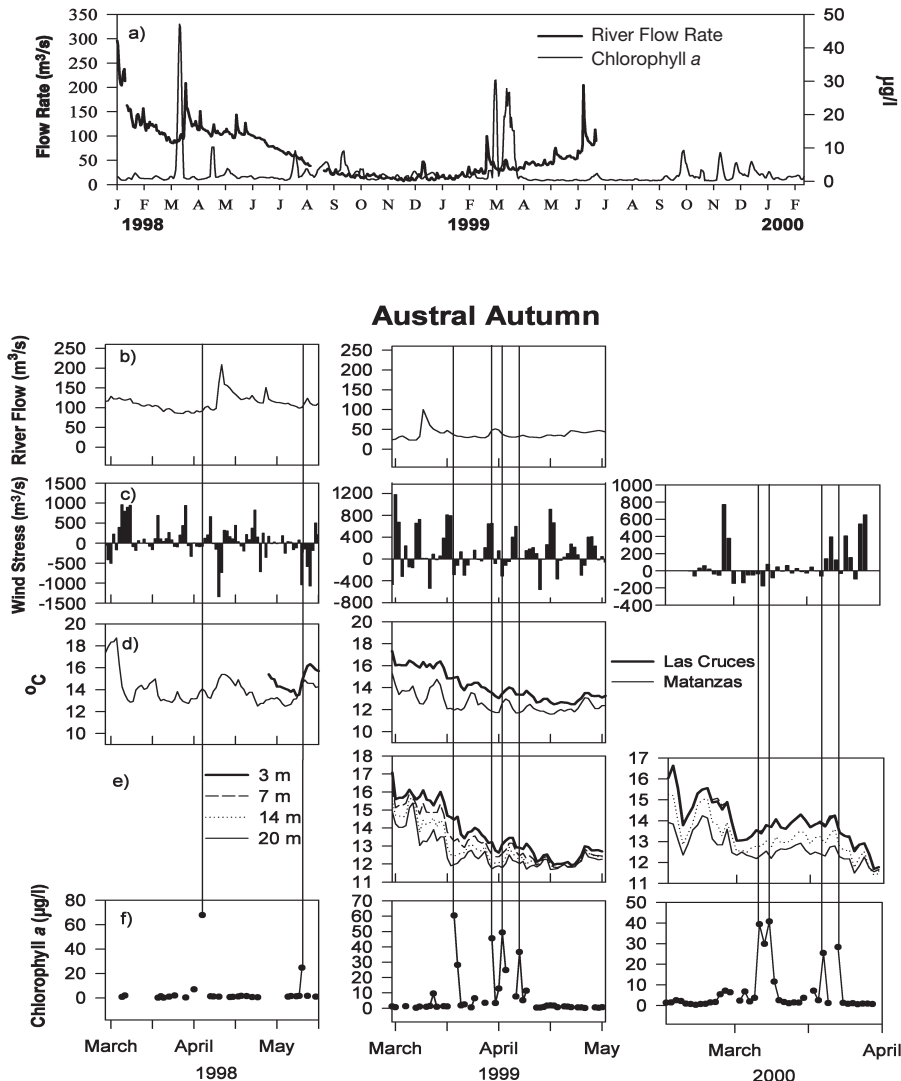
Fig. 7. (a) Daily flow rate for the Maipo River and chl *a* concentration at Las Cruces for the time series, (b) daily flow rate for the Maipo River, (c) wind stress values, (d) mean daily temperature for Matanzas and Las Cruces, (e) mean daily sea surface temperature (SST) at 3, 7, 14, and 20 m from moored temperature loggers, and (f) mean daily chl *a* concentration at Las Cruces during autumn months of each year of the study. Flow rates were measured 10 km from the mouth of the river. Positive wind velocity values indicate upwelling-favorable conditions. Vertical lines indicate peaks in chl *a* at Las Cruces

time peaks in chl *a*. Thus, it appears that runoff events and upwelling-relaxation conditions conspire to provide high levels of nutrients followed by stratification and the occurrence of these extreme bloom events.

