# **CAGU** PUBLICATIONS

### Journal of Geophysical Research: Oceans

### **RESEARCH ARTICLE**

10.1002/2017JC013111

#### **Key Points:**

- Front-eddy interaction in the early stages of intrathermocline eddy formation in the slope area off Concepción
- Intense submesoscale variability in nutrients and phytoplankton across the coastal upwelling and coastal transition zones
- A mixture of coastal and oceanic diatom species in the area of fronteddy interaction imply both offshore and onshore advection

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#### Citation:

Morales, C. E., Anabalón, V., Bento, J. P., Hormazabal, S., Cornejo, M., Correa-Ramírez, M. A., & Silva, N. (2017). Fronteddy influence on water column properties, phytoplankton community structure, and cross-shelf exchange of diatom taxa in the shelf-slope area off concepción (~36–37°S). *Journal of Geophysical Research: Oceans, 122*, 8944–8965. https://doi.org/10.1002/ 2017JC013111

Received 19 MAY 2017 Accepted 13 OCT 2017 Accepted article online 16 OCT 2017 Published online 21 NOV 2017

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### Front-Eddy Influence on Water Column Properties, Phytoplankton Community Structure, and Cross-Shelf Exchange of Diatom Taxa in the Shelf-Slope Area off Concepción (~36–37°S)

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Abstract In eastern boundary current systems (EBCSs), submesoscale to mesocale variability contributes to cross-shore exchanges of water properties, nutrients, and plankton. Data from a short-term summer survey and satellite time series (January-February 2014) were used to characterize submesoscale variability in oceanographic conditions and phytoplankton distribution across the coastal upwelling and coastal transition zones north of Punta Lavapié, and to explore cross-shelf exchanges of diatom taxa. A thermohaline front (FRN-1) flanked by a mesoscale anticyclonic intrathermocline eddy (ITE-1), or mode-water eddy, persisted during the time series and the survey was undertaken during a wind relaxation event. At the survey time, ITE-1 contributed to an onshore intrusion of warm oceanic waters (southern section) and an offshore advection of cold coastal waters (northern section), with the latter forming a cold, high chlorophyll-a filament. In situ phytoplankton and diatom biomasses were highest at the surface in FRN-1 and at the subsurface in ITE-1, whereas values in the coastal zone were lower and dominated by smaller cells. Diatom species typical of the coastal zone and species dominant in oceanic waters were both found in the FRN-1 and ITE-1 interaction area, suggesting that this mixture was the result of both offshore and onshore advection. Overall, front-eddy interactions in EBCSs could enhance cross-shelf exchanges of coastal and oceanic plankton, as well as sustain phytoplankton growth in the slope area through localized upward injections of nutrients in the frontal zone, combined with ITE-induced advection and vertical nutrient inputs to the surface layer.

**Plain Language Summary** The oceans exhibit high submesoscale (a few km in the horizontal axis) variability in physical processes, which influence plakton distribution and ecosystem dynamics. In this study, two common features in the oceans, fronts and eddies, were analyzed in terms of the submesoscale variability generated by their interaction in a region of coastal upwelling. We found that front-eddy interactions contribute to the transport of phytoplankton between the coast and the oceanic zone. This finding is surprising since, until now, it was thought that eddies in coastal upwelling areas contributed to a mostly offshore transport of plankton but not the other way around. This observation is relevant to understand potential changes in submesoscale dynamics under a climate change scenario and to predict the response of phytoplankton species to these changes.

### 1. Introduction

Eastern boundary current systems (EBCSs) are regions dominated, in the coastal zone, by wind-driven upwelling processes and, in the coastal transition zone (CTZ), by submesoscale and mesoscale activity associated with highly dynamic features, including eddies, filaments, fronts, jets, and meanders (Barth et al., 2005; Brink & Cowles, 1991; Hormazabal et al., 2004; Hösen et al., 2016; Pelegrí et al., 2005). These features

are closely related in the spatiotemporal context since their generation is usually linked to the period of upwelling-favorable winds, increased wind stress curl, and/or topographic/orographic effects (Batten, 1997; Castelao et al., 2006; Correa-Ramirez et al., 2012; Wang et al., 2015). Although each feature generates spatial



**Figure 1.** (a) Region of study off central-southern Chile, for which satellite time series (January–February, 2014) were analyzed and within which the PHYTO-FRONT survey (black dots: sampling stations) was undertaken (3–6 February 2014), and fixed-point time series data of (b) daily WS and (c) SST. The main current patterns in surface waters (CCC: equatorward Chile Coastal Current; CPC: equatorward Chile-Peru Current) and over the slope (PCUC: poleward Peru-Chile Undercurrent) are also shown. Data in Figure 1b represent a single position (blank square between St. 17 and 18 in Figure 1a) for WS values (black line: 6 hourly data; grey line, data filtered with a low-pass Godin-type filer). Data in Figure 1c represent two positions (coastal: cross in a circle symbol, shelf (St. 13): dashed line, and slope (St. 16): dashed-dotted line) for SST values. The location of a reference coastal upwelling time series, St. 18 (see section 3.5), is marked with a star. In Figures 1b and 1c, the grey bar denotes the survey time; W1–W8 (bottom axis) represent the weeks covered by the satellite time series and used in the calculation of weekly means of WS and WSC (Figure 2).

heterogeneity in the distribution of water properties, the interactions between them or the submesoscale dynamics within a mesoscale feature can further enhance such variability (Brannigan, 2016; Callbeck et al., 2017; D'Asaro et al., 2011; Johnston et al., 2011; Kaneko et al., 2013). Mesoscale turbulence is more energetic than submesoscale turbulence, but the dynamics of the latter is most strongly associated with sharp density gradients, ageostrophic circulation, and more intense, localized vertical exchanges in the water column (Capet et al., 2008; Klein & Lapeyre, 2009; Lévy et al., 2012; Mahadevan, 2016). Greater attention has been given in recent times to submesoscale and mesoscale variability in the oceans, and EBCSs, under the premise that they have a higher relevance to understanding phytoplankton community structure and functioning, organic matter export from the surface layer, and biogeochemical cycling, as well as in the prediction of the response of marine ecosystems to climate change (Lévy et al., 2012; Mahadevan, 2016; McGillicuddy, 2016).

