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River plume dynamic influences transport of barnacle larvae in the inner shelf off central Chile

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Off central Chile, around 33.5°S, the freshwater discharge of the River Maipo generates a small- to intermediate-size plume, which moves up to the north driven by the daily sea breeze and with localized effects on a costal zone of about 10–15 km. The influence of this river plume motion on abundance patterns of larval barnacles was studied in a ~12 km long transect, including 2–3 stations inside the river plume, one station on the visible turbidity front, and two stations outside the plume. Shipboard campaigns were conducted in January (summer), August (winter), and October 2003 (spring). On each occasion, conductivity–temperature–depth casts, bottom track acoustic Doppler current profiler current measurements, size-fractioned chlorophyll concentration, and stratified plankton sampling were conducted. A significantly higher abundance of barnacle nauplii was found at the river plume front than at the plume or outside the plume. Abundance was highest in the upper 10 m of the water column, where most nauplius larvae were found. The river plume appeared as a surface layer of less saline water moving north of the river mouth, with a buoyant frontal structure progressing at speeds of 5 to 20 cm s^{-1}. Although no peak in chlorophyll was observed at the buoyant front, the highest concentration of effective prey size for feeding nauplii (chlorophyl-*a* <5 and 5–20 μm) was generally associated with less saline plume waters. Thus, the accumulation of barnacle larvae at the front may facilitate foraging, potentially increasing larval growth and energy reserves. Our results suggest that the spatial structure and temporal dynamics of river plumes should be considered by benthic ecologists as transport mechanisms that potentially affect larval delivery and settlement of barnacles on rocky shores.

INTRODUCTION

Understanding the dynamics of coastal marine ecosystems requires knowledge of physical oceanographic conditions and their interplay with the biological components. For benthic invertebrates that produce planktonic larvae in the inner-shelf region (i.e. from the shoreline to ~5–10 km offshore), variation in the delivery of larvae to benthic habitats is a key and sometimes limiting process determining recruitment rates, population structure and gene flow among populations (Thorson, 1950). In this regard, a mechanistic and predictive understanding of variability in recruitment of benthic marine invertebrates could be achieved if these studies are coupled with the study of physical processes at appropriate spatial scales. Several mechanisms of larval transport have been identified, including onshore/offshore upwelling dynamics (Narváez et al., 2006), internal tidal bores (Pineda, 1991; Vargas et al., 2004) and freshwater discharge and river plumes (Thiébaut, 1996; Vargas et al., 2003). How these different mechanisms affect the transport of larvae might depend on the spatial distribution of larval stages in coastal waters.

Buoyant coastal discharges produce plumes and induce coastal currents, which are common features in continental and inner shelf habitats. Furthermore, these structures may have important ecological effects on phytoplankton, larval distribution, larval survival, and both cross-shore and along-shore transport of different larval stages (Kingsford & Suthers, 1994). Along the Chilean coast, the effects of river plumes and estuarine circulation on the horizontal and vertical distribution of larval stages have been scarcely studied. A few studies conducted on rivers producing large fresh water discharges (>100 m s^{-1}), such as the Itata river and the Valdivia estuary, have shown that these systems serve as sites of enhanced biological production as well as nursery areas for different marine organisms (Quiñones & Montes, 2001; Vargas et al., 2003).

Off central Chile, around 33.5°S, the freshwater discharge of the River Maipo generates a small- to intermediate-size plume (Piñones et al., 2005), with localized effects on a costal zone of about 10–15 km (Wieters et al., 2003; Narváez et al., 2004; Piñones et al., 2005). Since frontal circulation may act as a barrier to larvae dispersal, river plumes may enhance the accumulation of larvae at the front edge and facilitate transport to recruitment sites (Eggleston, 1998). Here, we evaluate whether invertebrate larvae found in surface waters near the River Maipo mouth, could be entrained by the

