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Facultad de Ciencias del Mar

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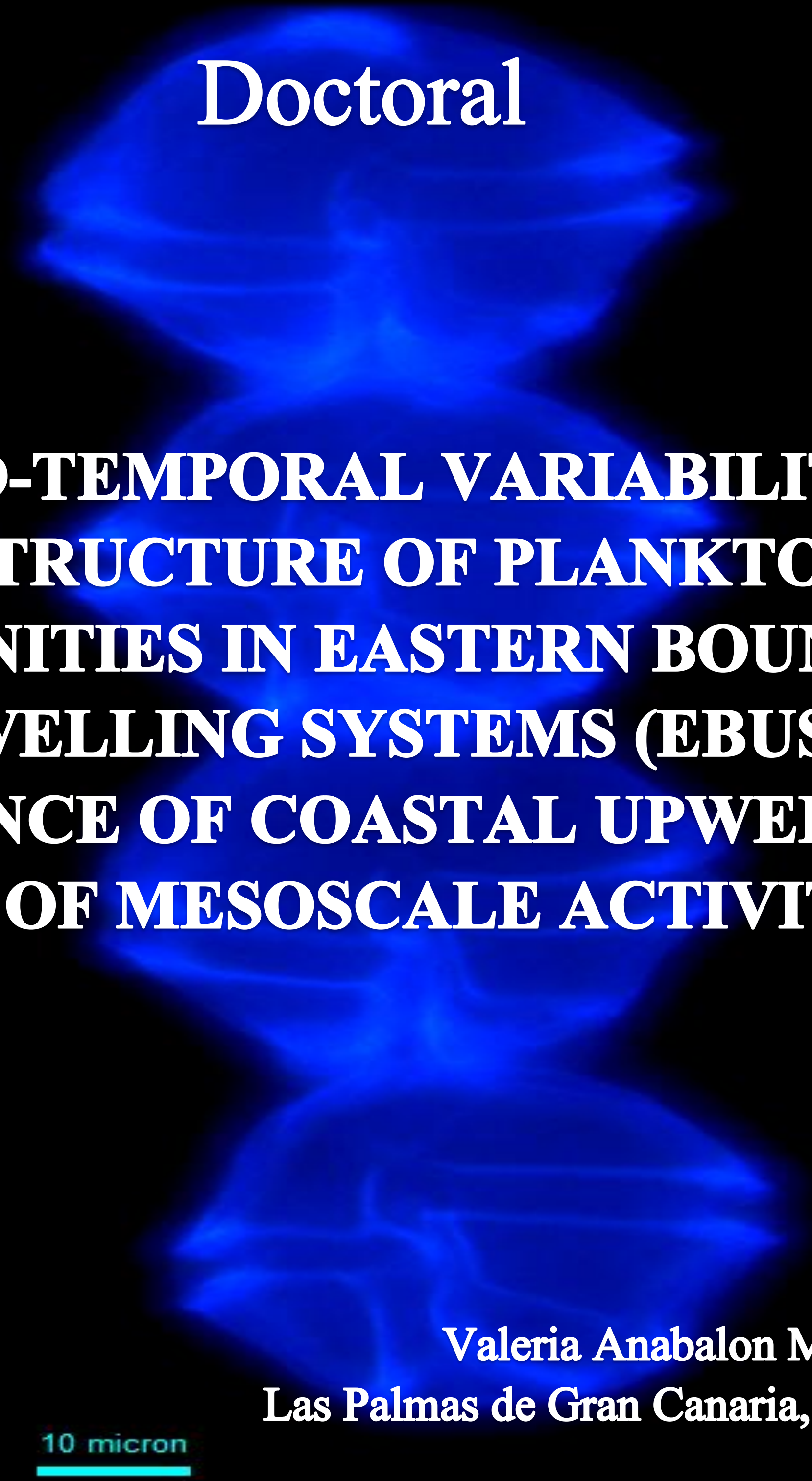

# SPATIO-TEMPORAL VARIABILITY IN THE STRUCTURE OF PLANKTONIC COMMUNITIES IN EASTERN BOUNDARY UPWELLING SYSTEMS (EBUS): INFLUENCE OF COASTAL UPWELLING AND OF MESOSCALE ACTIVITY

Valeria Anabalon Molina
Las Palmas de Gran Canaria, Octubre 2018

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DE GRAN CANARIA

**D/Dª: SANTIAGO HERNÁNDEZ LEÓN COORDINADOR/A DEL**

**PROGRAMA DE DOCTORADO EN OCEANOGRAFÍA Y CAMBIO GLOBAL**

**DE LA UNIVERSIDAD DE LAS PALMAS DE GRAN CANARIA,**

**INFORMA,**

Que la commission Académica del Programa de Doctorado, en su sesión de fecha a 14 de Octubre del 2018 tomó el acuerdo de dar el consentimiento para su tramitación, a la tesis doctoral titulada.

**"SPATIO-TEMPORAL VARIABILITY IN THE STRUCTURE OF PLANKTONIC COMMUNITIES IN EASTERN BOUNDARY UPWELLING SYSTEMS (EBUS): INFLUENCE OF COASTAL UPWELLING AND OF MESOSCALE ACTIVITY"**

presentada por el/la doctorando/a D/Dª : **Valeria Anabalón Molina** y dirigida por el Doctor **Javier Arístegui Ruiz.**

Y para que así conste, y a efectos de lo previsto en el Artº 11 del Reglamento de Estudios de Doctorado (BOULPGC 7/10/2016) de la Universidad de Las Palmas de Gran Canaria, firmo la presente en Las Palmas de Gran Canaria, a 14 de Octubre de dos mil dieciocho

UNIVERSIDAD DE LAS PALMAS
DE GRAN CANARIA

# UNIVERSIDAD DE LAS PALMAS DE GRAN CANARIA
# ESCUELA DE DOCTORADO

Programa de doctorado en Oceanografía y Cambio global

**Título de la Tesis**

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Tesis Doctoral presentada por D/Dª : Valeria Anabalón Molina

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Codirigida por el Dr/a. D/Dª: Carmen Morales Van de Wy ngard

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Las Palmas de Gran Canaria, a 14 de Octubre de 2018

UNIVERSIDAD DE LAS PALMAS DE GRAN CANARIA
Facultad de Ciencias del Mar

# SPATIO-TEMPORAL VARIABILITY IN THE STRUCTURE OF PLANKTONIC COMMUNITIES IN EASTERN BOUNDARY UPWELLING SYSTEMS (EBUS): INFLUENCE OF COASTAL UPWELLING AND OF MESOSCALE ACTIVITY

## VARIABILIDAD ESPACIO-TEMPORAL EN LA ESTRUCTURA DE COMUNIDADES PLANCTÓNICAS EN SISTEMAS DE BORDE ORIENTAL: INFLUENCIA DE LA SURGENCIA COSTERA Y DE LA ACTIVIDAD DE MESOESCALA

Tesis doctoral presentada por Valeria Anabalón Molina

dentro del Programa de Doctorado en Oceanografía y Cambio global

Dirigida por Dr. Javier Arístegui Ruiz

y Dra. Carmen E. Morales Van de Wyngard

**LAS PALMAS DE GRAN CANARIA,**

*“De la vida no quiero mucho, quiero apenas saber que*
*intenté todo lo que quise, tuve todo lo que quise, ame*
*lo que valía la pena y perdí apenas lo que nunca fue mío”*
**Pablo Neruda**

***A mis padres y hermana, gracias por amarme***
***incondicionalmente, por creer y confiar en mí,***
***incluso cuando dejé de creer en mí.***
*Mi padre dice que la mayor debilidad del*
*ser humano es rendirse la única manera de*
*tener éxito es intentarlo siempre una vez más*

***The genius is made with 1%***
***of talent and 99% of work***
*El genio se hace con1%*
*de talento y un 99% de trabajo*
***Einstein***

# ABSTRACT/ RESUMEN

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# ABSTRACT

Eastern boundary upwelling systems (EBUSs) are distinguished from other systems by the recurrent fertilizing effect of wind-induced upwelling processes, which stimulate a high productivity in coastal areas. Among the main EBUSs in the Atlantic and Pacific Oceans, some of them have been insufficiently researched in terms of the structure and dynamics of pelagic communities, which makes a difficult task to compare between systems or between regions in the same system. This thesis focuses on the characterization of microbial planktonic communities and on the analysis of their spatio-temporal changes associated with oceanographic variability in the coastal and coastal transition zones of two EBUSs with different oceanographic dynamics, the Cape Ghir system (31°N, Canary EBUS) and the Concepción system (36.5°S, Humboldt EBUS). A series of in situ oceanographic-biological samplings were carried out to accomplish the thesis objectives and these data were combined with satellite data to provide a wider spatio-temporal context to the samplings. Traditional microscopy and flow-cytometry techniques were used to identify taxa or functional groups and to estimate their abundance and biomass. The spatial and/or temporal similarity in microbial community structure in each EBUS and the influence of environmental factors on structure variability were evaluated with multivariate analyses. In Cape Ghir, where coastal upwelling is permanent, the spatio-temporal changes in the structure of microbial communities are related to variations in upwelling intensity and to the proportion of nutrients. A comparatively lower concentration of nutrients in the C. Ghir region contributes to the fact that the dominance of diatoms in the phytoplankton is infrequent but mixed photoautotrophic/mixotrophic assemblages are more often found. In Concepción, where coastal upwelling is highly seasonal, changes in upwelling intensity contribute to explain variations in microbial community structure, while nutrient concentrations remain high during the annual cycle; microplanktonic diatoms dominate the phytoplankton during the upwelling period. In addition, in the Concepción system, mesoscale activity represented by front-eddy interactions produces an intense exchange of diatom species between coastal and oceanic waters. The results obtained in this thesis reflect the high complexity associated with the structure of microbial communities in EBUSs but allow for making basic projections on community changes under a scenario of potential wind intensification in some of the EBUSs.