Several submesoscale and mesoscale mechanisms of physicalbiological interaction have been proposed for ocean systems. Some relate to transport of passive particles (e.g., stirring, trapping, and/or subduction processes) whereas others modulate biological rates in association with variations in nutrient and/or light availability (e.g., eddy pumping, eddy-wind interaction, eddy impacts on mixed-layer depth, re-stratification, and/or frontogenesis) (Mahadevan, 2016; McGillicuddy, 2016). In EBCSs, mesoscale eddies have been involved in the offshore advection of nutrient-rich waters and of plankton from the coastal upwelling zone, implying that phytoplankton biomass/production in the latter is negatively influenced (Chenillat et al., 2015; Gruber et al., 2011; Hernández-Carrasco et al., 2014; Nagai et al., 2015; Rossi et al., 2008). At the same time, different types of eddies and fronts, or the interactions between them, can contribute to local enhancements in phytoplankton biomass/primary production in the CTZ of EBCSs through processes which lead to nutrient injections toward the upper layer (Chenillat et al., 2015; Everett et al., 2015; Hyun et al., 2009; Kim et al., 2011; Krause et al., 2015). However, the observation of cross-isopycnal submesoscale intrusions of temperature, salinity, and chlorophyll-a (Chl-a) below the mixed layer between the coastal and CTZ waters off Peru suggests that vertical fluxes take place in both directions, with enhancements of phytoplankton growth in areas of localized upwelling of subsurface nutrient-rich waters and decreases in surface phytoplankton biomass due to localized downwelling (Pietri et al., 2013).

In the eastern South Pacific, the Humboldt Current System (HCS) displays relatively high submesoscale and mesoscale activity (Chaigneau et al., 2011; Hormazabal et al., 2013; Pietri et al., 2014; Thomsen et al., 2016). Elevated values of eddy-kinetic energy (EKE), associated with increased mesoscale activity, have been described for the northern (Peru) and southern (central-southern Chile) HCS (Hormazabal et al., 2004; Vergara et al., 2016). In the strongly seasonal coastal upwelling region of the southern HCS ( $\sim$ 33–40°S; Figure 1a), the equatorward Chile Coastal Current (CCC) dominates the surface flows, whereas the

poleward Peru-Chile Undercurrent (PCUC) dominates the subsurface (100–400 m depth); the equatorward Chile-Peru surface Current (CPC) is located further offshore (Fuenzalida et al., 2008; Llanillo et al., 2012; Strub et al., 1998; Vergara et al., 2016). Eddies, fronts, jets, and filaments are regularly generated in this region, especially during the spring-summer upwelling season (Aguirre et al., 2012; Correa-Ramirez et al., 2012; Hormazabal et al., 2013; Letelier et al., 2009; Morales et al., 2007, 2012; Wang et al., 2015). PCUC variability is highly relevant in the generation of mesoscale intrathermocline eddies (ITEs), also known as mode-water eddies, (Colas et al., 2012; Combes et al., 2015; Hormazabal et al., 2013; Johnson & McTaggart, 2010; Thomsen et al., 2016). Off Punta Lavapié ( $\sim$ 37°S), an abrupt change in coastline orientation plays a main role in creating current instabilities and meanders (Atkinson et al., 2002; Mesias et al., 2001). There, the CCC, which flows close to the coast south of this area, deviates offshore as a coastal jet, the position of which is denoted by values of zero in wind stress curl (Aguirre et al., 2012; Letelier et al., 2009; Mesias et al., 2009).

In the southern HCS, fronts can act as barriers to cross-shelf exchanges of phytoplankton (Morales et al., 2012), with different functional groups dominating in the coastal and oceanic zones around a front (Menschel et al., 2016). Eddies, however, facilitate such exchanges, at least in their early life-stages (Correa-Ramirez et al., 2007; Morales et al., 2012). During the upwelling season, when eddy formation and eddy movement close to the shelf-break area take place, intensive but transient front-eddy interactions are expected to occur and, thereby, generate a potential for submesoscale variability in the structure of phytoplankton communities. The influence of such interactions on water column characteristics and phytoplankton community structure remains mostly unknown. In the present study, front-eddy influence on water column structure and phytoplankton community structure was analyzed and evaluated in terms of its impact on cross-shelf exchanges of diatom taxa in the coastal upwelling and CTZ off Concepción ( $\sim$ 36–37°S).

### 2. Methods

### 2.1. Model-Derived Wind and Satellite Sea Surface Temperature, Sea Level, and Chl-a Time Series Data (January–February 2014)

Wind data (6 hourly) for the area between  $34.5-38.5^{\circ}S$  and  $72-76^{\circ}W$  (Figure 1a) were obtained from the Climate Forecasting System (CFS-v2) (Saha et al., 2011) and were used to calculate wind stress (WS), computed with the bulk aerodynamic formulation. The drag coefficient ( $C_D$ ) was calculated using the state-of-the-art Coupled Ocean Atmosphere Response Experiment (COARE) bulk algorithm COARE-v3.0 (Kara et al., 2005; Kochanski et al., 2006). The CFS-v2 parameters used in the calculations were air temperature at 2 m height, sea surface temperature, eastward (northward) component of wind velocity at 10 m height, atmospheric pressure reduced to mean sea level, and dew-point temperature. All CFS-v2 data were remapped onto a common regular grid with 0.2 of horizontal resolution using an interpolation algorithm (Akima, 1970).

Wind stress curl (WSC) was calculated using WS data from COARE algorithms. WS and WSC magnitudes were computed at each 6 h intervals, daily, and 7 d averaged to compare with sea surface temperature (SST). High-resolution (~1 km) daily (13:00 P.M.) observations of SST were obtained from the Multi-scale Ultra-high Resolution (MUR) SST (merged product from MODIS, 118 AMSR-E, and AVHRR; http://mur.jpl. nasa.gov/). The coefficient of correlation (Pearson) between MUR-SST data and SST measured at the sampling stations was significant (r = 0.901; p < 0.01), with MUR-SST values being ~1.4°C higher. In addition, high-resolution (1 km) daily sequences of Chl-a MODIS-A satellite data were obtained from Ocean Color Web (https://oceancolor.gsfc.nasa.gov) and gaps caused by cloud cover were filled with a time-space interpolation using the DINEOF method (Alvera-Azcárate et al., 2007; Correa-Ramirez et al., 2012).

### 2.2. Eddy Tracking

Satellite altimetry data from the SSalto/Duacs AVISO 2014 altimetry product (Duacs/AVISO, 2014) were used in the detection of eddies in the survey area during the January–February 2014 period. The SSalto/Duacs altimetry product 2014 accurately represents the circulation features in coastal regions of EBCSs where mesoscale activity is dominant (Capet et al., 2014). The eddy-tracking method used in this study was the "py-eddytracker" approach (http://imedea.uib-csic.es/users/emason/py-eddytracker) (Mason et al., 2014), based on previously described procedures for the detection of closed contours of sea level anomaly (Chelton et al., 2011; Kurian et al., 2011; Penven et al., 2005).