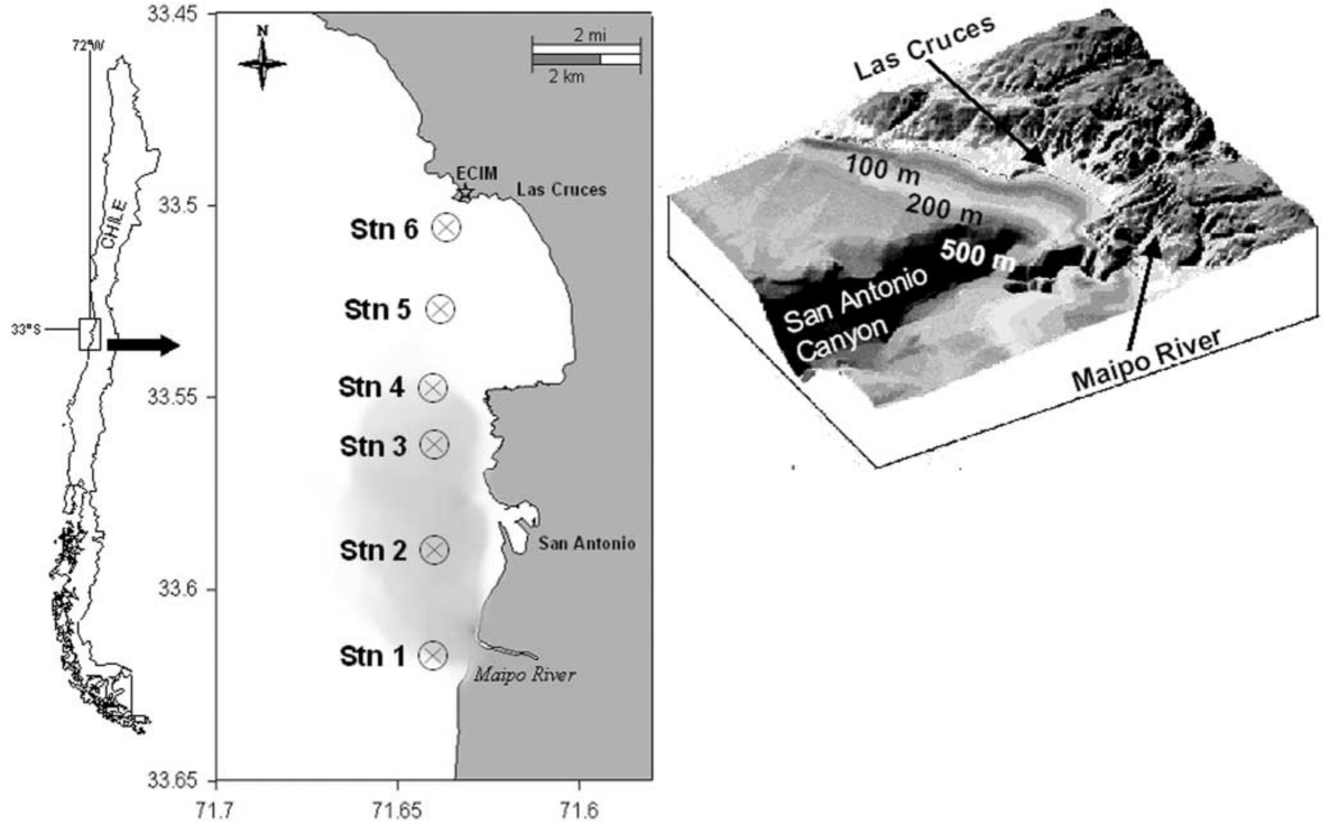

Figure 1. Map of the study area showing the River Maipo and the propagation of the plume parallel to shore. Locations of shipboard sampling stations (⊗) and rocky shore plankton sampling/conductivity–temperature–depth-mooring (◇) are indicated. The bathymetry of the study area, including the presence of the San Antonio Submarine Canyon is also shown.

buoyant plume and eventually delivered to rocky intertidal habitats. Since barnacle larvae can become sporadically one of the most dominant members of the larval invertebrate pool in the plankton (Lang, 1979; Vargas et al., 2006), we have chosen them as a study model to test the effect of river plume motion on larval distribution and transport along the shore. Barnacle larvae are distinguished by two stages, the nauplii stage, in which the larvae appears to be triangular, with two small spiky appendages. A few days later the nauplii stage gives way to the cypris larval stage, in which the larva resembles small seeds, and is unable to take in or digest food. Over the next few days the cypris swims in search of a suitable place to attach, and often chooses a rocky shore area that is already inhabited (Lang, 1979). In this respect, a number of recent studies have examined settlement and recruitment of intertidal barnacles in the area (Vargas et al., 2004; Lagos et al., 2005). The most abundant barnacle species inhabiting the intertidal zone along central Chile corresponds to the chthamaloids *Jehlius cirratus*, and *Notochthamalus scabrosus*, and the balanoid *Notobalanus flosculus* (Lagos et al., 2005). The work presented here describes the distribution of chthamaloid and balanoid barnacle larvae and their food supply in relation to the River Maipo plume and presents a preliminary evaluation of the importance of this process as an accumulation and transport mechanism for larvae of chthamalid and balanid barnacle species.

MATERIALS AND METHODS

Study area

The present study was conducted in central Chile between the locality of Las Cruces (33°30′S 71.40′W), and the mouth of the River Maipo (33°61′S 71.66′W) (Figure 1). The River Maipo enters the coastal ocean over a relatively narrow continental shelf, forming a plume of variable spatial structure (Piñones et al., 2005). The presence of the submarine canyon of San Antonio associated with the River Maipo (*Atlas hidrográfico de Chile*, Servico Hidrográfico de la Armada (SHOA), 1997),

Table 1. *Two way analysis of variance for barnacle nauplii abundance collected at three different positions with respect to the river plume (Factor 'Position': plume, front and ocean), and strata at two depths (Factor 'Depth': surface and sub-surface). The three different seasonal campaigns were considered as a random block (Factor: 'Date').*

Source of variation	df	MS	F	*P*
Date	2	2.231	–	–
Position	2	1.255	16.39	0.0007
Depth	1	0.629	8.21	0.0168
Depth×position	2	0.341	4.44	0.0416
Residual	10	0.077		