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# RESUMEN

Los sistemas de surgencia de borde oriental (EBUSs) se distinguen de otros sistemas por el efecto fertilizador recurrente que tienen los procesos de surgencia inducida por vientos y, con ello, se estimula una alta productividad en la zona costera. Entre los EBUSs principales en los océanos Atlántico y Pacífico, existen algunos que han sido insuficientemente investigados en términos de la estructura y dinámica de las comunidades pelágicas, lo que a su vez dificulta las comparaciones entre sistemas o entre regiones en un mismo sistema. Esta tesis se enfoca en la caracterización de las comunidades planctónicas microbianas y en el análisis de sus cambios espacio-temporales asociados a la variabilidad oceanográfica en la zona costera y de transición costera de dos EBUSs con distintas dinámicas oceanográficas, el sistema de Cabo Ghir (31°N, EBUS de Canarias) y el sistema de Concepción (36.5°S, EBUS de Humboldt). Se realizaron una serie de muestreos oceanográficos-biológicos in situ para el cumplimiento de los objetivos de la tesis y esta data fue, combinada con data satelital para proporcionar un contexto espacio-temporal mayor al de los muestreos. Se utilizaron técnicas de microscopía tradicional y citometría de flujo para identificación de taxa o grupos funcionales y para las estimaciones de abundancia y biomasa. La similitud espacial y/o temporal en la estructura comunitaria microbiana en cada EBUS y la influencia de factores ambientales sobre la variabilidad en dicha estructura fue evaluada mediante análisis multivariados. En C. Ghir, donde la surgencia costera es permanente, los cambios espacio-temporales en la estructura de comunidades microbianas están relacionados con las

variaciones estacionales en la intensidad de la surgencia y con las proporciones de nutrientes. Una comparativamente menor concentración de nutrientes en la región de C. Ghir contribuye a que la dominancia de diatomeas en el fitoplancton sea infrecuente pero que a menudo se presenten conjuntos de fotoautótrofos/mixótrofos. En Concepción, donde la surgencia costera es altamente estacional, los cambios estacionales en la intensidad de la surgencia contribuyen a explicar las variaciones en la estructura comunitaria microbiana, mientras que las concentraciones de nutrientes permanecen altas durante el ciclo anual; las diatomeas microplanctónicas dominan el fitoplancton durante periodo de surgencia. Además, en el sistema de Concepción, la actividad de mesoescala, representada por las interacciones frente-remolino, producen un intenso intercambio de especies de diatomeas entre aguas costeras y oceánicas. Los resultados obtenidos en esta tesis reflejan la alta complejidad asociada a la estructura de comunidades microbianas en los EBUSs pero permiten realizar proyecciones sobre los cambios comunitarios bajo un escenario de potencial intensificación de los vientos en algunos de los EBUSs.

***Try not to become a man of success ,***
***but rather try to become a man of value***
*Intenta no volverte un hombre de éxito,*
*sino un hombre de valor.*

***Einstein***

# THESIS PRESENTATION

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## THESIS PRESENTATION

This doctoral thesis, entitled SPATIO-TEMPORAL VARIABILITY IN THE STRUCTURE OF PLANKTONIC COMMUNITIES IN EASTERN BOUNDARY UPWELLING SYSTEMS (EBUS), has been developed under the supervision of Dr. Javier Arístegui Ruiz (Department of Biology of the University of Las Palmas of Gran Canarias (ULPGC), Spain) and Dra. Carmen E. Morales (Department of Oceanography of the University of Concepción (UDEC, Chile), and is associated to the Doctoral Program in Oceanography and Global Change at the ULPGC. The thesis consists of four original research papers, published in international indexed journals. The research in this doctoral thesis was financed by different sources: a CONICYT scholarship for graduate studies at ULPGC (Doctorate Scholarships Abroad for Own Management 2008 - Scholarships Chile 2009); CAIBEX Project (CTM2007-66408-CO2-02) " Spanish National R and D Plan " (MEC), under the coordination of Dr. J. Arístegui; FONDECYT 7070040, FONDECYT 1120504, and FONDECYT 1151299 Projects , Fisheries Research Fund, Projects (FIP 2004-20, 2005-01, 2006-12), FONDAP-COPAS Center (150100007), and the Millennium Institute of Oceanography (IMO-Chile), all under the coordination of Dr. C. E. Morales.

The thesis is organized following the typical structure of an academic text: a general introduction, where the background of the research is presented and the objectives and hypotheses to be studied are stated. Next, the four scientific contributions develop from hypotheses are presented following the conventional structure of a research article. Finally, the results are synthesized in a general discussion, from which the main conclusions are drawn. All the sections have been written entirely in English with the aim of complying with the normative; only the summaries of each chapter, hypotheses and objectives are presented in Spanish, as required by the regulation for the elaboration, tribunal, defense and evaluation of Doctoral Theses of the University of Las Palmas de Gran Canarias.

***A dark illimitable ocean, without bound, dimensions;***
***where length, breadth and height, and time and place,***
***are lost; where eldest night and chaos - ancestors of nature,***
***hold eternal anarchy.***
*Un océano ilimitado y oscuro, sin límites ni dimensiones;*
*donde se pierde la longitud, anchura y altura, el tiempo*
*y el espacio; donde la noche más antigua y el caos*
*– antecesores de la naturaleza - mantienen la anarquía eterna.*
**Milton**

# CONTENTS

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***Ti  Lüiku wechodkurakey ñi newengen***
***Mew nu,welu may ñi tüy-tüyleken new***
*La gota de agua perfora la roca. No*
*por su fuerza, sino por su constancia*
***Idioma y  Cultura mapuche***

# GENERAL INTRODUCTION

***Ti Lüiku wechodkurakey ñi newengen***
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# GENERAL INTRODUCTION

In planktonic communities, micro-organisms (0.2 to 200 µm) constitute a significant fraction of the biomass in the euphotic zone and they also represent a large proportion of it in deep ocean waters (Fuhrman et al., 1989; Kent et al., 2007; Hansell et al., 2009; Hansell and Carlson, 2015; Caron et al., 2017). The fine structure of microbial communities in pelagic systems (beyond its size categorization into picoplankton, nanoplankton, and microplankton) and its spatio-temporal variations are, until today, subjects which remain to be characterized in several coastal and ocean systems. These subjects are of the highest interest when considering that microbial communities play a major role in the trophic dynamics and carbon cycle in the oceans (Azam et al., 1983; Legendre and LeFévre, 1991; Freon et al., 2009; García-Reyes et al., 2015).

Among the pelagic systems in the oceans, eastern boundary upwelling systems (EBUSs) have been recognized to have high levels of primary production and biomass of phytoplankton, mostly dominated by micro-phytoplankton, in the coastal zone (Chavez and Messié, 2009; Arístegui et al., 2009; Capone and Hutchins, 2013). The structure of microbial communities in the main EBUSs and its spatio-temporal variations remain poorly characterized in some regions, mostly due to the lack or short period of in situ time series (Arístegui et al., 2009; Demarcq, 2009; Chavez and Messié, 2009; Hutchings et al., 2009; García-Reyes et al., 2015) and the complexities until today to identify phytoplankton functional groups using satellite approaches in coastal regions (Correa-Ramírez et al., 2018; Corredor-Acosta et al., 2018). The identification of the environmental and biological factors that control the structure of microbial communities in EBUSs not only is critical to understanding the functioning of these ecosystems, but it is also essential in the characterization of carbon cycling at the regional level and for the prediction of the responses of EBUSs to the effects of climate change.

## 1.1. EASTERN BOUNDARY CURRENT SYSTEMS

### 1.1.1. EBUSs: MAIN CHARACTERISTICS AND SPATIO-TEMPORAL VARIATIONS IN ENVIRONMENTAL CONDITIONS

The main EBUSs, which include the California, Humboldt (Chile-Peru), Canary/Iberian and Benguela systems, extend over large coastal areas on the western side of the continents and from equatorial to mid-latitude waters (review in Mackas et al., 2006). Each of them is composed of quite well-defined regions in terms of the physical, chemical and biological conditions (Chavez et al., 2009). EBUSs are associated with the positions of subtropical anticyclones in the Atlantic and Pacific Oceans, the eastern border of which are dominated by equatorward winds so that wind stress produces a divergence in the coastal zone. Such divergence contributes to the rise of subsurface, cooler waters towards the surface in the coastal band (coastal upwelling - Ekman transport), flow which is compensated by a subsurface flow towards the coast and poleward (Hill et al., 1998; Chavez et al., 2009).

EBUSs are also characterized by the presence of a Coastal Transition Zone (CTZ), where highly dynamic processes take place through sub-mesoscale and mesoscale structures, such as eddies, filaments, meanders, fronts, jets, as well as the interactions between them (Brink and Cowles, 1991;Williams and Follows, 2003; Hormazabal et al., 2004; Barth et al., 2005; Pelegrí et al., 2005; Hösen et al., 2016). Instabilities, mainly baroclinic, contribute to generate these types of structure (Leth and Shaffer, 2001; Leth and Middleton, 2004; Marchesiello et al., 2003; 2004). These structures tend to be related to the coastal upwelling season and/or to topographical effects (Batten, 1997; Castelao et al., 2006; Correa-Ramírez et al., 2012; Wang et al., 2015). Among the mechanisms that force vertical movements in the water column of the CTZ is Ekman pumping, induced by the wind stress curl and resulting in anticyclonic eddies (cyclonic) associated with areas of convergence (divergence) and sinking (upwelling) (Bakun and Nelson 1991; Hormazabal et al., 2004). Submeso-scale and mesoscale processes associated with these structures contribute to exchanges between coastal and oceanic waters, including nutrients and/or organic matter (Álvarez-Salgado et al., 2001; Mackas and Galbraith, 2002; Whitney et al., 2005; Hyun et al., 2009; Kim et al., 2011; Chenillat et al., 2015; Everett et al., 2015).

In the spatial dimension, coastal upwelling processes in EBUSs are dependent on latitude in terms of the Coriolis parameter. At low latitudes, the same magnitude of upwelling favorable winds produces a greater displacement of waters than at higher latitudes (Chavez et al., 2009). In addition, coastal upwelling occurs semi-permanently during the year at low latitudes, while it is highly seasonal at mid-latitudes due to the annual displacement of the subtropical anticyclones in each hemisphere (Mackas et al., 2006; Thomas et al., 2012).

These differences generate distinct regions in each of the main EBUSs, along with differences in intensity of mesoscale activity in the CTZ (Lachkar and Gruber, 2012).

In the time dimension, EBUSs are subjected to a wide range of oceanographic frequencies of variability, from high frequency (hourly, daily, event) to low frequency (years, decades, and multi-decades). In the low frequency, interannual processes, such as El Niño Southern Oscillation (ENSO), to inter-decadal processes, such as the Pacific Decadal Oscillation (PDO) and the North Atlantic Oscillation (NAO), can modulate the depth of the thermocline and of the nutricline and, in turn, can produce dramatic fluctuations in the productivity of EBUSs(Barber and Chavez, 1983; 1986; Philander, 1986; Gammelsrød et al., 1998; Yañez et al., 2001; Thomas et al., 2001; Carr and Kearns, 2003; Alheit et al., 2004; Lachkar and Gruber, 2012). At the annual scale, the oceanographic variability in the coastal areas of EBUSs has been widely characterized (Shannon et al. 1996; Morales et al., 2013; Pelegri et al., 2005a, 2005b), but much less is known at higher frequencies (Grados et al., 2016). In the case of the CTZ, time variability in oceanographic conditions remain far less analyzed (Correa-Ramirez et al., 2012).