To perform the eddy tracking algorithm, daily sea level anomaly (SLA) fields were spatially high-pass filtered by removing a smooth field obtained from a Gaussian filter with a zonal (meridional) major (minor) radius of 20° (10°). SLA contours were computed at 1 cm intervals for levels -100 to 100 cm and closed contours were searched from 100 (-100) cm downward (upward) to identify cyclones (anticyclones). To select the effective perimeter of an eddy, an identified closed contour must meet some criteria related to amplitude (1–150 cm), radius (0.35–4.46°), and number of local extremes (limited to 1). In order to detect the birth-time of the eddy analyzed in this study, we skipped the shape test, which is usually performed to filter out highly irregular closed contours.

### 2.3. Field Survey

A short-term survey (3–6 February 2014), the PHYTO-FRONT cruise, was undertaken and consisted of two transects perpendicular to the coast in the area north of P. Lavapié, between 36 and 37°S (Figure 1a). At each station, continuous hydrographic profiles (0–300 m depth) were obtained from a CTD (Sea Bird SBE-19 plus) equipped with dissolved oxygen (DO) and Wetstar fluorescence sensors. Also, in vivo spectral fluorescence data (0–60 m depth) were obtained from a submersible spectrofluorometer, the FluoroProbe (http:// www.bbe-moldaenke.de/en/products/chlorophyll/details/fluoroprobe.html). The continuous Chl-a data distribution from this profiling instrument were compared with those of discrete Chl-a data distribution detailed below.

Discrete water samples (8 L Niskin bottles) were obtained from the upper layer (<100 m depth) for analyzing nutrients, total and size fractionated Chl-a, and plankton; these analyses were completed a few weeks (Chl-a) or 2–3 months (nutrients and plankton) after the cruise. Nutrient samples were stored at  $-20^{\circ}$ C in 60 mL aseptic, high-density polyethylene flasks, and the analyses (Autoanalyzer) followed standard protocols (Atlas et al., 1971). Chl-a samples were filtered (GF/F filters) for both total and size fractions (<20 and <3  $\mu$ m); filters were then frozen and stored in the dark until analysis by fluorometry, using standard protocols (Anabalón et al., 2007, 2016).

Plankton samples were collected for analyses of composition, abundance, and biomass of pico, nano, and microplanktonic organisms. For picoplankton (<3  $\mu$ m), samples were taken in cryogenic vials (2 mL), immediately fixed with glutaraldehyde (0.1% final conc.), and stored in liquid-N until further analysis using a flow-cytometer (Becton-Dickinson FACScalibur with a 488 nm lon-Argon Laser) following standard protocols (Marie et al., 2000). Autotrophic picoplankton (*Prochlorococcus, Synechococcus*, and picoeukaryotes) were identified and counted based on the analysis of multiple bivariate scatter plots of size-scattered light, and red and orange fluorescence (runs at medium or high speed until 10,000 events were acquired; flow rate was determined volumetrically every 10 runs). A suspension of yellow-green, 1  $\mu$ m, latex beads (10<sup>5</sup> mL beads mL<sup>-1</sup>) was added as an internal standard (Polyscience Inc.).

Nanoplankton samples were collected (50 mL centrifuge tubes) and immediately fixed with a buffer of para-formaldehyde (1% final conc.), after which they were stored in cold (5°C) and darkness until further processing in the laboratory. Samples were stained with a mixture of DAPI (4,6-diamidino-2-phenylindole) and Proflavine (3–6 diaminoacridine hemisulfate) at a final concentration of 5  $\mu$ g mL<sup>-1</sup> (Verity & Sieracki, 1993). After this, samples were vacuum-filtered onto black polycarbonate membrane filters (0.6  $\mu$ m pore), immediately transferred to glass slides—immersion oil—glass cover slips, and stored in cold (–20°C) and darkness until subsequent analysis using an epifluorescence microscope (Nikon TI-U; 1,000x; UV, blue, and green filters). Counting included at least 100 cells of the most dominant groups in each sample (e.g., nano-flagellates, nanodinoflagellates, nanodiatoms, and nanociliates).

Microplankton samples were collected (250 mL plastic flasks) and immediately one sample was fixed with Lugol (2% final conc.) and another one with a buffer of paraformaldehyde (1% final conc.), after which they were maintained in conditions similar to the nanoplankton samples. Taxa composition and abundance of microplanktonic diatoms and autotrophic/mixotrophic dinoflagellates (evaluated as described in (Anabalón et al., 2014, 2016)) were analyzed using an inverted microscope (Nikon Eclipse TI-U, 1000x) and sedimentation chambers (100 mL), following the Utermöhl method (Anabalón et al., 2016; González et al., 2007). Ciliates were not included since their contribution has previously been found to be comparatively small in the coastal area off Concepción (González et al., 2007). At least 100 cells of the most common taxa (species level for the most part) in each sample were counted whenever possible, using a quarter or all of the fields of view (~5,000) depending on total cell abundance in each chamber. In the identification of diatom species

among the dominant genera, samples fixed with paraformaldehyde were acidified as to leave only the valves and analyze their morphological characteristics (Hasle, 1978). The relative abundance of valves corresponding to a species was used to recalculate the abundance of each species in the different samples. Taxonomic identification was based on existing descriptions/citations for the region of study (Rivera, 1968, 1985; Rivera & Valdebenito, 1979).

Nano and microphytoplankton carbon biomass (C-biomass) was obtained from cell volume estimates derived from geometric models, including a correction for Lugol-fixed samples (see Anabalón et al., 2016). At least 20 cells of each type/taxa were randomly selected and measured using a micrometer grid as a reference, and median values were obtained. Specific carbon/biovolume conversion factors for flagellates (Børsheim & Bratbak, 1987), diatoms (Strathman, 1967), and thecate-athecate dinoflagellates (Edler, 1979; Menden-Deuer & Lessard, 2000) were used; for mixotrophic dinoflagellates, 30% of the total cell biomass was allocated to the autotrophic fraction (Stoecker et al., 1996). Conversion factors for picoplankton C-biomass were 171 fg C cell<sup>-1</sup> for *Synechococcus* (Grob et al., 2007) and 2.0 pg C cell<sup>-1</sup> for picoeukaryotes (Zubkov et al., 2000).

### 3. Results and Discussion

### 3.1. Wind-Forcing and Satellite SST Short-Term Variability (January–February 2014)

Mean daily alongshore WS during the time series (Figure 1b), calculated for a fixed point close to the middle of the northern transect (Figure 1a), indicated the occurrence of two relatively strong coastal upwelling events (>0.2 N m<sup>-2</sup> for >5 d) during the first half of January (2–15) and another during the third week in February (19–23). A nonupwelling or wind relaxation event (<0.1 N m<sup>-2</sup>), lasting of ~1 week, was detected in the third week of January (16–23), followed by a moderate upwelling event during the fourth week (24–31) and, then, by a wind relaxation event during the first week in February (1–9), when the field work was undertaken (W5–W6). During the same period, mean daily MUR-SST distribution (Figure 1c), calculated for three fixed points (Figure 1a), denoted the presence of cold events in the coastal area (<14°C) for most of the first two weeks in January and during the last week in February, with an increase in SST during the time in between (>14.5°C and up to 17°C). In the shelf-break area (St. 16), SST fluctuated between 14 and 17°C and, for the most part, followed coastal SST variability. MUR-SST and WS displayed an inverse pattern, with cooling (warming) during active upwelling (relaxation) events, although increase or decrease in both variables were occasionally observed, especially at the most coastal station.