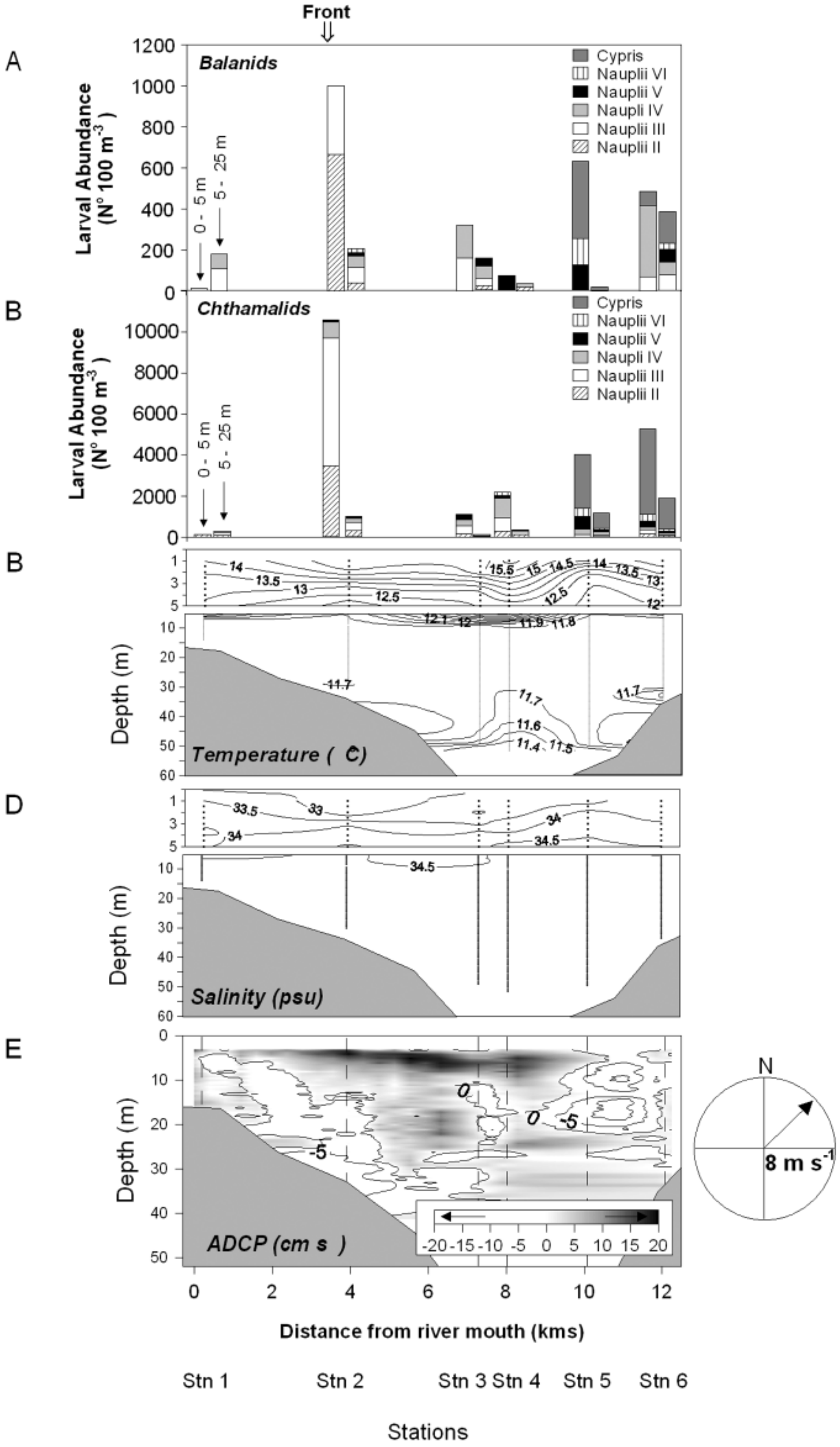

Figure 2. Summer (January 2003) campaign. Abundance (no. 100 m^{-3}) of different larval stages for: (A) balanid and (B) chthamalid barnacles, together with vertical sections of (C) temperature (°C); (D) salinity (psu); and (E) alongshore (v) current speed (cm s^{-1}). In the speed current panel, the grey scale is used for positive northward flows to Las Cruces, whereas labelled contours are used for negative southward flows to the river mouth. Position of the buoyant front is marked on the top panel. Dominant wind velocity and direction during each sampling are indicated at bottom right. Winds are shown in meteorological convention.

produces a significant break in the continental shelf (200 m) (Figure 1). Tidal ranges in the area are small (~1.5 m) and tidal currents are weak (<10 cm s^{-1}). The Coastal Marine Research Station (ECIM) is located at Las Cruces (Figure 1), where larval biology and settlement of intertidal barnacles has been recently investigated (e.g. Venegas et al., 2000; Lagos et al., 2005; Vargas et al., 2004, 2006). Furthermore, there is a general knowledge about the hydrodynamics of this area (e.g. Narváez et al., 2003, 2006; Wieters et al., 2003; Vargas et al., 2004; Piñones et al., 2005). The dynamics of the river plume are highly seasonal. During winter the plume remains close to