DISCUSSION

Surprisingly little is known about the scales of variation in phytoplankton biomass in nearshore environments, particularly for open coasts. Basic descriptive studies are scarce even in well-studied regions because of the short duration of records or limited cruises conducted during specific conditions or times of the year. Accounts of daily, or even weekly, variation of sufficient duration to quantitatively document seasonal changes are rare, let alone simultaneous records at more than 1 site along the shore. This deficiency has

lead to a predominant view of spatial homogeneity in nearshore chl *a* concentration and reinforced the traditional view of dominance by seasonal-scale variation. Here we report a unique data set describing the high-frequency (daily) and seasonal changes observed over 2.5 yr at multiple sites, which illustrate the dramatic contrast between nearshore chl *a* levels within upwelling centers and more sheltered areas between upwelling centers. We are unaware of any similar study of nearshore chl *a* patterns (daily data and multiple sites) anywhere. This study gains further importance in that it allows us to characterize temporal and spatial variability of chl *a* levels over scales relevant to other components of nearshore ecosystems. In what follows we compare these results to those obtained on other coasts of the world, but for the most part, comparisons are limited due to differences in the spatial and/or temporal extent of the studies.

The central coast of Chile is dominated by seasonally variable, wind-driven upwelling that forces cold, nutrient-rich waters into the upper water column (Poulin et al. 2002a,b, D. Narváez, S. A. Navarrete & J. C. Castilla unpubl. data, and see Strub et al. 1998 for review). Over large spatial scales, satellite (SeaWIFS) measured chlorophyll shows an offshore annual maximum in summer for central Chile, which coincides with the period of maximum upwelling-favorable winds for the region (Thomas et al. 2001). Our daily, shore-based measurements confirm a similar seasonal cycle onshore, with a summer maximum in chl *a* concentration occurring in spring-summer at all 3 of our study sites, which is in phase with seasonal, nearshore wind forcing and SST variability. However, our results also show that some sites can deviate significantly from this seasonal pattern, exhibiting high chl *a* concentrations in autumn months. Moreover, results showed persistent differences in overall chl *a* concentrations among sites 10s of km apart, with generally lower chl *a* levels at sites more strongly affected by upwelling.

Oceanographers have long recognized the localized nature of coastal upwelling (Currie 1953, Hart & Currie 1960), the major centers of which are often associated with alongshore variation in topography and coastline orientation (Jury 1985, Kelly 1985, Wolanski & Hamner 1988, Vergara 1993). The main upwelling centers within the region of our study, Punta Curaumilla and Punta Toro, have been previously identified and described in the literature (Silva 1973, Fonseca 1977, Johnson et al. 1980, Fonseca & Farías 1987, Vergara 1991, Bello Mejía 2001), and are clearly visible in thermal AVHRR images, as well as in our *in situ* temperature measurements from onshore sites located at the base of these centers (see records for Matanzas and Quintay). Like at other large upwelling centers (e.g. Andrews & Hutchings 1980, Taunton-Clark 1985), the forcing of equatorward winds was obvious at Matanzas and Quintay, where SST responded almost immediately (less than 1 d) to wind stress. In contrast to the well-documented, positive relationship between cold-upwelled water and pigment concentrations described over large spatial scales off the coasts of Chile and California (e.g. Abbott & Zion 1985, Strub et al. 1991, Van Camp et al. 1991, Thomas 1999, Thomas et al. 2001), at the smaller time- and space-scales of this study, we find a strong negative relationship, with lowest levels of chl *a* associated with cold water. This relationship holds true for time scales similar to or shorter than the time scale of spin-up of phytoplankton blooms. Thus, newly upwelled water has a very low chl *a* content, but water that has been near-surface for a few days is warmer and exhibits higher levels of chl *a*. This relationship is found in both spatial and temporal patterns. Given the advective nature of wind-driven upwelling, with export of surface waters from the nearshore, there is a length scale associated with the bloom time scale ($l = ut$, where ut = advection time) that defines the spatial extent of the cool clear waters that upwell and move away from upwelling centers. For example, by taking t of ca. 3 d, cross-shore u ca. 0.02 m s^{-1}, and alongshore u about one 0.1 m s^{-1}, obtains cross-shore l of about 5 km and alongshore l of about 25 km. The importance of offshore advection during strong upwelling in central Chile was evident in the study by Peterson et al. (1988), who described the offshore displacement of a chlorophyll-rich surface layer by cold, nutrient-rich, chlorophyll-free water during the active, spin-up phase of upwelling in front of Dichato, Chile. Carter (1982) also found that phytoplankton biomass declined to low or undetectable levels under active upwelling conditions. Our observations of persistently low chl *a* levels and cold water at Quintay are characteristic of a spatially restricted upwelling center, similar to those described for the southern Benguela system, where low chl *a* and high nutrient concentrations are consistently associated with newly upwelled water in the euphotic zone (Andrews & Hutchings 1980, Field et al. 1980, Barlow 1982, Hutchings et al. 1983, Olivieri 1983, Brown & Field 1985). Where upwelling is weaker, between upwelling centers, nearshore waters alternate between newly upwelled water and aged upwelled water that has been exported from a nearby upwelling center.