Regionally (34.5–38.5°S, from the coast to 76°W), the spatial distribution of mean weekly WS (Figure 2) reflected the occurrence of a strong upwelling event (>0.3 N m<sup>-2</sup>) along the entire coastal zone north of 38°S during the first week in January (W1). Moderate upwelling events were found during W2, W4, W6, and W7, with a focus of higher intensity in the southern section (36–38°S), whereas mean conditions during W3, W5, and W8 represented wind relaxation events. The mean weekly WSC spatial distribution (Figure 2) indicated strongly negative values (cyclonic; Ekman pumping) along the coastal zone and strongly positive values (anticyclonic) in the offshore zone during W1. After W1, a similar WSC distribution pattern was mostly restricted to the southern section during W2, W4, W6, and W7, whereas it was weakly cyclonic/neutral during W3, W5, and W8. Overall, the survey was preceded by moderate WS and WSC values (W4) and the conditions during it represented a transition from wind relaxation (W5) to moderate WS and weak WSC values (W6). Such high-frequency wind variability has already been described for the southern HCS in summer (Sobarzo et al., 2007), when quasi-weekly, southerly, coastal low-level jet events alternate with periods of weak southerly or even northerly flows in connection with the passage of coastal lows (Garreaud & Muñoz, 2005).

The spatiotemporal distribution of daily MUR-SST in the region of study (Figure 3, only for the initial dates of each week in Figure 1) was highly variable during January–February 2014. Colder waters (13.5–16°C) were found near the coast most of the time, except on 22 January when the most prolonged wind relaxation event (7 days) in the time series took place. Cold waters occasionally extended further offshore (8 and 15 January), in association with coastal upwelling events (W1–W2). For the most part, warmer waters (>16–18.5°C) were found offshore and separated from coastal waters by a SST gradient or thermal front (FRN-1). FRN-1 persisted throughout the time series, except under nonupwelling activity (16–23 January). It displayed a fairly irregular spatial pattern and it migrated further offshore (>100 km from the coast) during



**Figure 2.** Weekly means (W1–W8) of wind stress direction and magnitude (arrows; N m<sup>-2</sup>) and wind stress curl magnitude (color bar;  $10^{-7}$  N m<sup>-3</sup>) data series (January–February, 2014) for the region of study. The images on weeks W5 and W6 cover the survey period (see Figure 1c).



**Figure 3.** Daily satellite MUR-SST (color and thick lines) and altimetry (thin lines) data series (January–February, 2014) for the region of study. Selected images are shown for the first date in each week (W1–W8; left and central plots: a–h) and for the dates just previous to the cruise, during it, and at its end (right plots: i–k). The red dot represents the central position of ITE-1 and the red and grey lines its initial and final trajectories; the value in the center of ITE-1 is the eddy-kinetic energy (EKE, m<sup>2</sup> s<sup>-2</sup>).

strong coastal upwelling (8 and 15 January). Previous results in the same region have shown the satellite SST distribution changing from  $<14^{\circ}$ C near the coast to  $>17^{\circ}$ C in offshore zones in summer, separated by a frontal zone located, on average, at  $\sim$ 50–80 km from the coast (Letelier et al., 2009).

SST synoptic variability in the EBCS region off central Chile has been shown to be modulated by strengthening-relaxation cycles of southerly winds in the coastal zone and by daily heat fluxes in the adjacent CTZ (Aguirre et al., 2014). SST distribution in EBCSs has been found to reflect both Ekman-induced cross-shore temperature gradients and mesoscale activity associated with the upwelling dynamics (Desboilles et al., 2014). In addition, short-term and other intraseasonal SST variability could also be influenced by remote forcing (Dewitte et al., 2011; Goubanova et al., 2013; Hormazabal et al., 2001; Renault et al., 2009).

### 3.2. Eddy Activity in the PHYTO-FRONT Survey Area

Satellite altimetry data (Figure 3, overlaid on MUR-SST distribution) revealed, among other things, the presence of an anticyclonic mesoscale eddy located just north of P. Lavapié. This eddy appeared close to the shelf-break area at the very end of December 2013 and was detectable throughout January–February 2014, moving progressively westward. Previous satellite and field studies in this region have shown that anticyclonic eddies are recurrently generated in summer (Hormazabal et al., 2013; Letelier et al., 2009; Morales et al., 2012). The detected eddy was relatively weak (EKE < 0.10 m<sup>2</sup> s<sup>-2</sup>) during the first weeks in January when it moved in a mostly south-west direction. During the most prolonged wind relaxation event, the eddy movement changed to a mostly north-west direction, which was maintained until the end of the times series. In this eddy, EKE values increased from moderate during the first two weeks in February (~0.20–0.35 m<sup>2</sup> s<sup>-2</sup>) to strong during the second half (~0.40–0.60 m<sup>2</sup> s<sup>-2</sup>). At the end of January, the influence of the detected eddy on SST submesoscale variability was clear, generating cross-shore transport and mixing of cold coastal waters with offshore warmer CTZ waters.

During the short-term survey (3–6 February 2014), satellite altimetry and MUR-SST data indicated that the two sampling transects were distributed in a transitional area including coastal, frontal, and eddy waters (Figure 3, panels to the right). Also, a progressive intrusion of warm waters toward the coast took place from 2 to 6 February, consistent with the fact that the survey was carried out during a wind relaxation event preceded by moderate upwelling (Figures 2d and 2e). During the survey, the most offshore sampling stations in the southern transect were located in the south-eastern border of the anticyclonic eddy (4–5 February), but were closer to the eddy center in the northern transect (5–6 February). At this time, the eddy center was located  $\sim$ 200 km from the coast, had an approximate diameter of  $\sim$ 160–180 km, and was moving at  $\sim$ 1.9 km d<sup>-1</sup>. In the southern section, the south-eastern boundary of the anticyclonic eddy helped strengthen the thermal gradient of FRN-1 through the advection of warmer waters toward the coast, whereas in the northern section, the offshore.