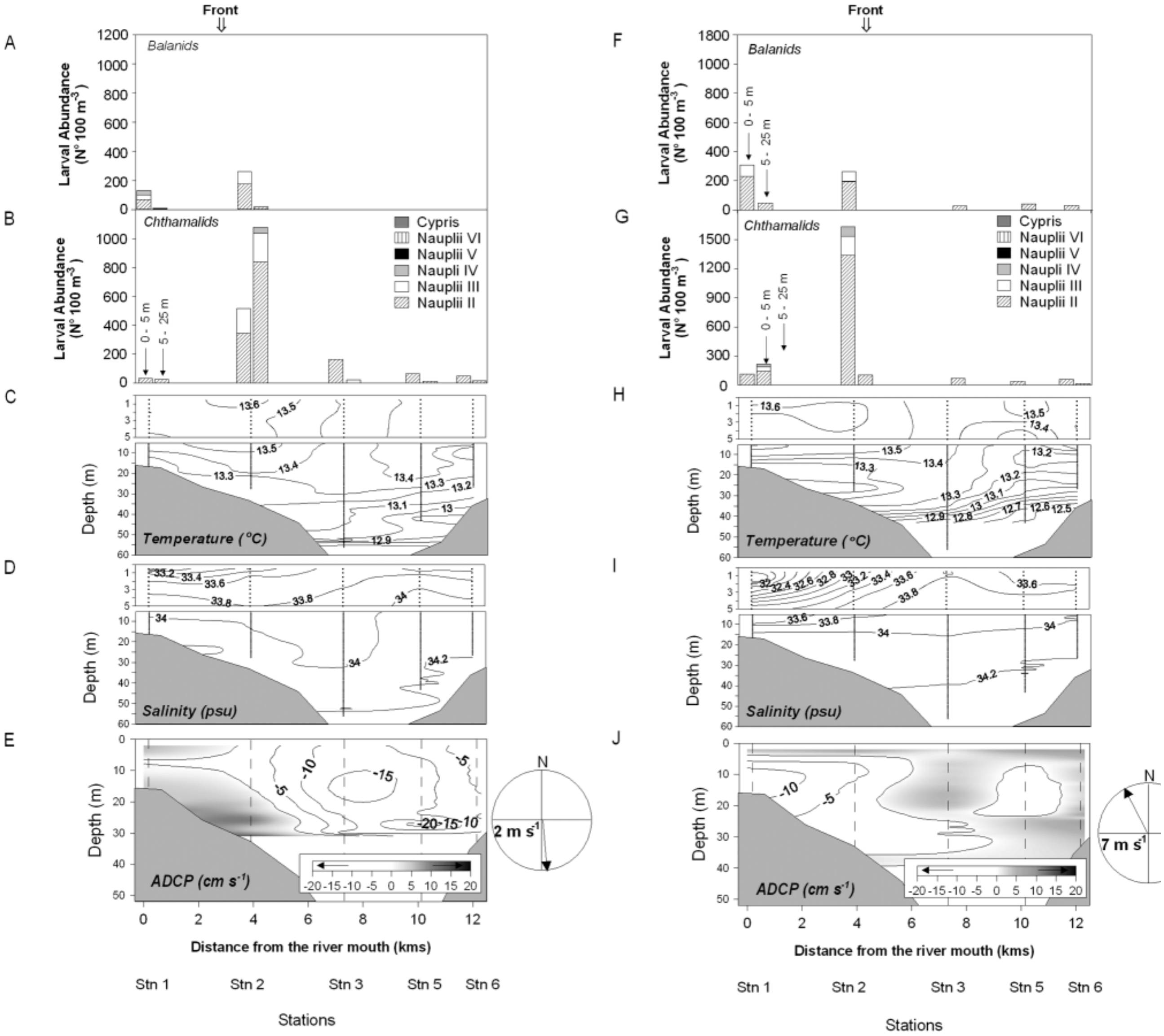

Figure 3. Winter (August 2003) campaign. Morning (left panels) and afternoon (right panels). Abundance (no. 100 m^{-3}) of different larval stages for: (A&F) balanid and (B&G) chthamalid barnacles, together with vertical sections of (C&H) temperature (°C); (D&I) salinity (psu); and (E&J) alongshore (v) current speed (cm s^{-1}). Legends as Figure 2.

the river mouth while in spring and summer it is daily advected northward to the Pelancura and Las Cruces area (Figure 1), as a response to the diurnal wind cycle (Piñones et al., 2005).

Sampling design

Sampling was conducted along a ~12 km long transect, between the River Maipo mouth and Las Cruces (Figure 1). Along the transect, we sampled 2–3 stations inside the river plume, one station on the visible turbidity front, and two stations outside the plume. The stations were sampled twice (morning and afternoon) during the three oceanographic campaigns: (1) summer, January 2003; (2) winter, August 2003; and (3) spring, November 2003. Due to weather conditions, the afternoon sampling of the summer campaign was too incomplete to be included in the analysis, except for chlorophyll samples. On each sampling station, conductivity, temperature and depth (CTD) profiles were obtained with a calibrated CTD Seabird-19. Current speed and direction were recorded with a 614.4-kHz broadband acoustic Doppler current profiler (ADCP, RD Instruments), mounted on a 2 m-long catamaran, which was towed from the starboard side of the vessel. The ADCP recorded velocity profiles that consisted of 1.4-s pings averaged about 1 min ensembles. Vertical resolution was 1 m, with the first bin located at 2 m below the surface, which was able to capture the flow within the buoyant plume. Since the maximum axis of current variability was well represented by the alongshore component (v), we present our results referred only to that component. The ADCP sampling track was dictated by the location of CTD and plankton sampling stations, which in turn sought to document the upstream migration of the plume. Local wind speed and direction were recorded every 20 min with a Campbell Metereological Station located at ECIM, Las Cruces. Information on the effect of sea breeze and wind condition on river plume motion was already reported in Piñones et al.