Overall, chl *a* concentrations were greater at Las Cruces, where water was consistently warmer. Such warm water areas between upwelling centers are fairly common along central Chile and other coasts of the world (Kelly 1985, Graham & Largier 1997, Broitman et al. 2001). Considering: (1) the considerably longer response time of Las Cruces temperature to local winds (up to 7 d), (2) that pronounced drops in Las Cruces temperature followed 2 to 3 d after the rapid SST drops observed at the upstream Matanzas upwelling center and (3) that the magnitude and duration of these cooling events were less intense and shorter than those observed at Matanzas, we conclude that upwelling at Las Cruces is rare and that upwelled waters normally intrude here from the Punta Toro upwelling center to the south, exhibiting similarities with the Monterey Bay upwelling shadow described by Graham & Largier (1997). As observed by others, and evident from the thermal satellite imagery (Fig. 1), cold water upwelled in the vicinity of Punta Toro expands north-northwest and quickly (approx. 3 to 4 d) occupies all the continental shelf (Fonseca & Farías 1987, Poulin et al. 2002b, D. Narváez, S. A. Navarrete & J. C. Castilla unpubl. data). The cold-water filament often appears to separate from the coast in the middle of the Bay of San Antonio and warmer water is typi-

cally observed inshore of the displaced cold plume at the northern end of the Bay of Cartagena (Fig. 1, and see Poulin et al. 2002b). A marked thermal front is observed between the warm nearshore waters and the cold upwelled waters streaming past offshore. Indeed, others have suggested that such warm water regions between upwelling centers can be trapped by surrounding cold water filaments (Kelly 1985, Graham & Largier 1997). Since the rapid drops in surface temperature at Las Cruces were never as cold as those observed at Matanzas (or Quintay), we believe these events mark the arrival of aged upwelled water that had upwelled days earlier and then was advected into the region from further upstream.

The sequence of events at Las Cruces thus represent the maturation of high-nutrient water. Most peaks in phytoplankton biomass at Las Cruces corresponded with surface warming, strong stratification of the water column, and reversal or relaxation in southerly winds that followed upwelling (as defined by rapid cooling). During upwelling, the water column was often well-mixed (decreased vertical gradient in SST) and peaks in chl a concentration occurred 1 to 2 d after the onset of surface warming. This time delay is critical, as the injection of nutrient-rich upwelled water has had several days to fertilize a bloom. Moreover, most blooms occurred during periods of relaxation or reversal of strong upwelling-favorable winds, when ageing upwelled water would tend to predominate. Similar dynamics have been described for the development of phytoplankton bloom events along the west coast of South Africa (see review by Shannon & Pillar 1986, Pitcher et al. 1995, 1998, Pitcher & Boyd 1996, Probyn et al. 2000).

Besides the spring-summer blooms at Las Cruces, Quintay, and El Quisco, we also observed regularly occurring autumn blooms at Las Cruces, which presented the highest chl a concentrations and were dominated by dinoflagellates (authors pers. obs.). These localized autumn events appeared as visible and spatially delimited patches of red water. Red-water blooms of similarly high concentrations observed in this study (up to 70 µg l^{-1}) have also been described to occur most frequently during autumn in the Southern Benguela (Horstman 1981, Pitcher & Boyd 1996, Pitcher et al. 1998, Mitchell-Innes et al. 2000). Because dinoflagellates grow well at low irradiances (Richardson et al. 1983) and are highly motile (e.g. Kamykowski & Yamazaki 1997, Pitcher et al. 1998), allowing them to position themselves within the water column, they are often considered to be competitively superior in exploiting both nutrient enrichment and the stratified conditions that typically occur in late summer and autumn along central Chile (Smayda 2000, D. Narváez, S. A. Navarrete & J. C. Castilla unpubl. data).