Interactions between fronts and eddies in EBCSs are probably restricted to the first stages of eddy development in the shelf-break area in the cases when the formation of an eddy is linked to upwelling jet-front instabilities. However, such instabilities could also arise from jet interaction with eddies generated from previous instabilities, in which case the interactions are expected to developed later and last as long as the eddy remains in the area of the jet influence (Harrison & Siegel, 2014). Because of the transient nature of such interactions, their effects on water column properties have remained elusive. Results from this study suggested that the front-eddy interaction started after the prolonged wind relaxation event in January and lasted for  $\sim$ 1 month, and that it contributed to localized exchanges of water properties between coastal and CTZ waters.

### 3.3. Water Column Structure During the PHYTO-FRONT Survey

The spatial distribution of oceanographic variables (0–300 m depth) along the two transects indicated intense submesoscale and mesoscale activity (Figure 4). Temperature, salinity, and DO displayed a characteristic trend of shallower isolines toward the coast, with colder (<16°C) and higher salinity (>34.2) waters distributed in the upper layer (<50 m depth) of the coastal zone versus warmer and fresher waters offshore in the CTZ. A clear signature of the PCUC in the slope area was denoted by a downward doming of isotherms and a high salinity–low DO core (Hormazabal et al., 2013; Letelier et al., 2009), with values characteristic of the Equatorial Subsurface waters (ESSW) (Llanillo et al., 2012; Silva et al., 2009; Strub et al., 1998). On both transects, FRN-1 was distinguishable by a SST gradient (0.12 and 0.22°C km<sup>-1</sup> in the northern and



**Figure 4.** Spatial distribution of oceanographic variables (0–300 m depth) during the PHYTO-FRONT survey. (a and b) Temperature ( $^{\circ}C$ ), (c and d) salinity, and (e and f) DO (mL L<sup>-1</sup>) in the (left) northern and (right) southern transects. Isopycnals are also included in all the graphs (white-dashed lines). The 17 $^{\circ}C$  isotherm (a and b) bold black line) represents the SST value associated with the area of maximum horizontal thermal gradient during the survey (white inverted triangles in the top axes).

southern transects, respectively) but also by a surface salinity gradient (0.02 and  $-0.06 \text{ km}^{-1}$  in the northern and southern transects, respectively), with the 16–17°C isotherms separating coastal and offshore CTZ waters. This front was located at  $\sim$ 70–100 km from the coast during the survey (Sts. 6–7, and 16–18, respectively). The thermal gradient was distributed in the upper  $\sim$ 50 m depth whereas the salinity gradient reached  $\sim$ 75 m depth. In the same region, thermal fronts with similar gradients ( $\sim$ 0.1–0.25°C km<sup>-1</sup>) and vertical distribution (0–50 m depth) have been previously described over the shelf-slope area in the summertime (Letelier et al., 2009).

In the offshore area, the isotherms below 100 m depth (Figures 4a and 4b) displayed strong vertical oscillations (amplitude of  $\sim$ 100 m in the northern section and  $\sim$ 50 m in the southern section), together with the presence of isolated subsurface (150–250 m depth) high salinity cores (>34.55) and steep up-lifting of the

34.2 isohaline (Figures 4c and 4d); submesoscale changes in subsurface DO were also observed (Figures 4e and 4f). At the most offshore stations, these oscillations coincided with the area where the satellite data indicated the presence of an anticyclonic eddy (section 3.2). Based on the characteristics of recurrent subsurface eddies in this region (Hormazabal et al., 2013; Letelier et al., 2009), the higher salinity – low DO core in this area signaled the presence of an intrathermocline eddy (ITE-1). This core was more intense in terms of salinity (>34.6) in the northern than in the southern transect (Figure 4), probably explained by the fact that the most offshore sampling stations were nearer to the eddy-center in the first case and toward its border or periphery in the second case (Figure 3f).

Additional isolated, subsurface, higher salinity – low DO cores (Figure 4) were located in the area of FRN-1 (Sts. 6–7 and 17–18) and ITE-1 (Sts. 10–11 and 23–24), together with a local down-lifting or subduction of the 10°C isotherm (~60 m amplitude). In these areas, surface salinity was characterized by lower values (<34.0), associated with Subantarctic waters (SAAW) in the region (Llanillo et al., 2012), which probably correspond to an intrusion of SAAW from offshore and along the southern border of ITE-1 and/or to an advection of SAAW from the south and along the coast. Off Concepción, this submesoscale to mesoscale variability has been linked to the presence of a meandering coastal jet, associated with fronts and eddies, which is subjected to a strong offshore deflection north of P. Lavapié (Letelier et al., 2009) and, thereby, generates instabilities in the water column.

### 3.4. Macro-Nutrient Distribution and Nutrient Ratios During the Survey

Nutrient distributions in the upper layer (0–100 m depth) also denoted submesoscale variability during the survey. Higher nitrate + nitrite (Figures 5a and 5b) and silicate or silicic acid (Figures 5c and 5d) concentrations in the subsurface layer, a characteristic of the ESSW (Llanillo et al., 2012), reached a shallower depth ( $\sim$ 20 m depth) in the coastal zone. In the upper layer (<20 m depth), nutrient content was higher in the coastal zone than in the CTZ, being nearly depleted in the area of front-eddy interaction (Sts. 7–9 and 16–18). Subsurface nutrient increases at a shallower depth (30 to 60 m depth) were also observed in the area of ITE-1 (Sts. 10–11 and 22–24), whereas a sharp decrease was observed in the area of front-eddy interaction (Sts. 8–9 and 20). The patterns of distribution of both nutrients, as well as that of phosphate (data not shown), closely followed the distribution of isopycnals, particularly that of 26.0 kg m<sup>-3</sup> (Figures 5a–5d).

The ratios between nitrogen (nitrate + nitrite) and silicate (N/Si) were clearly distinct between coastal waters and most of the CTZ (Figures 5e and 5f), with a strong deficit of silicate compared to nitrogen (>3:1) in the area of ITE-1. Silicate is depleted in the SAAW but enriched in the ESSW along the slope waters off central and northern Chile, but both have similar nitrate content (Llanillo et al., 2012; Silva et al., 2009). This deficit was more intense in the southern transect (southern border of ITE-1) than in the northern one (center and border of ITE-1), which suggests an intrusion of SAAW waters in the former and a subsequent mixing of water masses (SAAW and ESSW) toward the north, based also on SST (Figures 3e and 3f) and salinity distributions (Figures 4c and 4d).

High N/Si ratios (>2:1) have been previously detected in the upwelling waters of the equatorial Pacific (Leynaert et al., 2001; Raimbault et al., 1999) and in the subtropical eastern South Pacific, including the CTZ off central Chile (Gómez et al., 2007; Morales et al., 2012) and off Peru (Dugdale et al., 1995; Grasse et al., 2016). In contrast, values close to 1:1 have been described for the coastal upwelling zone off central Chile (Gómez et al., 2007), though interannual variation at a shelf station off Concepción (St. 18; Figure 1a) has been observed, with a significant increase from 1:1 (2002–2006) to 2:1 (2006–2009) (Anabalón et al., 2016). The source of coastal upwelling waters in the region off central Chile is ESSW, which enriches with Si the surface waters during seasonal upwelling periods and displaces SAAW to the offshore; an additional source of Si to coastal waters is provided by rivers in this region (Anabalón et al., 2016).