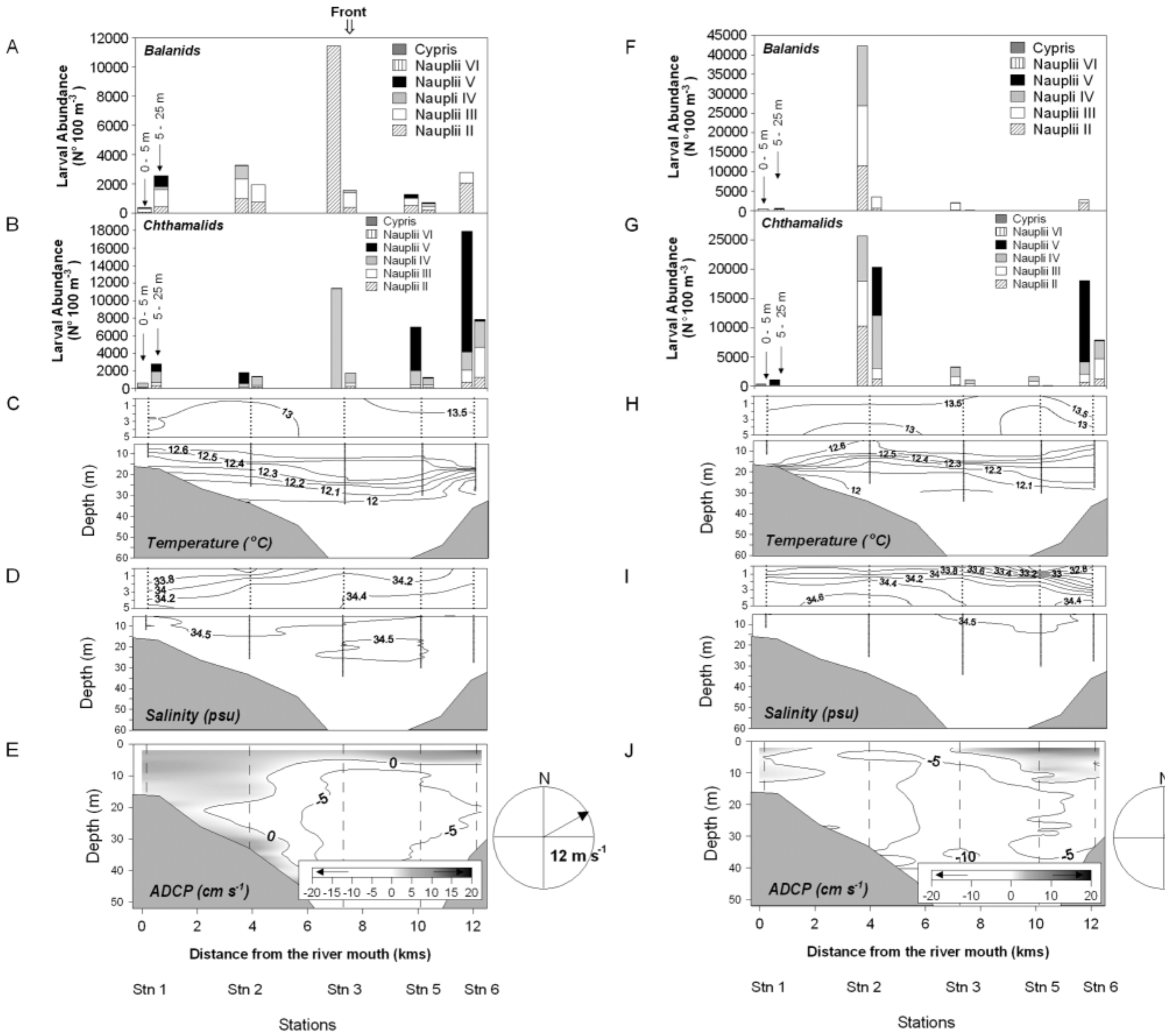

Figure 4. Spring (November 2003) campaign. Morning (left panels) and afternoon (right panels). Abundance (no. 100 m^{-3}) of different larval stages for: (A&F) balanid and (B&G) chthamalid barnacles, together with vertical sections of (C&H) temperature (°C); (D&I) salinity (psu); and (E&J) alongshore (v) current speed (cm s^{-1}). Legends as Figure 2.

(2005). Therefore, in the present study we are not going to include a detailed analysis about this mechanism of river plume motion, and we will only show a vector plot with the dominant wind speed and direction during each sampling occasion.

Vertical plankton net hauls to estimate barnacle larval abundance were carried out at each of two depth strata using a 200-μm mesh WP-2 net, equipped with closing devices and a calibrated Hydro-Bios Kiel flowmeter. Since our goal was to evaluate the influence of the surface structure on larval distribution, the chosen depth intervals were 0–5 m and 5–25 m. All plankton samples were preserved immediately after collection with 5% formaldehyde solution in seawater. In the laboratory the whole sample was analysed. Naupliar stages and cyprids were counted and separated into chthamalid and balanid larvae. Larval barnacles were staged in six classes according to Lang (1979) and Venegas et al. (2000): Nauplius (N) II, III, IV, V, VI and Cypris.

Distribution of larval food

Since previous studies in the same region have demonstrated that both chthamalid and balanid nauplii feed mostly on pico- and nanophytoplankton (Vargas et al., 2006), we measured size-fractioned chlorophyll concentration in order to establish the fraction that was actually available as food supply from the total phytoplankton standing stock. Water samples for size-fractioned chlorophyll-a (Chl-a), were collected at 1, 5, 10 and 25 m depths with a 5 litre GO-FLO Niskin bottle (General Oceanic Inc.). Phytoplankton size fractionations were carried out in three consecutive steps: (1) for the mid-size fraction (5.0–23 μm), seawater was pre-filtered using 23-μm Nitex mesh and collected on a 5.0-μm polycarbonate Millipore filter; (2) for the pico-nanoplankton fraction (0.45–5.0 μm) seawater was pre-filtered using a 5.0-μm Millipore and collected on a 0.45-μm GF/F filter; and (3) for the whole phytoplankton community, 100 ml of