Nearshore surface waters are subject to alongshore and alternating onshore-offshore advection in response to wind forcing. All dense autumn blooms (and many spring-summer blooms) at Las Cruces occurred during periods of wind reversal and the onshore movement of red water patches was easily visible. These observations suggest that the blooms represent offshore production (relative to *in situ* production onshore) occurring at offshore fronts that are subsequently transported onshore. Similarly, relaxation of upwelling winds often causes landward advection of plankton in the California Current System (Small & Menzies 1981, Roughgarden et al. 1991, Shanks 1995). Moreover, Pitcher et al. (1998) observed dinoflagellate-dominated, frontal blooms during the onshore movement of warmer, maturing-upwelled water following upwelling (i.e. during relaxation).

Several of the densest bloom events occurred when the above described upwelling-relaxation conditions coincided with increased flow rates of the Maipo River. The relative importance of nutrient enrichment via riverine inputs or upwelling to these dense dinoflagellate blooms awaits further study, as does the relative importance of river-induced salinity stratification versus temperature stratification due to surface warming, and the retention properties of the area surrounding Las Cruces. An improved understanding of the behavior of the river plume may also shed light onto the localized nature of the massive red-water bloom events in autumn.

Small-scale alongshore variation in nearshore chl a concentration along open coasts may have important consequences for other biological processes and ecosystem structure, potentially generating strong links between pelagic and nearshore benthic communities. For instance, observed differences in chl a levels could be magnified by benthic filter feeders, which would integrate these differences over longer periods of time. Indeed, observed among-site differences may explain why growth rates of sessile filter feeders (mussels and barnacles), dominant components of rocky intertidal habitats, tend to be lower at upwelling centers than sites downstream from upwelling (G. Finke & S. S. Navarrete unpubl. data). Moreover, if warm water regions downstream from upwelling centers are expected to receive greater particulate food supply and therefore present productivity 'hot spots', these areas may indeed be critical for marine conservation and resource management. Comparative studies among upwelling ecosystems and detailed nearshore oceanographic studies will provide tests of the generality of the proposed mechanisms and promise to shed light onto the context-dependency of regional- and local-scale phenomena.

LITERATURE CITED

Abbott MR, Zion PM (1985) Satellite observations of phytoplankton variability during an upwelling event. Cont Shelf Res 4:661–680

Alheit J, Bernal P (1993) Effects of physical and biological changes on the biomass yield of the Humboldt current ecosystem. In: Sherman K, Alexander LM, Gold B (eds) Large marine ecosystems: stress, mitigation and sustainability. AAAS Press, Washington, DC, p 252–267

Andrews WRH, Hutchings L (1980) Upwelling in the southern Benguela Current. Prog Oceanogr 9:1–88

Arar EJ, Collins GB (1997) Method 445.0. In vitro determination of chlorophyll *a* and pheophytin *a* in marine and freshwater algae by fluorescence. National Exposure Research Laboratory Office of Research and Development, US Environmental Protection Agency, Cincinnati, OH

Archambault P, McKindsey CW, Bourget E (1999) Large-scale shoreline configuration influences phytoplankton concentration and mussel growth. Estuar Coast Shelf Sci 49: 193–208

Arcos DF, Salamanca MA (1984) Distribución de clorofila y condiciones oceanográficas frente a Chile central (Latitudes 32°S–38°S, Febrero 1982). Biol Pesq 13:5–14

Arcos DF, Núñez SP, Castro L, Navarro N (1987) Variabilidad vertical de clorofila a en un área de surgencia frente a Chile central. Invest Pesq (Chile) 34:47–55

Barlow RG (1982) Phytoplankton ecology in the southern Benguela Current. 3. Dynamics of a bloom. J Exp Mar Biol Ecol 63:239–248

Barnes H (1956) *Balanus balanoides* in the Firth Clyde: the development and annual variation in the larval population and the causative factors. J Anim Ecol 25:72–84

Bello Mejía ME (2001) Variabilidad espacial y temporal de los eventos de surgencia costera en la zona central de Chile (32–36°S, 71–75°W), Octubre 1997–Septiembre 1999. Tesis para optar al título de Oceanógrafo, Universidad Católica de Valparaiso

Bertness MD, Gaines SD, Bermudez D, Sanford E (1991) Extreme spatial variation in the growth and reproductive output of the acorn barnacle *Semibalanus balanoides*. Mar Ecol Prog Ser 75:91–100

Broitman BR, Navarrete SA, Smith F, Gaines SD (2001) Geographic variation in southern Pacific intertidal communities. Mar Ecol Prog Ser 224:21–34