Coastal upwelling processes have often been associated with an input of subsurface nutrients into the surface layer in EBUSs (Hutchings et al., 1998; Wilkerson et al., 2000; Thomas et al., 2001; Pennington et al., 2006; Lachkar et al., 2011). At a local level, upwelling fronts and eddies can contribute to inject nutrients from the subsurface to the surface layer in EBUSs (Hyun et al., 2009; Kim et al., 2011; Chenillat et al., 2015; Everett et al., 2015; Krause et al., 2015; Morales et al., 2017). Despite this potential fertilization, limitation by iron has been detected in areas of EBUSs (Messié and Chavez 2015), especially in those with narrow continental platforms (Hutchins et al., 1998, 2002; Chase et al., 2007). In other cases, a limitation by silicon acid (or silicate) has been suggested, especially in the CTZ (Nelson and Treguer 1992; Dugdale et al., 1995; Morales et al., 2017). Altogether, spatial and temporal patterns of nutrient inputs to the surface layer in EBUSs, as well as the variability in nutrient ratios, have remain mostly understudied in most EBUSs. In turn, these unknowns prevent us from having a deeper understanding of the role of nutrients in structuring microbial communities and in predicting primary production levels in EBUSs.

### 1.1.2. EBUSs: PHYTOPLANKTON COMMUNITY STRUCTURE AND PRODUCTIVITY

EBUSs have been recognized as highly productive marine ecosystems on a global level, contributing about 5% of the global primary production (Carr, 2002) and 20% of the most important fisheries in the world (Pauly and Christensen, 1995; Bakun, 1990; 1996; Carr, 2001; Carr and Kearns, 2003; Chavez and Messié, 2009). Its high productivity potentially generates a high export of organic carbon, both vertically toward the sediments (Müller-Karger et al., 2005) and horizontally toward the open ocean (Arístegui et al., 2004; 2009; Lachkar and Gruber, 2012; Morales et al., 2017).

Coastal upwelling systems have usually been characterized by a structure of phytoplanktonic communities dominated by the microplankton, represented by a few genera of diatoms, mostly cosmopolitan and chain-forming cells, and which sustain a large fraction of the classical trophic transfer webs (Hutchings et al., 1995; Tilstone et al., 2000, Lassiter et al., 2006; Abrantes et al., 2016). Most recently, some studies have shown evidence indicating that community structure in these systems is spatially or temporally dominated by smaller phytoplankton and microbial food webs, particularly during non-upwelling periods (Sherr and Sherr, 2002; Vargas and Gonzalez, 2004a, 2004b; Böttjer and Morales, 2007; Crespo et al., 2012). In general, the smaller planktonic fractions have received less attention in EBUSs and there are only a few studies which have included the whole of the microbial size spectrum (from picoplankton to microplankton) or more than one of these fractions (Painting et al., 1992, Böttjer and Morales, 2007; Anabalón et al., 2007; Crespo et al., 2012, Arístegui et al., 2004, 2009; Baltar et al., 2009).

Among the EBUSs, as well as in regions within them, substantial differences in the concentration of phytoplankton biomass (as chlorophyll-a: Chl-a) and in net primary production (NPP) in the coastal upwelling zone have been found (Carr, 2001; Carr and Kearns, 2003; Patti et al., 2008; Correa-Ramirez et al., 2012; Rossi et al., 2008, 2009; Gruber et al., 2011; Lachkar and Gruber, 2012; Gómez-Letona et al., 2017). Together with this, fundamental differences between the EBUSs in the Atlantic and the Pacific have been described, with the latter having narrower platforms, relatively weaker winds along the coast and more intense mesoscale activity than in the Atlantic, altogether them leading to lower NPP levels in the Pacific (Lachkar and Gruber, 2012). Mesoscale and submesoscale processes in the CTZ of EBUSs can also have effects on the structure and dynamics of microbial communities, however, they remain relatively unknown for most of the cases. Among these effects, a coastal to offshore transport (by filaments or eddies) of planktonic organisms has been reported (Alvarez-Salgado et al., 2001; Mackas and Galbraith, 2002; Whitney et al., 2005). At the same time, such advection can have negative impacts in the coastal zone both in terms of nutrient and plankton losses over the shelf area (Gruber et al., 2011).

The structures of phytoplanktonic communities in the Canary and the Humboldt EBUSs are, among all, the least known in terms of the characterization of composition, abundance and biomass (beyond total Chl-a) and of their spatial and temporal variations. On this basis, this thesis focuses on two areas of these EBUSs, located at similar mid-latitude regions, one representing the Atlantic conditions with semi-permanent coastal upwelling (Cape Ghir; ~31°N), and the other representing the Pacific conditions with seasonal coastal upwelling (Concepción, ~36°S). This type of study is especially relevant in the current context of the impact of climate change on EBUSs, including Bakun hypothesis on an associated intensification of coastal upwelling in the main EBUSs (Bakun, 1990; Bakun et al., 2010). Evidence for this hypothesis remains controversial, mainly due to the fact that no significant changes in the Canary/Iberian System have been observed (Barton et al., 2013; Cropper et al., 2014; Sydeman et al., 2014). Wind intensification (weaking) is expected to happen in poleward (equatorward) regions of some of the EBUSs and during the warm season (García-Reyes et al., 2015). The potential effects of coastal upwelling intensification on total Chl-a and/or primary production have been evaluated in different EBUSs and heterogeneous results in their trends have been obtained depending on the dataset, production model and/or the region of EBUS analysed (see Gómez-Letona et al., 2017). However, the impact on the structure of phytoplanktonic communities remains unknown.

## 1.2. THE HUMBOLDT EBUS

The Humboldt Current system extends on the west coast of South America, from 4ºS up to 40ºS, which corresponds to waters off Peru and Chile. The large-scale atmospheric circulation that dominates the region is driven by the South Pacific Subtropical Anticyclone (SPSA), which is limited in the north by the Inter-Tropical Convergence Zone (ITCZ) and on the south by the Polar front (Strub et al., 1998). During the austral spring-summer season, the SPSA shifts to its southernmost position (~32ºS), favoring coastal upwelling all along the coast, while during the austral winter it moves north (~27ºS), weakening upwelling favorable winds off central Chile and increasing them off Peru (Bakun and Nelson, 1991). This movement generates three main sub-regions based the seasonality of coastal upwelling: a) the Peru sub-region (10-18°S), where upwelling is permanent throughout the year, but more intense in winter-spring; b) the northern Chile sub-region (18-30°S), where upwelling is permanent but weaker in intensity compared to the other two sub-regions; and c) the central Chile sub-region (30-40°S), where the upwelling has a marked seasonal cycle, with peaks in southern spring-summer (Correa-Ramírez et al., 2012). In this region, the CTZ is characterized by high levels of mesoscale activity, with higher levels off Peru and central Chile and lower in the sub-region in between (Hormazabal et al., 2004). Surface cyclonic and anticyclonic eddies are generated off Peru and central Chile, including the formation of subsurface intra-thermocline eddies or ITEs (Hormazabal et al., 2013).

### 1.2.1. EBUS CHARACTERISTICS OF CENTRAL-SOUTHERN CHILE – CONCEPCIÓN

The upwelling system off central Chile presents a seasonal maximum in upwelling favorable winds, the signal of which moves progressively in a southerly direction from spring to summer (Shaffer et al. 1999; Correa-Ramírez et al., 2012). In addition, there are episodes of intense winds along the coast (30-35ºS) during this period, known as atmospheric jets (Garreaud and Muñoz, 2005; Muñoz and Garreaud, 2005) and which have direct consequences on coastal upwelling (Renault et al., 2009, 2012; Aguirre et al., 2012; Bravo et al., 2015). In the central-southern sub-region, the continental shelf is relatively wide (50-60 km) in some areas (eg. Itata Terrace) and extremely narrow in others (eg. Point Lavapié); in addition, two submarine canyons (BioBio e Itata) are present and influence upwelling processes on the shelf area (Sobarzo et al., 2007). In terms of water masses, the upper layer is dominated by the Surface Subantarctic Waters (SAAW) and, immediately below it appears the Equatorial Subsurface Water (ESSW). The ESSW constitutes the main source of waters for coastal upwelling in this sub-region and it is associated with an intense oxygen minimum zone (OMZ; $< 0.5$ $mL^{-1}$) in the water column and over the sediments on the shelf and shelf-break (Sobarzo et al., 2007; Hormazabal et al., 2013). The contribution of freshwater inputs in the central-southern sub-region is locally important, with the Itata and Bio-Bio Rivers supplying high concentrations of silicic acid, nitrate and orthophosphate to the adjacent coastal area (Sánchez et al., 2008). Freshwater inputs from rivers and rainfall contribute to strong variations in the water column during autumn-winter, when the coastal waters are less saline and have a greater stratification compared to the upwelling season (Jutla et al., 2011; Sánchez et al., 2012). Solar radiation also has a strong seasonal cycle in this sub-region and it contributes to stratification in the upper layer, especially during the summer (Sobarzo et al., 2007).

### 1.2.2. COMMUNITY STRUCTURE AND PRODUCTIVITY IN THE CENTRAL-SOUTHERN CHILE EBUS – CONCEPCION

The seasonality in wind-driven coastal upwelling off central Chile develops in parallel with the seasonal increase in Chl-a concentration and, for this reason, it has been usually suggested that wind stress modulates the seasonal variability in phytoplankton biomass in the coastal zone (Thomas, 2001; Yuras et al., 2005; Correa-Ramirez et al., 2012; Morales et al., 2013). The seasonal cycle of solar radiation is also related to the seasonal increase in phytoplankton biomass and, together with wind stress, can explain the start of the phenological cycle of surface Chl-a (Corredor-Acosta et al., 2015). In the CTZ, the annual maximum in the annual cycle of Chl-a is associated with the propagation of Rossby waves and/or mesoscale activity (Correa-Ramirez et al., 2012). Also, the inter-annual variability of Chl-a in this region is closely associated with the ENSO cycle (Correa-Ramirez et al., 2012).