High N/Si ratios can arise from differences in the relative rates at which silica and nitrogen are recycled in the upper layer of a given region. A faster export of Si relative to N can be the result of a lower remineralization of Si in surface waters - the silica pump [Dugdale et al., 1995]. A Si-pump mechanism has been proposed to explain high N/Si ratios in the CTZ off Peru [Dugdale et al., 1995; Grasse et al., 2016], which can arise from direct diatom sedimentation or diatom-packing in fecal pellets produced by large zooplankton combined with their fast exportation from surface waters, in contrast to a rapid recycling of particulate organic nitrogen in the upper water column (Brzezinski et al., 2003; Dugdale et al., 1995; Dugdale & Wilkerson, 1998; Raimbault et al., 1999).

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**Figure 5.** Spatial distribution of macronutrient concentrations ( $\mu$ M) in the upper 100 m layer during the PHYTO-FRONT survey. Profiles of (a) nitrate + nitrite (N), (b) silicate, and (c) N/Si proportion in the (left) northern and (right) southern transects. The black lines correspond to isopycnals.

The silica pump has also been proposed for the region of the Antarctic Circumpolar Current (ACC), the Antarctic Surface Water (AASW) being relatively replete with nitrate but strongly depleted of Si, a signal which is exported toward lower latitudes by the Antarctic Intermediate Water (AAIW) and the Subantarctic Mode Water (SAMW), the latter providing nutrients to the thermocline of these latitudes in the southern hemisphere (Sarmiento et al., 2004). In summary, both local and remote processes can contribute to the Si depletion signal of the SAAW in the CTZ of the Humboldt Current System.

Seawaters with N/Si ratios close to 1:1 have been proposed to be favorable for diatom growth but species differ greatly in wall thickness, some of which have highly silicified and others have weakly silicified frustules, so that the value at which these ratios influence phytoplankton community composition or metabolism is variable (Davidson et al., 2012; Gilpin et al., 2004). Experimental studies have shown that conditions of Si-deficit (N/Si = 3:1) can produce a shift from chain-forming centric diatoms to pennate and small centric diatoms (Harrison & Davies, 1979). Also, N/Si ratios >2:1 can sometimes influence a diatom replacement by flagellates or affect the metabolism of the most abundant centric diatoms (Davidson et al., 2012; Gilpin et al., 2004). For the region of study, however, knowledge on phytoplankton nutrient requirements and nutrient uptake rates under different nutrient levels is scarce.

### 3.5. Phytoplankton Community Structure in the Coastal Zone and CTZ

Satellite surface Chl-a during the January–February 2014 time series (Figure 6) was highest (>3 mg m<sup>-3</sup>) in the coastal band, mostly to the north of 37°S, and patches of mostly moderate Chl-a concentration (1–2 mg m<sup>-3</sup>) appeared during the whole period in the CTZ. The latter coincided with the location of mesoscale structures, including eddies, meanders, and filaments, in concordance with previous observations in the region off central Chile (Correa-Ramirez et al., 2007; Letelier et al., 2009; Morales et al., 2007). In particular, the borders of the identified ITE-1 displayed higher Chl-a concentration during most part of the time series (~1.5 months; Figures 6a–6g). At the time of the PHYTO-FRONT survey, Chl-a values associated with ITE-1 were highest in its northern border, forming a filament, concurrent with an intrusion toward the coast of very low Chl-a values (Figure 6f); this intrusion persisted for >1 month (W4–W8; Figures 6d–6h) and it moved offshore in association with the trajectory of ITE-1 in the CTZ. A meander located immediately south of P. Lavapié apparently was also contributing to the advection of high Chl-a levels toward ITE-1 during W6–W8 (Figures 6f–6h).

During the survey, FluoroProbe-derived in vivo fluorescence profiles (0–60 m depth; Figures 7a and 7b) indicated that the highest Chl-a values (>5 mg m<sup>-3</sup>) were concentrated in the surface layer at the eastern (onshore) side of FRN-1 (Sts. 5 and 16) and in the subsurface layer (20–40 m depth) between FRN-1 and ITE-1 (Sts. 7–10 and 18–22); in contrast, values in the coastal stations were in the moderate range (2–5 mg m<sup>-3</sup>). A similar pattern was exhibited by extracted Chl-a samples obtained from discrete fluorometric measurements in the upper 100 m layer; Figures 7c and 7d). The magnitudes of the FluoroProbe data were almost twice as high compared with the latter, differences which can be attributed to the fact that the first one represents in vivo fluorescence measurements whereas the other corresponds to fluorescence after extraction. During the survey time, surface satellite Chl-a (Figure 6f) and in situ Chl-a data (Figures 7a–7d) presented a similar distribution, especially in the area of high values at FRN-1.

Phytoplankton size structure during the survey (Figures 7e and 7f) was, for the most part, dominated by the nanoplanktonic Chl-a fraction (~40–70% of total Chl-a) in both transects and in two layers (mean values: 0–30 and >30–100 m depth). The contribution of the microplanktonic Chl-a fraction was highly variable along both transects but was maximum (~40–70%) at FRN-1 (Sts. 5 and 16–18) and ITE-1 (Sts. 10–11 and 22), combined with a slight decrease in the proportion of nanoplanktonic Chl-a in the surface layer. In the coastal zone, the microplanktonic Chl-a contribution was relatively low (<30%), contrary to the expected pattern for this upwelling zone (Anabalón et al., 2016). The picoplanktonic Chl-a fraction was, for the most part, lowest in the survey area, but its proportion was highest in the coastal zone compared with the CTZ; This pattern is also unexpected for coastal surface waters in this region (Collado-Fabri et al., 2011) and can be explained by the decrease in the contribution of the microplanktonic fraction.

In terms of phytoplankton C-biomass by size fraction (Figure 8), a very similar pattern of distribution compared to that of Chl-a fractions (Figures 7e and 7f) was found, with primary maxima (>40 mg C m<sup>-3</sup>) for both the micro and nanoplankton in the surface layer at FRN-1 and secondary maxima (>20 mg C m<sup>-3</sup>) in the subsurface layer (20–40 m depth) of the CTZ. In the coastal zone, secondary maxima in C-biomass were contributed by the nanoplankton (Figures 8c and 8d) and the picoplankton (Figures 8e and 8f). This pattern of community size-structure differs from that previously found in the area of study, including coastal waters and eddies in the adjacent waters of the CTZ during the summer period (January 2009), with dominance of microplanktonic Chl-a in coastal waters and smaller cells in the mesoscale eddies (Morales et al., 2012). The differences may be attributed to the fact that most part of the sampling in the previous study took place during upwelling favorable conditions.