Brown PC (1992) Spatial and seasonal variation in chlorophyll distribution in the upper 30 m of the photic zone in the southern Benguela/Agulhas ecosystem. S Afr J Mar Sci 12:515–525

Brown PC, Field JG (1985) Factors limiting phytoplankton

production in a nearshore upwelling area. J Plankton Res 8:55–68

Bustamante RH, Branch GM, Eekhout S, Robertson B and 7 others (1995) Gradients of intertidal primary productivity around the coast of South Africa and their relationship with consumer biomass. Oecologia 102:189–201

Cabrera FN (2003) Estado de las aguas continentes y marinas de Chile. Report 10 of SUMA 21 program, Universidad de Santiago de Chile, Santiago

Carter RA (1982) Plankton biomass and production in a southern Benguela kelp bed system. Mar Ecol Prog Ser 8:9–14

Cole J, McGlade J (1998) Clupeoid population variability, the environment and satellite imagery in coastal upwelling systems. Rev Fish Biol Fish 8:445–471

Currie R (1953) Upwelling in the Benguela Current. Nature 171:497–500

Cury P, Roy C, Faure V (1998) Environmental constraints and pelagic fisheries in upwelling areas: the Peruvian puzzle. S Afr J Mar Sci 19:159–167

Demers S, Therriault JC, Bourget E, Desilets H (1989) Small-scale gradients of phytoplankton productivity in the littoral fringe. Mar Biol 100:393–399

Duggins DO, Simenstad CA, Estes JA (1989) Magnification of secondary production by kelp detritus in coastal marine ecosystems. Science 245:170–173

Field JG, Griffiths CL, Linley EA, Carter RA, Zoutendyk P (1980) Upwelling in a nearshore marine ecosystem and its biological implications. Estuar Coast Mar Sci 11: 133–150

Fonseca T (1977) Proceso de surgencia en Punta Curaumilla con especial referencia a la circulación. Tesis para optar al título de Oceanógrafo, Universidad Católica de Valparaíso

Fonseca TR, Farías M (1987) Estudio del proceso de surgencia en la costa de Chile utilizando percepción remota. Invest Pesq 34:33–46

Graham WM, Largier JL (1997) Upwelling shadows as nearshore retention sites: the example of northern Monterey Bay. Cont Shelf Res 17:509–532

Grebmeier JM, McRoy CP, Feder HM (1988) Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. I. Food supply source and benthic biomass. Mar Ecol Prog Ser 48:57–67

Hart TJ, Currie RI (1960) The Benguela current. Disc Rep 31:123–298

Hentschel BT, Emlet RB (2000) Metamorphosis of barnacle nauplii: effects of food variability and a comparison with amphibian models. Ecology 81:3495–3508

Horstman DA (1981) Reported red-water outbreaks and their effects on fauna of the west and south coasts of South Africa, 1959–1980. Fish Bull (S Afr) 15:71–88

Hutchings L, Nelson G, Horstman DA, Tarr R (1983) Interaction between coastal plankton and sand mussels along the Cape coast, South Africa. In: McLachlan A, Erasmus T (eds) Sandy beaches and ecosystems. W. Junk, The Hague, p 481–500

Huyer A (1983) Coastal upwelling in the California Current System. Prog Oceanogr 12:259–284

Johnson DR, Fonseca T, Sievers H (1980) Upwelling in the Humboldt Coastal Current near Valparaíso, Chile. J Mar Res 38:1–15

Jury MR (1985) Case studies of alongshore variations in wind-driven upwelling in the Southern Benguela Region. In: Shannon LV (ed) South African Ocean colour and upwelling experiment. Galvin and Sales, Cape Town, p 29–46

Kamykowski D, Yamazaki H (1997) A study of metabolism-influenced orientation in the diel migration of marine dinoflagellates. Limnol Oceanogr 42:1189–1202

Kelly KA (1985) The influence of the winds and topography on the sea surface temperature patterns over the northern California slope. J Geophys Res 90:11783–11798

Legendre P, Legendre L (1998) Numerical ecology. Elsevier, Amsterdam

Leichter JJ, Shellenbarger G, Genovese SJ, Wing SR (1998) Breaking internal waves on a Florida (USA) coral reef: a plankton pump at work? Mar Ecol Prog Ser 166:83–97