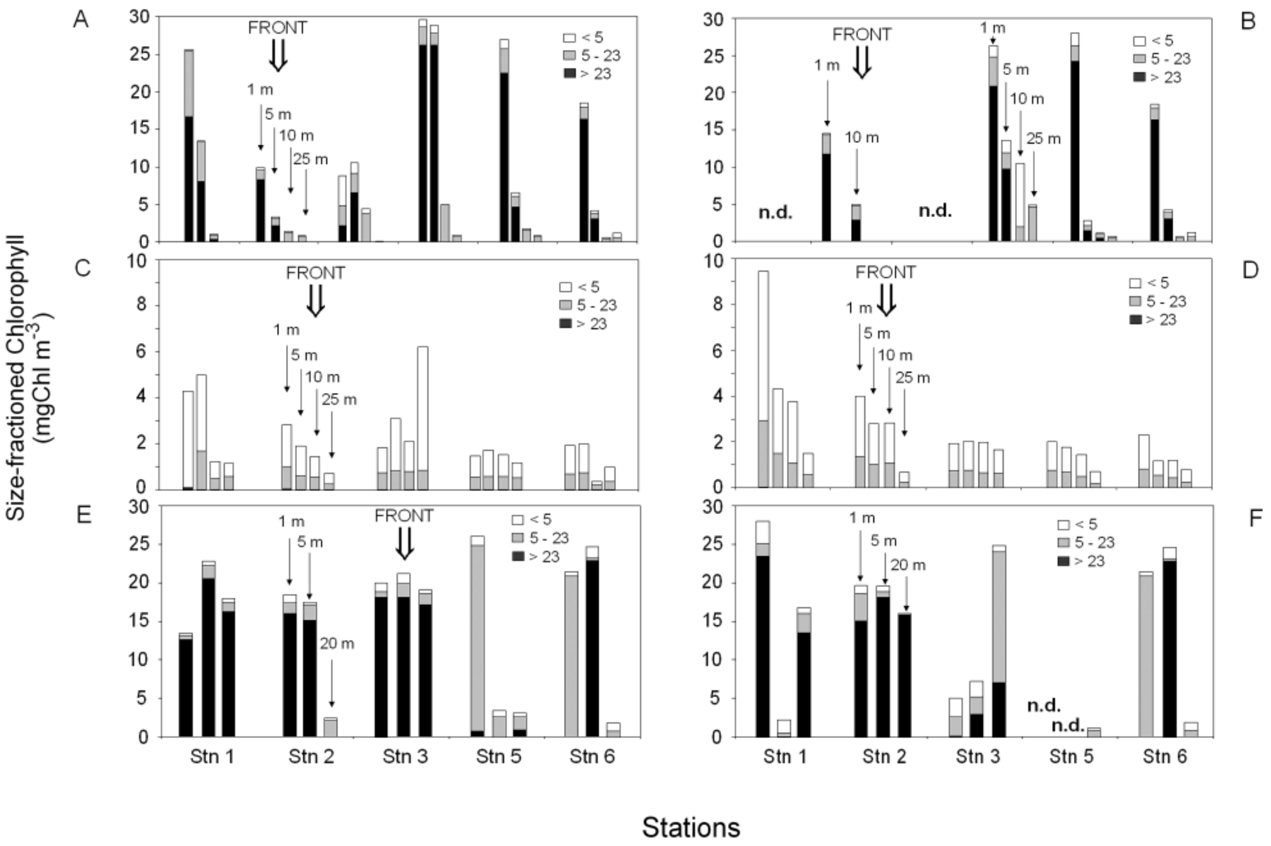

Figure 5. Morning (left panel) and afternoon (right panel) size-fractioned concentrations of chlorophyll-*a* (mg Chl-*a* m^{-3}) along the sampled transect during the (A&B) summer; (C&D), winter; and (E&F) spring campaigns. Position of the buoyant front is marked at the top panel.

seawater were filtered with a 0.45-μm GF/F filter. The micro-phytoplankton fraction (>23 μm) was obtained by subtracting the concentration estimated in steps 1 and 2 from the concentration estimated in step 3. Chlorophyll-*a* and phaeopigment concentrations were measured with a TD 700 Turner Fluorometer, before and after acidification of the sample obtained from a 24 h extraction in 90% acetone (Strickland & Parsons, 1972).

We conducted a two way analysis of variance (ANOVA) to compare the abundance of nauplii between depths ['surface (0–5 m)' and 'sub-surface (5–25 m')] and position with respect to the river plume (Table 1). Three different positions were considered by averaging all sampling stations inside the river plume, the stations sampled at the buoyant front and the stations outside the plume to the north. The morning and afternoon legs were also averaged before analysis, except for the summer campaign, when complete data were available only for the morning leg. The three different campaigns were considered as a random block in the analysis and data were log-transformed to improve normality and variance homogeneity. Cyprids were not included in this analysis.

RESULTS

Hydrographic features and larval distribution along the river plume

Results obtained from the campaigns conducted at different times of the year showed the variability in the position and dynamics of the River Maipo plume, as well as temporal changes in the horizontal and vertical distribution of larvae. Stratified plankton samples showed higher abundance of chthamalid than balanid larvae (maximum of 10,000 and 1000 ind 100 m^{-3}, respectively, Figure 2A,B), and higher abundance of both in the upper 5 m depth. Peak abundance of nauplius stages was found at Station 2, where the buoyant front was located at the time of sampling. Larval stages were not homogeneously distributed along the transect; early stages (NII and NIII) were concentrated at the plume front, whereas older stages (NIV–V and cyprids) were found outside the plume, near Las Cruces (Figure 2A,B). Patterns of horizontal distribution were similar for surface and subsurface waters. During the summer campaign, vertical sections of temperature showed high stratification of the upper 10 m of the water column, ranging from 11.8 to 15.5°C, without a clear horizontal gradient (Figure 2C). Less saline waters (33 psu) were observed at the surface (<3 m depth) in association with the river mouth (Stations 1&2), and increased to the north towards Las Cruces (Figure 2D). On this campaign, the edge of the river plume was visible as a turbidity front between Stations 3 and 4. However, salinity values indicated that the buoyant front caused by the freshwater input was found between Stations 2 and 3. Hereafter, we use the area of stronger horizontal salinity gradient as an indication of the position of the river plume front (Figure 2D). The alongshore component of the ADCP currents (v)