**Figure 6.** MODIS daily satellite Chl-a (mg m<sup>-3</sup>; color scale; 1 km resolution) and altimetry (lines) data in the region of study during selected dates (as in Figure 3 for SST) in the January–February 2014 period. Red dot: central position of ITE-1; gray lines: ITE-1 trajectory.

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**Figure 7.** Chl-a concentration (mg m<sup>-3</sup>) in the upper layer during the PHYTO-FRONT survey. Profiles of total Chl-a (in vivo fluorescence) obtained from the (a and b) FluoroProbe and from (c and d) extracted samples, together with the contribution of different Chl-a size fractions to (e and f) total Chl-a (micro: red; nano: blue; and pico-plankton: green lines) in the (left) northern and (right) southern transects. The continuous lines in Figures 7e and 7f represent the mean values in the upper layer (0–30 m depth) and the broken lines in the subsurface (>30–100 m depth). The black lines correspond to isopycnals.

Localized patches of higher microplankton biomass in the inshore (Sts. 1 and 25; Figures 8a and 8b) were contributed by dinoflagellates ( $\sim$ 10 mg C m<sup>-3</sup>) and they were also the dominant component in the coastal zone in both transects (>60%). In the CTZ, microplankton C-biomass was dominated (>60%) by diatoms in

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**Figure 8.** Phytoplankton C-biomass (mg C m<sup>-3</sup>) in each size fraction in the upper layer (0–60 m depth) during the PHYTO-FRONT survey. Profiles for the (a and b) microphytoplankton, (c and d) nanophytoplankton, and (e and f) the picophytoplankton biomass in the (left) northern and (right) southern transects. The black lines correspond to isopycnals.

surface waters of the FRN-1 area (Sts. 5 and 16: 25–70 mg C m<sup>-3</sup>) and subsurface waters of the ITE-1 area (Sts. 10–11 and 20–24; 10–15 mg C m<sup>-3</sup>). In the rest of the area or layers the microdinoflagellates were dominant (southern transect) or presented similar contributions as the microdiatoms (northern transect). These results reveal the importance of dinoflagellates in CTZ waters of this region and their relative importance during wind relaxation events; in contrast, coastal time series data off Concepción (St. 18) have rarely found them to be of equal or higher importance than the diatoms (Anabalón et al., 2016).

C-biomass in the nanophytoplankton was largely dominated by nanoflagellates in both transects (70–100%), as previously reported for the region of study (Böttjer & Morales, 2007; Morales & Anabalón, 2012). In the picophytoplankton, *Synechococcus* and picoeukaryotes made similar contributions to the total of this fraction in the coastal zone of the southern transect (40–60%), but the cyanobacteria increased offshore of FRN-1 (Sts. 7–9) and that of picoeukaryotes did so in surface waters of ITE-1 area (Sts. 10–11). In the northern transect, *Synechococcus* was dominant (>60%) in the coastal zone and in FRN-1 but picoeukaryotes dominated in the ITE-1 area (Sts 20–24).

Phytoplankton dominance by microdiatoms in coastal waters during the upwelling season in the region off Concepción has been found in monthly time-series studies in the region off Concepción (Anabalón et al., 2016; González et al., 2007), however, nanophytoplankton maxima also appear during the upwelling period in the coastal zone (Böttjer & Morales, 2007). The lack of both microplankton Chl-a and microdiatom dominance in coastal waters probably is the result of the wind relaxation event that characterized the PHYTO-FRONT survey (Figures 1b and 2e). Data on short-term variability (days to a week) of phytoplankton community structure remains relatively unknown for this and other coastal areas in the HCS. However, Chl-a concentration and primary production rates during a short-term study (3 weeks during January–February 2007) were shown to vary by 3–6 times, respectively (Daneri et al., 2012). These results suggest that event scale forcing can strongly influence phytoplankton biomass and primary production, and possibly community structure, in the HCS region off central Chile. On the other hand, macronutrient levels in surface waters of the coastal zone during the PHYTO-FRONT survey (Figures 5a–5d) were not depleted, as it was the case in the upper layer of the CTZ, and N/Si ratios in the coast did not suggest N or Si-limitation as to explain the observed pattern in phytoplankton community structure.

Maxima in phytoplankton abundance and biomass in frontal areas, as found in this study, have been associated with submesoscale dynamics stimulating intense vertical flows, which drives nutrients to the upper layer and also subducts organic matter (Lévy et al., 2012). In EBCSs, this dynamics acts in combination with (i) an offshore Ekman transport of nutrients and organic matter as a result of coastal upwelling, and (ii) the generation of filaments and eddies in the shelf-break area, features which transport nutrients and plankton further offshore (Gruber et al., 2011; Krause et al., 2015; Morales et al., 2012; Nagai et al., 2015). In the case of ITEs, their surface layer act as surface cyclonic eddies, pumping waters upward at its center; therefore, both type of eddies can stimulate increases in biological production in this and other EBCS (Chenillat et al., 2015; Morales et al., 2012). The mechanisms for these increases are related to the contribution of eddies to a redistribution of coastal upwelling communities and nutrients, referred as "eddy trapping" (Gruber et al., 2011; Lathuilière et al., 2010), and/or to a local enhancement of phytoplankton biomass (Morales et al., 2012) and primary new production in the CTZ (Chenillat et al., 2015), referred as "eddy pumping."

#### 3.6. Cross-Shore Distribution of Diatom Taxa

The distribution of different microplanktonic diatom species along the cross-shore transects, as well as of total microdinoflagellates, was evaluated in terms of abundance (Figure 9). Diatom abundances were around one order of magnitude higher (>1,000 \* 10<sup>6</sup> cells m<sup>-2</sup>) in the FRN-1 (Sts. 6 and 16) and ITE-1 zones compared with the coastal zone, where their contributions were similar to those of autotrophic/mixotrophic dinoflagellates (Figures 9a and 9b). Among the numerically dominant diatom species (>100 × 10<sup>6</sup> cells m<sup>-2</sup> at any station), the centric and chain-forming *Skeletonema* sp., *Chaetoceros debilis*, and *Thalassiosira anguste-lineata* (Figures 9c and 9d) are usually found in the coastal waters of the region of study (Anabalón et al., 2016; González et al., 2007; Sánchez et al., 2012). The highest abundances of these taxa were found mostly in both FRN-1 and ITE-1, as was the case of the other dominant taxa, including *C. convolutus* and the pennate *Pseudo-nitzschia delicatissima* and *P. pseudodelicatissima* (Figures 9e and 9f).