In the area off Concepción, primary production, respiration and phytoplankton abundance or biomass in the coastal upwelling area display significant spatial-temporal fluctuations (Daneri et al., 2000; Cuevas et al., 2004; Anabalón et al., 2007; Morales et al., 2007). Results from studies based on a time series in a coastal fixed station (St. 18, about 36 km from the coast) have shown significant increases in Chl-a and in cell abundance and/or carbon biomass of the microphytoplankton during spring-summer (Gonzalez et al., 2007; Sánchez et al., 2012). The microphytoplankton in this area is composed mostly of diatoms and it is dominated by a few genera during the upwelling period: *Skeletonema*, *Chaetoceros*, *Thalassiosira* (Anabalón et al., 2007; Sánchez et al., 2012). Beyond this knowledge, still too few studies have characterized the spatial and temporal changes in the structure of microbial planktonic communities (other than total Chl-a) and their associations with oceanographic variability. In addition, the effects of sub-mesoscale and mesoscale variability in the CTZ on the structure of microbial communities in this sub-region remain mostly under-investigated. Hence, the interest in this thesis to address these issues.

## 1.3. THE CANARY EBUS

The Canary EBUS forms part of a more general system, the Canary Current Large Marine Ecosystem (Arístegui et al., 2006), which includes the west coast of the Iberian Peninsula and the NW coast of Africa (12-43ºN). The Gulf Stream, which flows north along the east coast of North America, becomes separated from the mainland at ~35ºN and travels north-eastward in the ocean generating several branches around 40ºN. One of these branches gives rise to the Azores Current, which becomes divided into three smaller branches flowing southwest. The most eastern branch constitutes the Canary Current (CanC), which is also fed by some branches of the North Atlantic Current, such as the Portugal Current (Barton, 1998; Hernandez-War et al., 2005). The Canary EBUS has been divided into five large sub-regions, based on the extent of seasonality in coastal upwelling and on biogeographic aspects (Arístegui et al., 2009). On the west coast of the Iberian Peninsula, the Galician (42-43ºN) and Portuguese (37-42ºN) sub-regions are strongly influenced by freshwater inputs, which increase northward. Coastal upwelling in these sub-regions occur between April and September, being more intense during the summer. The sub-region of the Gulf of Cadiz (33-37ºN) represents a significant disruption in the continuity of the system due to the configuration of the coast, which is not favorable for upwelling and, therefore, this process disappears in the area around the Strait of Gibraltar. In the coast NW Africa, two sub-regions are located, Morocco (21-33ºN) and Mauritania-Senegal (12-21ºN). The first one is characterized by permanent upwelling during the year, being more intense between 20ºN and 25ºN, and having a relatively higher mesoscale variability. The second is defined in its northern border by the separation of the CanC from the coast and in its southern border by the southern limit of the upwelling favorable winds. This seasonal and zonal behavior is related to the seasonal variation of the trade winds, which in turn is associated with the southern displacement of the Azores High (Marcello et al., 2011).

### 1.3.1. CHARACTERISTICS OF THE MOROCCO EBUS - CAPE GHIR

The Morocco sub-region is characterized by a relatively wide continental shelf, with an average extension of 70 km and a maximum of 140 km offshore. At least two main upwelling areas have been identified (Marcello et al., 2011): between Cape Ghir and C. Juby (25-33ºN) and between C. Bojador and C. Blanc (20-25ºN). In terms of water masses, the upper layer is dominated by the central waters of the North Atlantic (NACW), the main source of coastal upwelling in this sub-region; in the intermediate layers (600 to 1500 m depth), the Antarctic Intermediate Water (AAIW) and the Mediterranean Water (MW) are present. Another feature of this sub-region is that the area between 24 and 33ºN has been shown to present a relatively low concentration of nitrate in the surface layer in comparison with the sub-region to the south, the Mauritania-Senegal sub-region (Arístegui et al., 2006; Lathuiliere et al., 2008; Schafstall et al., 2010). On the other hand, solar radiation has a strong seasonality in this sub-region, with a maximum in summer and in co-occurrence with maximum upwelling favorable winds (Bozzano et al., 2002).

The area of Cape Ghir (~31ºN) has been one of the least studied in this N. Atlantic EBUS in terms of the dynamics of coastal upwelling and of mesoscale activity (Van Camp et al., 1991; Hagen et al, 1996; Nykjaer and Van Camp, 1994; Freudenthal et al., 2001, 2002). Coastal upwelling in C. Ghir is permanent, but with peaks during boreal summer and autum, associated with the increase in upwelling favorable winds (Marcello et al., 2011). The area is characterized by the presence of a submarine plateau that extends towards the open ocean (150 km from the coast), being a branch of the Atlas Mountains (Hagen et al., 1996; Barton et al., 1998). Mesoscale activity in this area is relatively moderate and includes the formation of fronts, eddies and filaments in the CTZ (Hagen et al., 1996, Hernández-War and Nykjaer, 1997, Barton et al., 1998, Nieto et al., 2012). In particular, a recurrent filament has been detected, the C. Ghir filament, which has a highly variable length (30 to 300 km) (Hagen et al., 1996, Hernández-War and Nykjaer, 1997, Barton et al., 1998). North of C. Ghir, a recurrent positive wind stress curl is present, which has been attributed to the orographic influence of the Atlas Mountains and the concave shape of the coast south of C. Ghir (Hagen et al., 1996). All of these features generate high temporal and spatial variability in the oceanographic conditions in this area (Van Camp et al., 1991; Zhao et al, 2000; Sicre et al., 2001).

## 1.3.2. COMMUNITY STRUCTURE AND PRODUCTIVITY IN THE MOROCCO EBUS - CAPE GHIR

The effects of upwelling processes and of moderate mesoscale activity on the pelagic ecosystem off C. Ghir have been evaluated primarily in terms of the export of organic matter and the distribution of Chl-a (Head et al., 1996; Neuer et al., 2002; Freudenthal et al., 2001, 2002; Arístegui and Harrison 2002; García-Muñoz et al., 2005; Pelegrí et al., 2005a, 2005b), with few details on the structure of microbial communities and their spatio-temporal variability. Satellite surface Chl-a time series have shown that the region between 24 and 33°N presents weak seasonality and higher values are limited to a narrow coastal band, probably in response to nutrient limitation (Lauthuiliére et al., 2008). In areas close to C. Ghir, lower values of primary production and Chl-a have been found (Pelegrí et al., 2005a; Garcías-Muñoz et al., 2005; Demarcq and Benazzouz, 2015; Gómez-Letona et al., 2017), and have been associated with low nutrient concentrations, especially of silicates (Mines et al., 1982; Treguer and Le Corre, 1978; Fanning, 1992). A shortfall in the supply of phosphates in surface waters of this sub-region has also been observed (Arcos-Pulido et al., 2014), which, in turn, could inhibit the rates of N-fixation (Fernández et al., 2013).

In the Morocco sub-region, phytoplankton communities are mostly composed of microplanktonic diatoms and dinoflagellates. The most abundant diatom genera include

*Chaetoceros*, *Thalassiosira*, *Leptocylindrus*, and *Pseudo-nitzschia* (Makaoui et al., 2005; García-Muñoz et al., 2005), whereas among the dinoflagellates, the most common genera are *Protoperidinium*, *Prorocentrum* and *Gymnodinium*. The relative abundance of diatoms and dinoflagellates vary depending mainly on the differences in the intensity of coastal upwelling (Makaoui et al., 2005; Elghrib et al., 2012). In general, studies on microbial communities in this sub-region have been of short duration and with few details on their detailed structure. In this sense, part of this thesis aims to investigate the effects of variations in the oceanographic conditions on the spatial and temporal variability of microbial communities in the surface waters of the coastal upwelling and CTZ off C. Ghir.

## 1.4. **REFERENCES**

Abrantes, F., Cermeño, P., Lopes, C., Romero, O., Matos, L., Van Iperen, J., Rufino, M., Magalhães, V., 2016. Diatoms Si uptake capacity drives carbon export in coastal upwelling systems. Biogeosciences 13, 4099–4109.

Aguirre, C., Pizarro, O., Strub, P. T., Garreaud, R. D., Barth J., 2012. Seasonal dynamics of the near-surface alongshore flow off central Chile, J. Geophys. Res., 117, C01006, doi:http://dx.doi.org/10.1029/2011JC007379.

Alheit, J. and Niquen, M., 2004. Regime shifts in the Humboldt Current ecosystem. Prog. Oceanogr. 60(2-4): 201-222. doi:10.1016/j.pocean.2004.02.006.

Alvarez-Salgado, X.A., Doval, M.D., Borges, A.V., Joint, I., Frankignoulle, M., Woodward, E.M.S., Figueiras, F.G., 2001. Off-shelf fluxes of labile materials by an upwelling filament in the NW Iberian upwelling system. Prog. Oceanogr. 51, 321–337.

Anabalón, V., Morales, C.E., Escribano, H.R., Varas, M.A., 2007. The contribution of nano- and micro-planktonic assemblages in the surface layer (0–30 m) under different hydrographic conditions in the upwelling area off Concepción, central Chile. Prog. Oceanogr. 75, 396–414.

Arcos-Pulido, M., Rodríguez-Santana, A., Emelianov, M., Paka,V., Arístegui, J., Benavides, M., Sangrá, P., Machín, F., García-Weil, L., Estrada-Allis, S., 2014. Diapycnal nutrient fluxes on the northern boundary of Cape Ghir upwelling region Deep Sea Res. Part I, 840, pp. 100-109

Arístegui, J., Harrison, W.G., 2002. Decoupling of primary production and community respiration in the ocean: implications for regional carbon studies. Aquat. Microb. Ecol., 29, 199-209.

Arístegui, J., Barton, E.D., Tett, P., Montero, M.F., García-Muñoz, M., Basterretxea, G., Cussatlegras, A.S., Ojeda, A., de Armas, D., 2004. Variability in plankton community structure, metabolism, and vertical carbon fluxes along an upwelling filament (Cape Juby, NW Africa). Prog. Oceanogr. 62, 95–113.

Arístegui, J., Álvarez-Salgado, X.A., Barton, E.D., Figueiras, F.G., Hernández-León, S., Roy, C., Santos, A.M.P., 2006. Oceanography and fisheries of the Canary Current Iberian region of the Eastern North Atlantic. In: Robinson, A., Brink, K.H. (Eds.), The Global Coastal Ocean: Interdisciplinary Regional Studies and Syntheses, The Sea: Ideas and Observations on Progress in the Study of the Seas, vol. 14. Harvard University Press, pp. 877–931.

Arístegui J., Barton E.D., Álvarez-Salgado, X.A., Santos A.M.P., Figueiras, F.G., Kifani, S., Hernández-León, S., van Mason, E., Machú, E., Demarcq, H., 2009. Sub-regional ecosystem variability in the Canary Current upwelling. Prog. Oceanogr. 83, 33-48.