Longhurst A (1998) Ecological geography of the sea. Academic Press, San Diego

Lubchenco J, Allison GW, Navarrete SA, Menge BA and 6 others (1995) Coastal systems. In: Heywood VH, Watson RT (eds) Global biodiversity assessment. United Nations Environmental Programme, Cambridge, p 370–381

Menge BA (1992) Community regulation: under what conditions are bottom-up factors important on rocky shores? Ecology 73:755–765

Menge BA, Daley BA, Wheeler PA, Dahlhoff E, Sanford E, Strub PT (1997a) Benthic-pelagic links and rocky intertidal communities: bottom-up effects on top-down control? Proc Natl Acad Sci (USA) 94:14530–14535

Menge BA, Daley BA, Wheeler PA, Strub PT (1997b) Rocky intertidal oceanography: an association between community structure and nearshore phytoplankton concentration. Limnol Oceanogr 42:57–66

Mitchell-Innes BA, Pitcher GC, Probyn TA (2000) Productivity of dinoflagellate blooms on the west coast of South Africa, as measured by natural fluorescence. S Afr J Mar Sci 22: 273–284

Morales CE, Blanco JL, Braun M, Reyes H, Silva N (1996) Chlorophyll *a* distribution and associated oceanographic variables in the upwelling region off northern Chile during the winter and spring 1993. Deep-Sea Res 43: 269–289

Morales CE, Blanco JL, Braun M, Silva N (2001) Chlorophyll *a* distribution and mesoscale physical processes in upwelling and adjacent oceanic zones off northern Chile (summer-autumn 1994). J Mar Biol Assoc UK 81:193–206

Olivieri (1983) Colonizations, adaptations and temporal changes in diversity and biomass of a phytoplankton community in upwelled water off the Cape Peninsula, South Africa, in December 1979. S Afr J Mar Sci 1:77–109

Page HM, Hubbard DM (1987) Temporal and spatial patterns of growth in mussels *Mytilus edulis* on an offshore platform: relationships to water temperature and food availability. J Exp Mar Biol Ecol 111:159–179

Parsons TR, Takahashi M, Hargrave B (1984) Biological oceanographic processes. Pergamon Press, Oxford

Peterson W, Arcos D, McManus G, Dam H, Bellantoni D, Johnson T, Teselius P (1988) The nearshore zone during coastal upwelling: daily variability and coupling between primary and secondary production of central Chile. Prog Oceanogr 20:1–40

Pitcher GC, Boyd AJ (1996) Cross-shelf and alongshore dinoflagellate distributions and the mechanisms of red tide formation within the southern Benguela upwelling system. In: Yasumoto T, Oshima Y, Fukuyo Y (eds) Harmful and toxic algal blooms. Intergovernmental Oceanographic Commission of UNESCO, Paris, p 243–246

Pitcher GC, Agenbag JJ, Calder DA, Horstman DA, Jury MR, Taunton-Clark J (1995) Red tides in relation to the meteorology of the southern Benguela upwelling system. In: Lassus P, Arzul G, Erard E, Gentien P, Marcaillou C (eds) Harmful marine algal blooms. Technique et Documentation. Levoisier, Paris, p 657–662

Pitcher GC, Boyd AJ, Horstman DA, Mitchell-Innes BA (1998) Subsurface dinoflagellate populations, frontal blooms and the formation of red tide in the southern Benguela upwelling system. Mar Ecol Prog Ser 172:253–264

Poulin E, Palma AT, Leiva G, Hernández E, Martínez P, Navarrete SA, Castilla JC (2002a) Temporal and spatial variation in the distribution of epineustonic competent larvae of *Concholepas concholepas* (Gastropoda: Muricidae) in the central coast of Chile. Mar Ecol Prog Ser 229: 95–104

Poulin E, Palma AT, Leiva G, Narváez D, Pacheco R, Navarrete SA, Castilla JC (2002b) Avoiding offshore transport of competent larvae during upwelling events: the case of the gastropod *Concholepas concholepas* in central Chile. Limnol Oceanogr 47:1248–1255

Probyn TA, Pitcher GC, Monteiro PMS, Boyd AJ, Nelson G (2000) Physical processes contribution to harmful algal blooms in Saldanha Bay, South Africa. S Afr J Mar Sci 22: 285–297

Ricciardi A, Bourget E (1999) Global patterns of macroinvertebrate biomass in marine intertidal communities. Mar Ecol Prog Ser 185:21–35