*Pseudo-nitzschia* species have been reported to be a dominant component in the CTZ off central Chile (Gómez et al., 2007; Menschel et al., 2016) and in oligotrophic waters of the tropical central Pacific (Gómez

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**Figure 9.** Cross-shelf distribution of integrated microphytoplankton abundance (cells\*10<sup>6</sup> m<sup>-2</sup>) in the upper 60 m layer during the PHYTO-FRONT survey: (left) northern and (right) southern transects. (a and b) Total diatom and autotrophic/mixotrophic dinoflagellate; (c and d) *Skeletonema* sp., *Chaetoceros debilis*, and *Thalassiosira anguste-lineata*; (e and f) *C. convolutus*, *Pseudo-nitzschia pseudo-delicatissima*, and *P. delicatissima*; (g and h) *Guinardia delicatula*, *P. seriata*, and *Fragilaria* sp.; (i and j) *Haslea* sp., *Cylindrotheca longissima*, and *Fragilariopsis doliolus*; (k and l) *Leptocylindrus minimus*, *C.*, and *Navicula directa*. Note a log-10 scale and scales differences between plots.

et al., 2007), but they are not usually dominant in the coastal upwelling waters off Concepción (Anabalón et al., 2016; Sánchez et al., 2012). In general, *Pseudo-nitzschia* species are known to have lower Si requirements and weakly silicified frustules compared to other diatoms, in contrast to the genera which are common in coastal upwelling zones (Sommer, 1994). In particular, weakly silicified *P. delicatissima* populations have been shown to be dominant in Si-deficient waters in the High-Nutrient Low-Chl-a (HNLC) regions in the tropical central Pacific and in the PCC area (CTZ off Chile) during the austral summer (Gómez et al., 2007).

Diatom species with lower abundance values presented distribution patterns similar to those described above. *Pseudo-nitzschia seriata* (Figures 9g and 9h) and *Haslea* sp. (Figures 9i and 9j) were concentrated in the ITE-1 zone, whereas *Fragilariopsis doliolus* was distributed in both the FRN-1 and ITE-1 zones (Figures 9i and 9j). The latter species has been found in oligotrophic oceanic waters of the South Pacific (Gómez et al., 2007) but in very low numbers in the upwelling system off Concepción (Sánchez et al., 2012). *Guinardia delicatula* (Figures 9g and 9h) was part of the community in the FRN-1 and ITE-1 zones but was absent from the coastal zone although it is a nondominant component in coastal waters off Valparaíso and Concepción (Gómez et al., 2007; Sánchez et al., 2012). In contrast, *Navicula directa* was distributed between the coast and FRN-1 (Figures 9k and 9l).

Higher abundances of coastal and mostly oceanic taxa in the FRN-1 and ITE-1 zones compared to the coastal zone coincided with a short-term wind relaxation event in the region of study (Figure 2). In other EBCSs, coastal formations of *Pseudo-nitzschia* blooms have been found to be associated with events of wind relaxation or weak upwelling (Díaz et al., 2014; Kudela et al., 2004; Louw et al., 2016). Populations of *Pseudo-nitzschia* species are thought to develop in offshore retention areas ("incubators") and then to be advected to the coast during periods of downwelling-favorable winds on time scales of a few days (Adams et al., 2006; Fawcett et al., 2007; Trainer et al., 2002, 2012). Based on this and the observations of lower nutrient concentrations in surface waters of the area between FRN-1 and ITE-1, combined with Si-limitation in this area, we suggest that an increase in the abundances of *Pseudo-nitzschia* species closer to the coast is the result of both, a wind relaxation event combined with an advection of waters toward the coast by mesoscale eddies located in the shelf-break area. Thus, increases in *Pseudo-nitzschia* abundance near the coastal zone in the region off central Chile may be favored by wind relaxation events, especially the long ones ( $\sim$ 1 week) such as that observed in January 2014, and by front-eddy activity facilitating the cross-shore exchange of diatom taxa between coastal and CTZ waters.

### 4. Summary and Implications

Cross-shelf exchanges of physical (e.g., heat, salts) and chemical (e.g., DO, nutrients) properties, and of organic matter (e.g., dissolved organic carbon, plankton), are a central aspect of how coastal dynamics in systems like the upwelling areas in EBCSs influence or are influenced by oceanic systems, especially in the CTZ. Overall, our observations suggest that coastal and oceanic diatom taxa accumulate in the upwelling frontal zone and that mixing between them is a result of the interactions between the coastal front and a relatively young mesoscale eddy located in the shelf-break area. These results indicate that front-eddy interactions in EBCSs could enhance cross-shelf exchanges of coastal and oceanic plankton taxa through localized upward injections of nutrients in the frontal area, favoring enhanced plankton growth/aggregation there, combined with ITE-induced advection and vertical injections of nutrients, which contribute to sustain both coastal and oceanic phytoplankton in the eddy center.

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#### Acknowledgements

We are thankful to the captain and crew of the R/V Abate Molina (IFOP, Chile), and to the technical staff and students participating in the PHYTO-FRONT survey for their invaluable help at sea and initial data processing. V. Anabalón benefited from a CONICYT fellowship (Becas de Doctorado en el Extranjero por Gestión Propia 2008 -Becas Chile 2009) and this work was completed while V. Anabalón was a Ph.D. student in the IOCAG Doctoral Programme in Oceanography and Global Change at the ULPGC in Spain. C.E. Morales and S. Hormazabal were supported by CONICYT-FONDECYT (Projects 1120504 and 1151299) and, together with M. Cornejo, by the Instituto Milenio de Oceanografía (IMO-Chile). We acknowledge the contribution of Pierre-Amael Auger with the eddy-tracking algorithm and his comments on this subject. Satellite Chl-a data used in this study are available from SeaWiFS/MODIS-Seaviewing Wide Field-of-view Sensor/ Moderate Resolution Imaging Spectroradiometer on the NASA Aqua satellites (http://oceancolor.gsfc.nasa. gov). The Group for High Resolution Sea Surface Temperature (GHRSST) Multi-scale Ultra-high Resolution (MUR) SST data were obtained from the NASA EOSDIS Physical Oceanography Distributed Active Archive Center (PO.DAAC) at the Jet Propulsion Laboratory, Pasadena, CA (https://doi.org/10.5067/GHGMR-4FJ01). Multimission altimeter products are produced by SSALTO/ Duacs and distributed by AVISO (www. aviso.oceanobs.com). The data included in this study are listed in the figures, URLs in the text, and/or references. In addition, in situ and satellite data used in this study are available upon request from C.E. Morales (camorale@udec.cl) and S. Hormazabal (samuel.hormazabal@ pcuv.cl), respectively. Finally, we thank the very useful comments by two anonymous reviewers.

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