Azam, F., Fenchel, T., Field, J.G., Gray, J.S., Meyer-Reil, L.A., Thingstad, T.F., 1983. The ecological role of water-column microbes in the sea. Mar. Ecol. Prog. Series 10, 257–263.

Bakun, A. 1990. Global Climate Change and Intensification of Coastal Ocean Upwelling. Science 247(4939): 198-201.

Bakun, A., 1996. Patterns in the ocean: ocean processes and marine population dynamics. University of California Sea Grant, San Diego, California, USA, in cooperation with Centro de Investigaciones Biologicas de Noroeste, La Paz, Baja California Sur, Mexico. pp. 323

Bakun, A., Nelson, C.S., 1991. The seasonal cycle of wind stress curl in subtropical boundary current regions. J. Phys. Oceanogr. 21, 1815– 1834.

Bakun, A., Field, D.B., Redondo-Rodriguez, A., Weeks, S., 2010. Greenhouse gas, upwelling-favorable winds, and the future of coastal ocean upwelling ecosystems. Glob. Chang. Biol. 16 (4), 1213–1228. http://dx.doi.org/10.1111/j.1365-2486.2009.02094.x.

Baltar, F., Arístegui, J., Montero, M.F., Espino, M., Gasol, J.M., Herndl, G.J., 2009. Mesoscale variability modulates seasonal changes in the trophic structure of nano- and pico-plankton communities across the NW Africa–Canary Islands transition zone. Prog. Oceanogr. 83 (1–4), 180–188.

Barber, R.T., Chavez, F.P., 1983. Biological consequences of El Niño. Science 222, 1203–1210.

Barber, R.T., and Chavez, F.P. 1986. Ocean variability in relation to living resources during the 1982-83 el Niño. Nature 319: 279-285.

Barth, J.A., Pierce, S.D., Castelao, R.M., 2005b. Time-dependent, wind- driven flow over a shallow midshelf submarine bank. J. Geophys. Res. 110. http://dx.doi.org/10.1029/2004JC002761, C10S05.

Barton, E.D., Arístegui, J., Tett, P., Cantón, M., García-Braun, J., Hernández-León, S., Nykjaer, L., Almeida, C., Almunia, J., Ballesteros, S., Basterretxea, G., Escánez, J., García-Weill, L., Hernández-Guerra, A., López-Laatzen, F., Molina, R., Montero, M.F., Navarro-Pérez, E., Rodríguez, J.M., van Lenning, K., Vélez, H., Wild, K., 1998. The transition zone of the Canary Current upwelling region. Prog. Oceanogr. 41, 455–504.

Barton, E. D., Field, D. B., Roy, C., 2013. Canary Current upwelling: more or less? Prog. Oceanogr. 116, 167–178. doi: 10.1016/j.pocean.2013.07.007

Batten, M. L.,1997. Wind-forced modeling studies of currents, meanders, and eddies in the California Current system, J. Geophys. Res., 102(C1), 985-1010.

Böttjer, D., Morales, C.E., 2007. Nanoplanktonic assemblages in the upwelling area off Concepción (36°S), central Chile: abundance, biomass, and grazing potential during the annual cycle. Prog. Oceanogr. 75, 415–434.

Bozzano, G., Kuhlmann, H., Alonso, B., 2002. Storminess control over African dust input to the Moroccan Atlantic margin (NW Africa) at the time of maxima boreal summer insolation: a record of the last 220 kyr. Palaeogeography, Palaeoclimatology, Palaeoecology, 183 (2002), pp. 155-168, doi.org/10.1016/S0031-0182(01)00466-7

Bravo, L., Ramos, M., Astudillo, O., Dewitte, B., Goubanova, K., 2015**.** Seasonal variability of the Ekman transport and pumping in the upwelling system off central-northern Chile (~ 30°S) based on a high-resolution atmospheric regional model (WRF) Ocean Sci. Discuss., 12 (6), pp. 3003-3041, 10.5194/osd-12-3003-2015

Brink, K.H., Cowles, T.J., 1991. The coastal transition zone program. J. Geophys. Res. 96, 14637–14647.

Capone, D.G., Hutchins, D.A., 2013. Microbial biogeochemistry of coastal upwelling regimes in a changing ocean. Nat. Geosci., 6, 711–717.

Caron, D. A., Connell, P. E., Schaffner, R. A., Schnetzer, A., Fuhrman, J. A., Countway, P. D., Kim, D. Y., 2017. Planktonic food web structure at a coastal time-series site: I. Partitioning of microbial abundances and carbon biomass. Deep Sea Res. Part I: Oceanogr. Res. Pap. http://dx.doi.org/10.1016/j.dsr.2016.12.013.

Carr, M., Kearns, E., 2003. Production regimes in four eastern boundary current systems. Deep Sea Res. Part II 50, 3199–3221.

Carr, M., 2001. Estimation of potential productivity in Eastern Boundary Currents using remote sensing,.Deep Sea Res., 49, 59–80, doi:10.1016/S0967-0645(01)00094-7.

Carr, M.E., Strub, P.T., Thomas, A., Blanco, J.L., 2002. Evolution of 1996–1999 La Niña and El Niño conditions off the western coast of South America: a remote sensing perspective. J. Geophys. Res. 107, C12, 3236. doi:10.1029/2001JC001183.

Castelao, R. M., Mavor, T. P., Barth, J. A., Breaker, L. C., 2006. Sea surface temperature fronts in the California Current System from geostationary satellite observations, J.

Geophys. Res., 111, C09026, doi:10.1029/2006JC003541.

Chase, Z., Strutton, P. G., and Hales, B., 2007. Iron links river runoff and shelf width to phytoplankton biomass along the US West Coast. Geophys. Res. Lett., 34, 4 pp., L04607, doi:10.1029/2006GL028069, 2007.

Chavez, F.P., Messié, M., 2009. A comparison of eastern boundary upwelling systems. Prog. Oceanogr. 83, 80–96.

Chenillat, F., Franks, P. J. S., Rivière, P., Capet, X., Grima, N., Blanke, B., 2015. Mesoscale activity in the Southern California Current System. Biological dynamics of a coastal eddy, J. Geophys. Res. Oceans, http://dx.doi.org/10.1002/2015JC010826.

Correa-Ramirez, M. A., Hormazabal, S., Morales C.E., 2012. Spatial patterns of annual and inter-annual surface chlorophyll-a variability in the Peru–Chile Current System. Prog. Oceanogr., 92, 8-17. doi:10.1016/j.pocean.2011.07.008.

Correa-Ramirez, M., Morales, C.E., Letelier, R., Anabalon, V., Hormazabal, S., 2018. Improving the Remote Sensing Retrieval of Phytoplankton Functional Types (PFT) Using Empirical Orthogonal Functions: A Case Study in a Coastal Upwelling Region. Remote. Sens. 10, 498; doi:10.3390/rs10040498

Corredor-Acosta, J.A., Morales, C.E., Hormazabal, S., Andrade, I., Correa-Ramirez, M. A., 2015. Phytoplankton phenology in the coastal upwelling region off central- southern Chile (35ºS–38ºS): time-space variability, coupling to environmental factors, and sources of uncertainty in the estimates. J. Geophys. Res. Oceans. http://dx.doi.org/10.1002 /2014JC010330.

Corredor-Acosta, A., Morales C. E., Brewin, R. J., Auger, P. A., pizarro, O., Hormazabal S., Anabalón V., 2017. Phytoplankton Size Structure in Association with Mesoscale

Eddies off Central-Southern Chile: The Satellite Application of a Phytoplankton Size-Class Model. Remote Sens.10, 834; doi:10.3390/rs10060834

Crespo, B.G., Espinoza-González, I.O., Teixeira, I.G., Castro, C.G., Figueiras, F.G., 2012. Structure of the microbial plankton community in the NW Iberian margin at the end of the upwelling season. J. Marine Syst. 95, 50–60.

Cropper T. E., Hanna, E., Bigg G. R., 2015. Spatial and temporal seasonal trends in coastal upwelling off Northwest Africa, 1981-2012. Deep Sea Res. Part I Oceanogr. Res. pp. **86**, 94–111. doi:10.1016/j.dsr.2014.01.007.

Cuevas, L.A., Daneri, G., Jacob, B., Montero, P., 2004. Microbial activity and organic carbon flow in the upwelling area off Concepción (36°S), central Chile**.**Deep-Sea Res. Pt. II, 51 (2004), pp. 2427-2440.

Daneri, G., Dellarossa, V., Quinones, R., Jacob, B., Montero, P., Ulloa O., 2000. Primary production and community respiration in the Humboldt Current System off Chile and associated oceanic areas, Mar. Ecol., 197, 41–49.

Demarcq, H., 2009. Trends in primary production, sea surface temperature and wind in upwelling systems (1998–2007). Prog. Oceanogr. 83, 376–385, http://dx.doi.org/ 10.1016/ j.pocean. 2009.07.022.

Dugdale, R. C., Wilkerson, F. P., Minas H. J., 1995. The role of a silicate pump in driving new production, Deep Sea. Res. I, 42, 697-719.

Elghrib, H., Somoue, L., Elkhiati, N., Berraho, A., Makaoui, A., Bourhim, N., Salah, S. and Ettahiri, O., 2012. Phytoplankton distribution in the upwelling areas of the Moroccan Atlantic coast localized between 32°30'N and 24°N. Comptes rendus biologies, 335 (8), pp. 541– 554. doi:10.1016/j.crvi.2012.07.002

Everett, J.D., Macdonald, H., Baird, M.E., Humphries, J., Roughan, M., Suthers I.M., 2015. Cyclonic entrainment of preconditioned shelf waters into a frontal eddy, J. Geophys. Res. Oceans, 120, 677–691, doi:10.1002/2014JC010301.

Fanning, K.A., 1992. Nutrient Provinces in the Sea: Concentration Ratios, Reaction Rate Ratios, and Ideal Covariation. J. Geophys. Res. 97 (C4), 5693 – 5712.

Fernández, A., Graña, R., Mouriño-Carballido, B., Bode, A., Varela, M., Domínguez- Yanes, J.F., Escánez, J., de Armas, D., Marañón, E., 2013. Community N2 fixation and *Trichodesmium* spp. abundance along longitudinal gradients in the eastern subtropical North Atlantic. ICES J. Mar. Sci 70, 223–231.

Freon, P., Barange, M., Arístegui, J., 2009. Eastern boundary upwelling ecosystems: integrative and comparative approaches. Prog. Oceanogr. 83, 1–14.

Freudenthal, T., Meggers, H., Henderiks, J., Kuhlmann, H., Moreno, A., Wefer, G., 2002. Upwelling intensity and filament activity off Morocco during the last 250,000 years. Deep-Sea Res. I 49, 3655–3674.