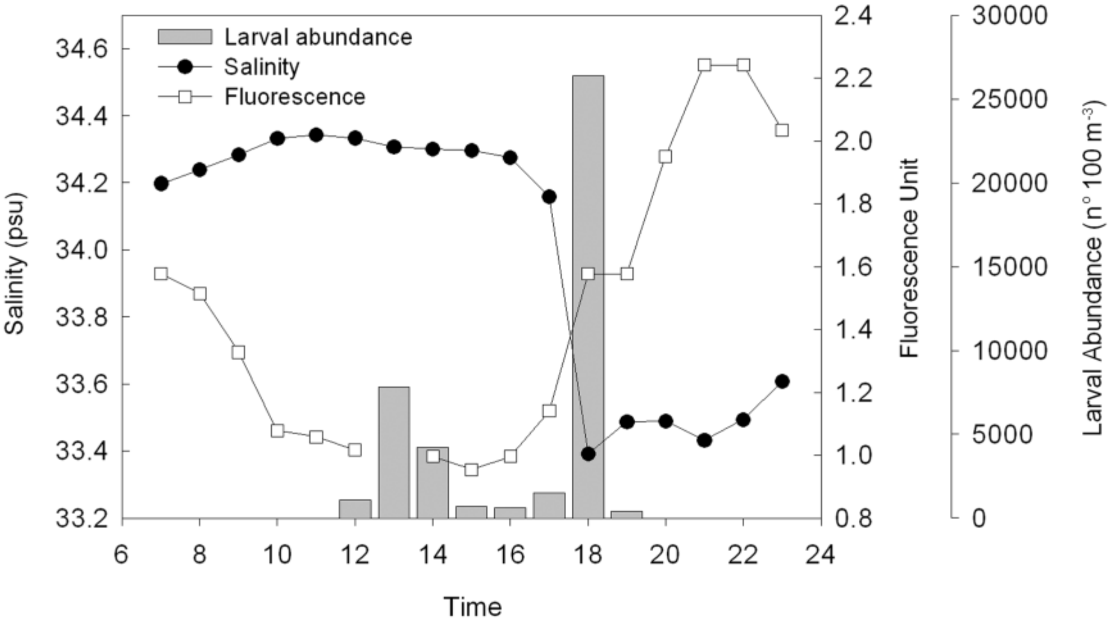

Figure 6. Hourly record of salinity (psu), fluorescence and larval abundance (no. 100 m^{-3}) at a rocky intertidal site (ECIM) in Las Cruces (see Figure 1) during the summer campaign in January 2003.

showed that the river plume was a shallow wedge of buoyant water of around 5–6 m depth that moved northward at about 15 to 20 cm s^{-1} (Figure 2E) towards the Las Cruces area (ECIM), and probably driven by the southerly winds (Figure 1). Below 10 m depth we observed weak currents flowing south in some sections of the transect (Figure 2E).

During the winter campaign in August 2003 (Figure 3), sampling was conducted in two legs: in the morning (0800–1200) and afternoon (1300–1800) hours. In both legs, chthamalids were more abundant than balanids, and overall larval abundance was much lower than observed in summer (Figure 3). No clear thermal stratification was observed, which is typical of winter conditions in coastal areas. The river plume was clearly visible as a layer of less salty waters (~32 psu) near the river mouth in the morning and reaching Station 2 in the afternoon (Figure 3D&I).

Alongshore currents measured during the morning leg showed a surface layer of water moving north of the river mouth to the vicinity of Station 2, where the buoyant front was located (Figure 3E). An opposite, vertically homogeneous flow of 10–15 cm s^{-1} was observed between Las Cruces and the buoyant front. The river plume remained within 4 km of the river mouth in the morning hours (Figure 3D). Then, through the afternoon the surface current progressed slightly to the north along the entire transect (Figure 3J), the buoyant front moved around 1.5–2 km north and it was evidenced by the shoaling of isohalines still close to the river mouth (Figure 3I). The maximum abundance of early chthamalid larvae (1100 to 1600 ind 100 m^{-3}) was associated with the buoyant frontal structure, which was progressing at ~7 cm s^{-1} towards the north direction (Figure 3A,B and 3F,G for Leg I and II, respectively). Current velocity in the river plume (7 cm s^{-1}=252 m h^{-1}; Figure 3E), correspond well with the buoyant front displacement of about 1.5 km between morning and afternoon sampling.

An influence of the river plume on the nearshore environment was also observed, though less evident, during the spring campaign conducted in November 2003. During the morning leg, less saline waters were observed close to the river mouth and out to Station 3, ~7 km north of the river mouth (Figure 4D). At this time, the surface layer moved northward at about 5 cm s^{-1} (Figure 4E). Abundance of barnacle larvae observed during the spring campaign was higher than in summer, and especially in winter months. High abundance of early balanid larvae (NII and NIII) was observed at Station 3, where the buoyant front was located (Figure 4A). On the other hand, high concentrations of late chthamalid larvae (NIV and NV) were found at Station 6, near Las Cruces (Figure 4B). Later in the day, less saline waters were observed at the north end of the transect off Las Cruces (Figure 4I). However, when the southerly wind relaxed (from 12 to 8 m s^{-1}), the plume motions reversed, resulting in an opposite flow between Station 1 and Station 2 (Figure 4J). Coincidentally, high concentrations of chthamalid and balanid larvae (20,000 to 250,000 ind 100 m^{-3}) were observed near Station 2 (Figure 4F,G).

Our results show that naupliar stages of both cthamalids and balanids were mostly concentrated at surface waters during all different campaigns. The pattern of larval distribution, or position with respect to the river plume, differed according to sampling depth (significant 'position×depth' interaction in ANOVA, Table 1). Significantly higher larval concentrations were observed at the front stations than at the plume or outside the plume, and the pattern was clearer at the surface, where most nauplii were found (Table 1, and a posteriori Tukey comparisons for each depth level). We did not conduct a similar statistical analysis for larval cyprids because they were not available during all campaigns. However, results from the summer campaign suggest that they were also more abundant at surface waters off Las Cruces area.