Richardson K, Beardall J, Raven JA (1983) Adaptation of unicellular algae to irradiance: an analysis of strategies. New Phytol 93:157–191

Roughgarden J, Pennington JT, Stoner D, Alexander S, Miller K (1991) Collisions of upwelling fronts with the intertidal zone, the cause of recruitment pulses in the barnacle populations of central California. Acta Oecol 12:35–51

Roy C, Cury P, Kifani S (1992) Pelagic fish recruitment success and reproductive strategy in upwelling areas: environmental compromises. S Afr J Mar Sci 12:135–146

Sanford E, Menge BA (2000) Spatial and temporal variation in barnacle growth in a coastal upwelling system. Mar Ecol Prog Ser 209:143–157

Shanks AL (1995) Mechanisms of cross-shelf dispersal of larva invertebrates and fish. In: McEdward LR (ed) Ecology of marine invertebrate larvae. CRC Press, Boca Raton, FL, p 323–368

Shannon LV, Pillar SC (1986) The Benguela ecosystem, Part III. Plankton. Oceanogr Mar Biol Annu Rev 24:65–170

Shannon LV, Walters NM, Mostert SA (1985) Satellite observations of surface temperature and near-surface chlorophyll in the Southern Benguela region. In: Shannon LV (ed) South African Ocean Colour and Upwelling Experiment. Galvin and Sales, Cape Town, p 183–210

Sievers HA, Silva N (1979) Variación temporal de las condiciones oceanográficas frente a Punta Curaumilla, Valparaíso, Chile (Mayo 1974–Abril 1975). Invest Mar 7:2–30

Silva N (1973) Variaciones estacionales de temperatura, salinidad y contenido de oxígeno en la zona costera de Valparaíso. Invest Mar 4(3):89–112

Smaal AC, Van Stralen M (1990) Average annual growth and condition of mussels as a function of food source. Hydrobiologia 195:179–188

Small LF, Menzies DW (1981) Patterns of primary production and biomass in a coastal upwelling region. Deep-Sea Res 28:123–149

Smayda TJ (2000) Ecological features of harmful algal blooms in coastal upwelling ecosystems. S Afr J Mar Sci 22: 219–253

Strub PT, Kosro PM, Huyer A, (1991) The nature of cold filaments in the California Current System. J Geophys Res 96:14743–14768

Strub PT, Mesías JM, Montecinos-Banderet V, Rutllant J, Salinas-Marchant S (1998) Coastal ocean circulation off western South America. In: Robinson AR, Brink KH (eds) The sea, Vol 11. J Wiley & Sons, New York, p 273–313

Taunton-Clark J (1985) The formation, growth and decay of upwelling tongues in response to the mesoscale wind field during summer. In: Shannon LV (ed) South African Ocean Colour and Upwelling Experiment. Galvin and Sales, Cape Town, p 47–62

Thomas AC (1999) Seasonal distribution of satellite-measured phytoplankton pigment concentration along the Chilean coast. J Geophys Res 104:25877–25890

Thomas AC, Huang F, Strub PT, James C (1994) Comparison of the seasonal and interannual variability of phytoplankton pigment concentrations in the Peru and California Current Systems. J Geophys Res 99:7355–7370

Thomas AC, Blanco JL, Carr ME, Strub PT, Osses J (2001) Satellite-measured chlorophyll and temperature variability off northern Chile during the 1996-98 La Niña and El Niño. J Geophys Res 106:899–915

Van Camp L, Nykjaer L, Mittelstaedt E, Schlittenhardt P (1991) Upwelling and boundary circulation off northwest Africa as depicted by infrared and visible satellite observations. Prog Oceanogr 26:357–402

Vergara J (1991) Un modelo numérico bi-dimensional continuamente estratificado para el estudio de la surgencia costera. Invest Pesq 36:39–50

Vergara J (1993) Effects of coastline geometry on wind-induced upwelling in the Chilean coast: a numerical study. Preprints Fourth Int Conf Southern Hemisphere Meteorology and Oceanography, Hobart

Walker G, Yule AB, Noitt JA (1987) Structure and function in balanomorph larvae. In: Southward AJ (ed) Barnacle biology. AA Balkema, Rotterdam, p 307–328

Wolanski E, Hamner WM (1988) Topographically controlled fronts in the ocean and their biological influence. Science 245:177–181

Wroblewski JS (1977) A model of phytoplankton plume formation during variable Oregon upwelling. J Mar Res 35: 357–394