Freudenthal, T., Neuer, S., Meggers, H., Davenport, R., Wefer, G., 2001. Influence of lateral particle advection and organic matter degradation on sediment accumulation and stable nitrogen isotope ratios along a productivity gradient in the Canary Islands region. Marine Geology 177, 93–109.

Fuhrman, J.A., Sleeter, T.D., Carlson, C.A., Proctor, L.A., 1989. Dominance of bacterial biomass in the Sargasso Sea and its ecological implications. Mar. Ecol. Progr. Series 57, 207-217.

Gammelsrød, T., Bartholomae, C.H., Boyer, D.C., Filipe, V.L.L., O'Toole, M.J., 1998. Intrusion of warm surface water along the Angolan–Namibian coast in February–March 1995: the 1995 Benguela Niño. S. Afr. J. Mar. Sci. 19, 41–56.

García-Muñoz, M., Arístegui, J., Pelegrí, J.L., Antoranz, A., Ojeda, A., Torres, M., 2005. Exchange of carbon by an upwelling filament off Cape Guir (NW Africa). J. Mar. Syst. 54, 83–95.

García-Reyes M., Sydeman W.J., Schoeman D.S., Rykaczewski R.R., Black B.A., Smit A.J. Bograd S.J., 2015. Under pressure: climate change, upwelling, and ecosystem boundary upwelling ecosystems, Front. Mar. Sci. 2, 109. http://dx.doi.org/10.3389/ fmars. 2015.00109.

Garreaud, R.D., Munoz, R.C., 2005. The low level jet off the west coast of subtropical South America: structure and variability. Mon. Weather Rev. 133, 2246–2261. http://dx.doi.org/10.1175/MWR2972.1.

González, H.E., Menschel, E., Aparicio, C., Barría, C., 2007. Spatial and temporal variability of microplankton and detritus, and their export to the shelf sediments in the upwelling area off Concepción, Chile ($36S), during 2002– 2005. Prog. Oceanogr. 75, 435–451.

Gómez- Letona, M., Ramos, A.G., Coca J., Arístegui, J., 2017. Trends in Primary Production in the Canary Current Upwelling System—A Regional Perspective Comparing Remote Sensing Models. Front.Mar.Sci., 14 November 2017.https://doi.org/10.3389/ fmars. 2017.00370

Grados, D., Bertrand, A., Colas, F., Echevin, V., Chaigneau, A., Gutiérrez, D., Vargas, G., Fablet, R., 2016. Spatial and seasonal patterns of fine-scale to mesoscale upper ocean dynamics in an Eastern Boundary Current System. Prog. Oceanogr. 142, 105–116.

Gruber, N., Lachkar, Z., Frenzel, H., Marchesiello, P., Münnich, M., McWilliams, J.C., Nagai, T., Plattner, G.K., 2011. Eddy-induced reduction of biological production in eastern boundary upwelling systems. Nat. Geosci. 4 (11), 787–792.

Hagen, E., Zulicke, C., Feistel, R., 1996. Near-surface structures in the Cape Ghir filament off Morocco. Oceanologica Acta 19, 577–598.

Hansell, D. A., Carlson, C. A., 2015. Dissolved organic matter in the ocean carbon cycle. Eos, 96 (15), 8-12.

Hansell, D. A., Carlson, C. A., Repeta, D. J., Schlitzer, R., 2009. Dissolved organic matter in the ocean: A controversy stimulates new insights. Oceanography 22, 52–61 (2009).

Head, E.J.H., Harrison, W.G., Irwin, B.I., Horne, E.P.W., Li, W.K.W., 1996. Plankton dynamics and carbon flux in an area of upwelling off the coast of Morocco. Deep-Sea Res. I 43, 1713–1738.

Hernández-Guerra, A., Nykjaer, L., 1997. Sea surface temperature variability off north-west Africa: 1981–1989. Int. J. Rem. Sens. 18, 2539–2558.

Hernández-Guerra, A., Fraile-Nuez, E., Lopez-Laatzen, F., Martínez, A., Parrilla, G., Vélez-Belchí, P., 2005. Canary Current and North Equatorial Current from an inverse box model. J. Geophys. Res. 110, C12019. doi:10.1029/ 2005JC003032.

Hill, A.E., Hickey, B.M., Shillington, F.A., Strub, P.T., Brink, K.H., Barton, E.D., Thomas, A.C., 1998. Eastern Ocean boundaries. In: Robinson, A.R., Brink, K.H. (Eds.), The Sea, Vol. 11. Global Coastal Ocean: Regional Studies and Syntheses the Sea. John Wiley and Sons, New York, pp. 29–67.

Hormazabal, S., Shaffer, G., Leth, O., 2004. Coastal transition zone off Chile. J. Geophys. Res.-Oceans 109(C1): // 000188867600002.

Hormazabal, S., Combes, V., Morales, C. E., Correa-Ramirez, M. A., Di Lorenzo E. and Nuñez S., 2013. Intrathermocline eddies in the coastal transition zone off central Chile (31–41°S). J. Geophys. Res. Oceans, 118, 4811-4821, doi:10.1002/jgrc.20337.

Hösen, E., Möller, J., Jochumsen, K.,and Quadfasel, D., 2016. Scales and properties of cold filaments in the Benguela upwelling system off Lüderitz, J. Geophys. Res. Oceans, 121, 1896-1913, doi:10.1002/2015JC011411.

Hutchings, L., Pitcher, G.C., Probyn, T.A., Bailey, G.W., 1995. The chemical and biological consequences of coastal upwelling. In: Summerhayes, C.P., Emeis, K.-C., Angel, M.V., Smith, R.L., Zeitzschel, B. (Eds.), Upwelling in the Ocean Modern Processes and Ancient Records. Dahlem Workshop Reports. Environmental Sciences Research Report 18. Wiley, pp. 67–72.

Hutchings, L., van der Lingen, C., Shannon, L., Crawford, R., Verheye, H.M.S., Bartholomae, C., van der Plas, A., Louw, D., Kreiner, A., Ostrowski, M., Fidel, Q., Barlow, R., Lamont, T., Coetzee, J., Shillington, F., Veitch, J., Currie, J., Monteiro, P. 2009. The Benguela Current: an ecosystem of four components. Prog. Oceanogr. doi:10.1016/j.pocean.2009.07.046.

Hutchins, D.A., Hare, C.E., Weaver, R.S., Zhang, Y., Firme, G.F., DiTullio, G.R., Alm, M.B., Riseman, S.F., Maucher, J.M., Geesey, M.E., Trick, C.G, Smith, G.J., Rue, E.L., Conn, J., Bruland, K.W., 2002. Phytoplankton iron limitation in the Humboldt Current and Peru Upwelling. Limnol. Oceanogr. 47, 997–1011. http://dx.doi.org/10.4319/lo.2002.47.4.0997.

Hutchins, D.A., Bruland, K.W., 1998. Iron-limited diatom growth and Si:N uptake ratios in a coastal upwelling regime. Nature 393, 561–564. http://dx.doi.org/ 10.1038/31203.

Hyun, J.H., Kim, D., Shin, C. W., Noh, J. H., Yang, E. J., Mok, J. S., Kim, S. H., Kim, H. C., Yoo, S., 2009. Enhanced phytoplankton and bacterioplankton production coupled to coastal upwelling and an anticyclonic eddy in the Ulleung Basin. East Sea. Aquat. Microb. Ecol. 54(1), 45–54.

Jutla I.S., Jeub L.G.S., Mucha P.J.A. 2011. Generalized louvain method for community detection implemented in MATLAB. http://netwiki.amath.unc.edu/GenLouvain/GenLouvain.

Kim D., Yang, E. J., Kim, K. H., Shin, C.W., Park, J., Yoo, S., Hyun, J. H., 2011. Impact of an anticyclonic eddy on the summer nutrient and chlorophyll a distribution in the Ulleung Basin, East Sea (Japan Sea). ICES J. Mar. Sci. 69(1), 23–29.

Krause, J. W., Brzezinski, M. A., Goericke, R., Landry, M. R., Ohman, M. D., Stukel, M. R., and Taylor, A. G., 2015. Variability in diatom contributions to biomass, organic matter production and export across a frontal gradient in the California Current Ecosystem, J. Geophys. Res. Oceans, 120, 1032–1047, doi:10.1002/2014JC010472.

Lachkar, Z., and Gruber, N., 2011. What controls biological productivity in coastal upwelling systems? Insights from a comparative modeling study, Biogeosciences, 8, 9901–9941, doi:10.5194/bgd-8- 9901-2011.

Lachkar, Z., and Gruber, N., 2012. A comparative study of biological production in eastern boundary upwelling systems using an artificial neural network. Biogeosciences 9, 293–308.

Lassiter, A.M., Wilkerson, F.P., Dugdale, R.C., Hogue, V.E., 2006. Phytoplankton assemblages in the CoOP-WEST coastal upwelling area. Deep-Sea Res. Part II 53, 3063–3077.

Lauthuilière, C., Echevin, V., Lévy, M., 2008. Seasonal and intraseasonal surface chlorophyll-a variability along the northwest African coast. J. Geophys. Res.113, C05007. http://dx.doi.org/10.1029/2007JC004433.

Legendre, L., LeFèvre, J., 1991. From individual plankton cells to pelagic marine ecosystems and to global biogeochemical cycles. In: Demers, S. (Ed.), Particle Analysis in Oceanography. Springer, Berlin, pp. 261–300.

Leth, O., and Middleton J.F., 2004. A mechanism for enhanced upwelling off central Chile: Eddy advection, J. Geophys. Res., 109, C12020, doi:10.1029/2003JC002129.

Leth, O. and G Shaffer, G., 2001. A numerical study of the seasonal variability in the circualtion off central Chile. Jounal of Geophysical Rresearch 106(C10): 22229-22248.

Mackas, D., and Galbraith, M.D., 2002. Zooplankton distribution and dynamics in a North Pacific eddy of coastal origin: I. Transport and loss of continental margin species. J. Oceanogr. 58, 725–738.

Mackas, D., Strub, P.T., Thomas, A.C., Montecino, V., 2006. Eastern ocean boundaries pan-regional view. In: Robinson, A.R., Brink, K.H. (Eds.), The Sea. Harvard Press Ltd., Boston, pp. 21–60, Chapter 2.

Makaoui, A., Orbi, A., Hilmi, K., Zizah, S., Larissi, J., Talbi, M., 2005. L'upwelling de la côte atlantique du Maroc entre 1994 et 1998. Comptes Rendus Geosci. 337 (16), 1518–1524.