Food availability associated with river plume

As is typical in nearshore waters off central Chile (e.g. Wieters et al., 2003, Vargas et al., 2006), large differences in total Chl-*a* concentration ($\sim$1 up to 30 mg Chl-*a* m^{-3}) were recorded among the campaigns conducted in winter and those in spring and summer months (Figure 5). We did not find consistent differences in Chl-*a* concentration between morning and afternoon hours throughout the sampled transect. During summer, high Chl-*a* concentration was associated with surface waters of the river plume (Station 1) as well as outside the plume (Stations 4 & 5), with values ranging from 20 to 25 mg Chl-*a* m^{-3} (Figure 5A,B). No clear peak in Chl-*a* was observed at the buoyant plume front, and most of the Chl-*a* was found in the microplankton ($>23\,\mu$m) fraction. Pico- and nanophytoplankton, the most important size fraction for nauplii feeding (Vargas et al., 2006), were most concentrated at Station 1, in the river plume (Figure 5). Contrastingly, the microplankton fraction was absent in the winter campaign, and all the Chl-*a* was in the pico- and nanophytoplankton fraction (0.5 to 6 mg Chl-*a* m^{-3}; Figure 5C,D). In spring, high Chl-*a* concentration was again observed, with values up to $\sim$30 mg Chl-*a* m^{-3} and dominance of the large $>23\,\mu$m microphytoplankton fraction (Figure 5E,F), corresponding to large chain-forming diatoms *Skeletonema costatum* and *Eucampia cornuta* (C.A. Vargas, personal observation). Total Chl-*a* concentration was relatively homogeneous along the transect; however, the highest concentrations of pico- nano-phytoplankton were observed in the northern area outside the plume, at Stations 5 and 6. Thus, small sized phytoplankton were common in the river plume waters, but no peak in Chl-*a* was associated with the buoyant front.

DISCUSSION

Our results, though very limited in the temporal scale, are suggestive of the effect that the river plume may have on barnacle larval distribution, and its potential as a transport mechanism for larvae concentrated at the front. The less saline water of the river plume tended to form a frontal buoyancy structure, which lagged behind the visually conspicuous turbidity front. Influence of the plume was appreciable only within the upper $\sim$5 m of water, and its dynamics is not clearly affected by tidal currents (Piñones et al., 2005). According to the theory of plume advection (Yankosvsky & Chapman, 1997), the River Maipo plume can be classified as a 'pure surface-advected plume'. The strong southerly winds, typical of this coastal area in spring and summer months (Narváez et al., 2004), move the plume from near the river mouth to the area of Las Cruces, $\sim$12 km further north (Piñones et al., 2005).

During our study larval barnacles were not homogeneously distributed in the water column. Both nauplius and cyprids were predominantly found in surface waters. Maximum numbers of barnacle larvae at the surface were observed at the plume front, especially in spring and summer months. Differences in zooplankton abundance near river plumes have been previously found over small scales (10s metres, e.g. Kingsford & Suthers, 1994) and mesoscales (1 to 100 km, Vargas et al., 2003). Abundance of planktonic organisms (mostly fish larvae) in these studies was also highest at the buoyancy fronts. In a similar study, Kingsford & Suthers (1994) showed that barnacle larvae were commonly associated with river plume waters and fronts in eastern Australia. Thus, aggregation of invertebrate larvae around these fronts, even a small front such as the River Maipo, seems to be a general feature in coastal areas. Several studies have shown that fronts do not act as static boundaries between water masses and could therefore act as a barrier to small organisms. For instance, in the Bay of Seine, Thiébaut (1996) found that plume fronts may act as a physical barrier and promote the accumulation of polychaete larvae, which are then transported along a coastal band. Govoni (1993) found that fish larvae in the River Mississippi plume may be transported over the shelf by advective stirring.

Since the buoyant front can concentrate larvae, and the front itself is displaced to the north by the sea breeze, larvae entrained by the front can be transported several kilometres up the coast. When the front makes contact with an appropriate habitat, competent larvae may attach to the substratum, thus enhancing settlement at local scales. Indeed, during spring and early summer, when sea breezes advect the surface layer upstream (Piñones et al., 2005), the buoyant plume and its turbid frontal edge was almost daily observed northward at Las Cruces. Preliminary results obtained at the Coastal Marine Research Station (ECIM) in Las Cruces support this proposition. Hourly time series of salinity and fluorescence obtained with a CTD moored at 1.5 m below the lowest low tide, and hourly plankton samples obtained with a bilge pump directly from the water adjacent to the intertidal rocky platform showed a striking pattern (Figure 6). When the buoyant front collided with the shore at ECIM, surface salinity dropped abruptly, and a sharp peak in abundance of chthamalid larvae (up to 250 ind m^{-3}) was observed, followed by an increase in fluorescence (Figure 6). Most larvae collected at the site corresponded to late nauplii (NV and NVI; C.A. Vargas, personal observation). A previous study (Lagos et al., 2005) has shown that Pelancura and ECIM (Figure 1) are indeed sites of high barnacle recruitment, even for a region of generally high recruitment rates. Further larval sampling in relation to the arrival of the river plume, and high frequency settlement data are needed to fully evaluate the importance of this mechanism for barnacle settlement at Las Cruces.

Buoyancy fronts are usually sites of enhanced phytoplankton production. In this kind of physical structure, maximum Chl-*a* concentrations tend to be found below the surface, within the front and associated with the pycnocline (Franks & Anderson, 1992). However, that was not the case in our study, as the peak of total Chl-*a* was weakly associated with less saline plume water and outside the front rather than at the front itself. This is consistent with results reported by Franks & Anderson (1992), in which a bloom of *Alexandrium tamarense* was associated with the buoyant front, but the Chl-*a* peak, generated by diatoms of the genus *Eucampia,* occurred offshore.

Nevertheless, the highest concentration of effective prey size for nauplii (<5 and 5–20 μm pico- and nanophytoplankton, Vargas et al., 2006) was generally associated with less saline plume waters. Therefore, the accumulation of barnacle larvae at the front may facilitate foraging, potentially increasing larval growth and energy reserves.

In conclusion, in the present study we argue that the aggregation of larval stages is one of the most important roles that river plume fronts may play in larval dynamics at nearshore areas. Their consequences for larval transport will depend on the dynamic of the river plume and local forcing factors. In the case of the River Maipo, the plume might enhance larval delivery to the area of Las Cruces. Numerous small rivers, like the Maipo, interrupt the Chilean coastline and most coasts around the world. The study of the spatial structure and temporal dynamics of their plumes should be considered by benthic ecologists as transport mechanisms that potentially may affect larval delivery and settlement on rocky shores.

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