Marcello, J., Hernandez-Guerra, A., Eugenio, F., Fonte, A. 2011. Seasonal and temporal study of the northwest African upwelling system. Int. J. Rem. Sens. 32, 1843–1859.

Marchesiello, P., McWilliams, J.C., Shchepetkin, A., 2003. Equilibrium structure and dynamics of the California Current System. J. Phys. Oceanogr. 33, 753–783.

Marchesiello, P., Herbette, S., Nykjaer, L., Roy, C., 2004. Eddy-driven dispersion processes in the Canary Current upwelling system: comparison with the California system. GLOBEC International Newsletter 10, 5–7.

Menden-Deuer, S., and Lessard, D.J., 2000. Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. Limnol. Oceanogr., 45, 569-579.

Messié and F. Chavez. 2015. Seasonal regulation of primary production in eastern boundary upwelling systems, Prog. Oceanogr., 134,1–18.

Minas, H.J., Codispoti, L.A., Dugdale, R.C., 1982. Nutrients and primary production in the upwelling region off Northwest Africa. Rapports et Proces-verbaux des Réunions. Conseil International pour l'Éxploration de la Mer 180, 148–183.

Miranda, P.M.A., Alves, J.M.R., Serra, N., 2012. Climate change and upwelling: response of Iberian upwelling to atmospheric forcing in a regional climate scenario. Clim. Dyn. 40, 2813–2824.

Morales, C.E., González H.E., Hormazabal, S.E., Yuras, G., Letelier J., Castro L.R., 2007. The distribution of chlorophyll-a and dominant planktonic components in the coastal transition zone off Concepción, central Chile, during different oceanographic conditions. Prog. Oceanogr. 75(3):452-469.

Morales, C.E., Hormazabal, S., Andrade, I., Correa-Ramirez, M.A., 2013. Time-space variability of chlorophyll-a and associated physical variables within the region off Central-Southern Chile. Remote Sens. 5, 5550–5571.

Morales, C.E., Anabalon, V., Bento, J.P., Hormazabal, S., Cornejo, M., Correa-Ramirez, M.A., Silva, N., 2017. Front-eddy influence on water column properties, phytoplankton community structure, and cross-shelf exchange of diatom taxa in the shelf-slope area off Concepcion (36–37°S). J. Geophys. Res. Ocean, 122, 8944–8965.

Müller-Karger, F.E., Varela, R., Thunell, R., Luerssen, R., Hu, C., Walsh, J.J., 2005. The importance of continental margins in the global carbon cycle. Geophys. Res. Lett. 32, L01602.

Muñoz, R., and  Garreaud R., 2005. Dynamics of the low-level jet off the subtropical west coast of South America. Mon. Wea. Rev., 133, pp. 3661-3677

Nelson, D.M., and Tréguer, P., 1992. On the role of silicon as a limiting nutrient to Antarctic diatoms: evidence from kinetic studies in the Ross Sea ice-edge zone. Mar. Ecol. Progr. Ser. 80: 255-264

Neuer, S., Freudenthal, T., Davenport, R., Llinás, O., Rueda, M.J., 2002. Seasonality of surface water properties and particle flux along productivity gradient off NW Africa. Deep Sea Res. II 49, 3561–3567.

Nieto, N., Demarcq, H., McClatchie, S., 2012. Mesoscale frontal structures in the Canary Upwelling System: new front and filament detection algorithms applied to spatial and temporal patterns. Remote  Sens.  Environ. 123, 339– 346.

Nykjaer, L., Van Camp, L., 1994. Seasonal and interannual variability of coastal upwelling along Northwest Africa and Portugal from 1981 to 1991. J. Geophys. Res. 99 (C7), 14197–14207.

Painting, S.J.,  Moloney, C.L., Probyn, T.A., Tibbles, B., 1992. Microheterotrophic pathways in the southern Benguela upwelling system. S. Afr. J. Mar. Sci., 12, pp. 527-543

Pauly, D., Christensen, V., 1995. Primary production required to sustain global fisheries. Nature 374, 255–257.

Pelegrí, J, Arístegui J, Cana L, Gonzalez-Davila M, Hernandez-Guerra A, Hernandez-Leon S, Marrero-Dıaz A, Montero M, Sangra P, Santana-Casiano M., 2005a. Coupling between the open ocean and the coastal upwelling region off northwest africa: water recirculation and offshore pumping of organic matter. J. Marine Syst. 54(1-4):3–37

Pelegrí, J, Marrero-Dıaz A, Ratsimandresy A, Antoranz A, Cisneros-Aguirre J, Gordo C, Grisolıa D, Hernandez-Guerra A, Laiz I, Martınez A, Parrilla G, Perez-Rodrıguez P, Rodrıguez-Santana A, Sangra P., 2005b. Hydrographic cruises off northwest africa: the canary current and the cape ghir region. J. Marine Syst. 54(1-4):39–63

Pennington, J.T., Mahoney, K.L., Kuwahara, V.S., Kolber, D.D., Calienes, R., Chavez, F.P., 2006. Primary production in the eastern tropical Pacific: a review. Prog. Oceanogr. 69, 285–317. http://dx.doi.org/10.1016/j.pocean.2006.03.012

Philander, S. G. H., 1986. Unusual conditions in the tropical Atlantic Ocean in 1984. Nature, 332,236-238.

Renault, L., Dewitte, B., Falvey, M., Garreaud, R., Echevin, V., Bonjean, F., 2009. Impact of atmospheric coastal jets on SST off central Chile from satellite observations (2000–2007), J. Geophys. Res., 114, C08006, doi:10.1029/2008JC005083.

Renault, L., Dewitte, B., Marchesiello, P., Illig, S., Echevin, V., Cambon, G., Ramos, M., Astudillo, O., Minis, P., Ayers, J.K., 2012. Upwelling response to atmospheric coastal jets off central Chile: A modeling study of the October 2000 event. J. Geophys. Res., 117, C02030, doi: 10.1029/2011JC007446.

Sánchez, G.E., Pantoja, S., Lange, C.B., González, H.E., Daneri, G., 2008. Seasonal changes in particulate biogenic and lithogenic silica in the upwelling system off Concepción

(36 S), Chile, and their relationship to fluctuations in marine productivity and continental input. Cont. Shelf. Res. 28, 2594–2600.

Sánchez, G. E, Lange, C.B., González, H. E., Vargas, G., Muñoz, P., Cisternas, C., and Pantoja S., 2012. Siliceous microorganisms in the upwelling center off Concepción, Chile (36°S): Preservation in surface sediments and downcore fluctuations during the past ~150 years. Prog. Oceanogr., 92-95, 50-65.

Schafstall, J., Dengler, M., Brandt, P., Bange, H., 2010. Tidal-induced mixing and diapycnal nutrient fluxes in the Mauritanian upwelling region. J. Geophys. Res. 115, C10014, http://dx.doi.org/10.1029/2009JC005940.

Shaffer, G., Hormazábal, S., Pizarro, O., Djurfeldt, L., Salinas, S., 1999. Seasonal and interannual variability of currents and temperature over the slope off central Chile. J. Geophys. Res. 104, 29951–29961. http:// dx.doi.org/10.1029/1999JC900253.

Shannon, L.V., and Nelson, G., 1996. Wefer, G. (Ed.), The Benguela: large- scale features and processes and system variability. The South Atlantic: Present and Past Circulation, pp. 163–210.

Sherr, E. B., and Sherr, B. F., 2002. Significance of predation by protists in aquatic microbial food webs. Antonie van Leeuwenhoek, 81(1-4), 293-308.

Sicre, M.A., Ternois, Y., Paterne, M., Martinez, P., Bertrand, P., 2001. Climatic changes in the upwelling region off Cap Blanc NW Africa over the last 70 k year: a multi-biomarker approach. Organic Geochemistry 32, 981–990.

Sobarzo, M., Bravo, L., Donoso, L., Garcés-Vargas, J., Schneider, W., 2007. Coastal upwelling and seasonal cycles that influence the water column over the continental shelf off central Chile. Prog. Oceanogr. 75, 363–382.

Strub, P., Mesías, J., Montecino, V., Ruttlant, J., 1998. Coastal ocean circulation off western South America. In: Robinson, A., Brink, K. (Eds.), The Global Coastal Ocean. The Sea, vol. 11. John Wiley and Sons, Inc., N.Y., pp. 273–313.

Sydeman, W.J., García-Reyes, M., Schoeman, D.S., Rykaczewski, R.R., Thompson, S.A., Black, B.A., Bograd, S.J., 2014. Climate change and wind intensification in coastal upwelling ecosystems. Science 345, 77–80.

Thomas, A.C., Carr, M.E., Strub, P.T., 2001. Chlorophyll variability in eastern boundary currents. Geophysical Research Letters 28, 3421–3424. http:// dx.doi.org/10.1029 /2001GL013368.

Thomas, A.C., Strub, P.T., Weatherbee, R.A., James, C., 2012. Satellite views of Pacific chlorophyll variability: comparisons to physical variability, local versus nonlocal influences and links to climate indices. Deep Sea Res. Part II 77–80, 99– 116.

Tilstone, G.H., Míguez, B.M., Figueiras, F.G., Fermin, E.G., 2000. Diatom dynamics in a coastal ecosystem affected by upwelling: coupling between species succession, circulation and biogeochemical processes. Mar. Ecol. Prog. Ser. 205, 23–41.

Treguer, P., and Le Corre, P.,1978. The ratios of nitrate phosphate, and silicate during uptake and regeneration phases of the Moroccan upwelling regime. Deep-Sea Res., 26A, 163-184.

Thompson, G.A., 2004. Tintinnid diversity trends in the southwestern Atlantic Ocean (29 to 60° S). Aquat. Microb. Ecol. 35, 93–130.

Van Camp, L., Nykjaer, L., Mittelstaedt, E., Schlittenhakdt, P.,1991. Upwelling and boundary circulation off Northwest Africa as depicted by infrared and visible satellite observations. Progr. Oceanogr. 26, 357–402.

Vargas, C.A., and González, H.E., 2004a. Plankton community structure and carbon cycling in a coastal upwelling system. I. Bacteria, microprotozoans and phytoplankton in the diet of copepods and appendicularians. Aquat. Microb. Ecol. 34, 151–164.

Vargas, C.A., and González, H.E., 2004b. Plankton community structure and carbon cycling in a coastal upwelling system. II. Microheterotrophic pathway. Aquat. Microb. Ecol. 34, 165–180.

Wang, Y., Castelao, R.M., Yuan, Y., 2015. Seasonal variability of alongshore winds and sea surface temperature fronts in Eastern Boundary Current Systems, J. Geophys. Res. Oceans, 120, 2385–2400, doi:10.1002/2014JC010379.

Whitney, F.A., Crawford, W.R., Harrison, P.J., 2005. Physical processes that enhance nutrient transport and primary productivity in the coastal and open ocean of the subarctic NE Pacific. Deep-Sea Res. II 52, 681–706.

Wilkerson, F.P., Dugdale, R.C., Kudela, R.M., Chavez, F.P., 2000. Biomass and productivity in Monterey Bay, California: contribution of the large phytoplankton. Deep-Sea Res. Part II 47, 1003–1022.

Williams R.G. and Follows M. J.,2003. Physical transport of nutrients and the maintenance of biological production. In: “Ocean Biogeochemistry: The Role of the ocean carbon cycle in global change”. Editado por M. Fasham. Springer, pp. 19-51, ISBN: 3-540-42398-2

Yáñez, E., Barbieri, M. A., Silva, C., Nieto, K., Espíndola, F., 2001. Climate variability and pelagic fisheries in northern Chile. Prog. Oceanogr. 49, 581–596. doi: 10.1016/S0079-6611(01)00042-8

Yuras G., Ulloa, O., Hormazabal S., 2005. On the annual cycle of coastal and open ocean satellite chlorophyll off Chile (18 degrees-40 degrees S). Geophysical Research Letters 32(23): //000233936000001.

Zhao M., Eglinton G., Haslett S.K., Jordan R.W., Sarnthein M., Zhang Z., 2000. Marine and terrestrial biomarker records for the last 35,000 years at ODP site 658C off NW Africa. Organic Geochemistry. 31(9), pp. 919-930.

***Rimü mew kimün, Müñchüle rume***
***Ti aliwen, witralekey Müten***
*Del otoño aprendí, aunque las*
*hojas caigan el árbol sigue en pie*
***Idioma y Cultura mapuche***

# OBJECTIVES OF THE THESIS

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## 2. OBJECTIVES OF THE THESIS

Considering that EBUSs are highly relevant in terms of their large contribution to total biological productivity in the oceans, that these systems are characterized by high levels of oceanographic variability in both the space and time dimensions, and that climate change might significantly affect some or part of these systems through progressive intensification of wind-driven l upwelling, the main objectives of this thesis are to characterize the structure of microbial communities in two coastal upwelling systems which have different oceanographic conditions and to describe the spatio-temporal variability in the structure of these communities and in the forcing associated with these changes. The specific objectives of each chapter are detailed below.

CHAPTER 1. The structure of planktonic communities under variable coastal upwelling conditions off Cape Ghir (31°N) in the Canary Current System (NW Africa).

This chapter focuses on the effects of spatial (cross-shore transect with 7 stations) and temporal (5 dates: from December 2008 to October 2009) variations in oceanographic conditions on the structure of planktonic communities (functional groups, size and taxa composition, abundance and carbon biomass). The specific objective of the study was:

To characterize seasonal variation in oceanographic conditions of the coastal upwelling zone and the CTZ off C. Ghir and its influence on changes in the structure of microbial communities.

CHAPTER 2. Phytoplankton biomass and microbial abundances during the spring upwelling season in the coastal area off Concepción, central-southern Chile: Variability around a time series station .

This chapter focuses on the spatial variability of oceanographic conditions in the upwelling zone (data from St. 18 collected during monthly in the spring and each cruise, 8 stations located on the shelf and shelf break, in the area around St. 18 ) and its effects on the structure of the planktonic community (size fractionated chlorophyll-a and microbial abundances) in the upper layer during the upwelling season (springs of 2004, 2005 and 2006). The specific objective of the study was:

To evaluate the representativeness of St. 18 as typical of the coastal upwelling system in the central-southern region off Chile in terms of oceanographic variability and of microbial communities during the upwelling season.

CHAPTER 3. Micro-phytoplankton community structure in the coastal upwelling zone off Concepción (central Chile): Annual and interannual fluctuations in a highly dynamic environment.

In this chapter, annual and inter-annual variability in microbial community structure (total and taxa-specific abundance and biomass) and its association with oceanographic fluctuations were analyzed using in situ time series data (2002–2009) from a shelf station off Concepcion (36.5ºS), in the region of strong seasonal coastal upwelling in the southern HCS. The specific objective of the study was:

To characterize the seasonal and interannual oceanographic variability in the coastal upwelling zone off Concepción and its influence on the variations in the structure of micro - phytoplankton communities.

CHAPTER 4. 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)

In this chapter, mesoscale and submesoscale processes in the water column (eg. eddies, fronts) and phytoplankton distribution across the coastal upwelling and coastal transition zones off Concepción were characterized, and cross-shelf exchanges of diatom taxa were explored. The specific objective of the study was:

To evaluate the influence of front-eddy interactions on the structure of phytoplanktonic communities and the extent of diatom exchanges between the coastal upwelling zone and the CTZ off Concepción.

***Intelligence is the ability***
***to adapt to change***
*La inteligencia es la habilidad*
*para adaptarse al cambio*
***Hawking***

# CHAPTER 1

## The structure of planktonic communities under variable coastal upwelling conditions off Cape Ghir (31°N) in the Canary Current System (NW Africa).

**V. Anabalón, J. Arístegui, C.E. Morales, I. Andrade, M. Benavides, M.A. Correa-Ramírez, M. Espino, O. Ettahiri, S. Hormazabal, A. Makaoui, M.F. Montero, A. Orbi.**

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# 1

CHAPTER

# The structure of planktonic communities under variable coastal upwelling conditions off Cape Ghir (31°N) in the Canary Current System (NW Africa).

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## Abstract

Cape Ghir (~31°N), in the Canary Current System, is an area of permanent coastal upwelling with maximum intensity in summer–autumn, when a strong across-shore thermal gradient and increased mesoscale activity are present. The effects of spatial (cross-shore transect with 7 stations) and temporal (5 dates: from December 2008 to October 2009) variations in upwelling conditions on the structure of planktonic communities (functional groups, size and

taxa composition, abundance and carbon biomass) were investigated. Multivariate analysis of the environmental variables enabled both spatial separation of the stations, based primarily on differences in nutrient concentration, and a temporal distinction of upwelling phases, based mostly on differences in sea surface temperature and number of days favourable to upwelling. These clusters were also representative of the time–space variability in the planktonic communities, suggesting that upwelling conditions directly influence their structure. For most of the cruises, the microplankton (mainly diatoms and auto/mixotrophic dinoflagellates) made the highest contributions to photoautotrophic carbon (C) biomass but the nanoplankton (mainly flagellates and dinoflagellates) made the largest contributions to total chlorophyll-a (Chl-a). Mean heterotrophic:autotrophic biomass ratios (from pico-to microplankton during three cruises) were mostly ≤1 (normal pyramid), as expected for productive coastal areas, only when the contribution of mixotrophy was considered. A mixed composition of functional groups of autotrophs/mixotrophs in the coastal and coastal transition zones off C. Ghir is probably the result of the nutrient contents in the upwelled waters since potential silicate or nitrate limitation together with a relatively high C:Chl-a in the micro-phytoplankton were detected during some of the cruises. Temporal changes in diatom taxa with different nutrient requirements also suggested a strong influence of nutrients. The comparatively lower nutrient contents in the upwelled waters off Cape Ghir are linked to the regional circulation patterns, a relatively narrow shelf (lower residence time of the upwelled waters), a higher level of mesoscale activity, and with weak to moderate wind intensities for most part of the year.

## 3.1. Introduction

The coastal waters off NW Africa in the Canary Current System (CCS; 10–33°N) are among the most productive in the world in terms of pelagic and demersal resources (Arístegui and Montero, 2005; Arístegui et al., 2009; Chavez and Messié, 2009), sustained by the upwelling of cold, higher nutrient waters in the coastal band which stimulate high levels of primary production (up to 5 gC $m^{-2}$ $d^{-1}$) and of phytoplankton biomass (Chl-a up to 10 mg $m^{-3}$) (Van Camp et al., 1991; Freudenthal et al., 2001; Arístegui and Montero, 2005; Lauthuilière et al., 2008; Arístegui et al., 2009). Latitudinal shifts in the Azores subtropical high- pressure system and in the tropical deep-pressure system related to the Intertropical Convergence Zone (ITCZ) generate temporal variations in intensity of upwelling (Barton et al., 1998; Pelegrí et al., 2005a). In addition, other features (e.g. bathymetry, coastal geometry, and topography) contribute to strengthen the coastal upwelling processes, especially in the areas around capes. At least 3 main upwelling areas have been identified in this region (Marcello et al., 2011): between Cape Ghir and C. Juby (25–33°N); from C. Bojador to C. Blanc (20–25°N); and around C. Vert (12–20°N).

In the area off Cape Ghir (~31°N), coastal upwelling processes are favoured by the dominance of trade winds (NE direction) (Barton et al., 1998). This area is characterized by the presence of a submarine plateau (a branch of the Atlas Mountains) which extends offshore for ~150 km (Hagen et al., 1996; Barton et al., 1998). C. Ghir also displays high mesoscale activity, including the formation of fronts, eddies and filaments in the coastal transition zone (Hagen et al., 1996; Hernández-Guerra and Nykjaer, 1997; Barton et al., 1998; Nieto et al., 2012). In particular, a recurrent filament (C. Ghir filament) has been detected, having a highly variable length (from 30 to 300km) (Hagen et al., 1996; Hernández-Guerra and Nykjaer, 1997; Barton et al., 1998). North of C. Ghir, a high positive wind stress curl is also recurrent and it has been attributed to the orographic influence of the Atlas Mountains and the concave shape of the coastline just south of C. Ghir (Hagen et al., 1996). All these features stimulate considerable temporal and spatial variability in the oceanographic conditions in this area (Van Camp et al., 1991; Sicre et al., 2001). However, studies describing in detail the dynamics of coastal upwelling and mesoscale structures in the area off C. Ghir are still few and sporadic in time and space (Van Camp et al., 1991; Hagen et al., 1996; Nykjaer and Van Camp, 1994; Freudenthal et al., 2001, 2002). Only recently, the variability in upwelling conditions in this area, and the whole of the CCS, has been analyzed using a 20-year time series on winds and surface temperature (Marcello et al., 2011). Also, the mesoscale frontal and filament variability has been analyzed in detail for this system, using high resolution surface temperature data (Nieto et al., 2012). Altogether, these studies indicate that coastal upwelling off C. Ghir is almost permanent but with peaks during summer and fall, associated with a strengthening of the upwelling favourable winds and the formation of stronger coastal–ocean gradients in sea surface temperature (SST) during that period.

The effects of upwelling processes and mesoscale features on the pelagic ecosystem in the area off Cape Ghir have been assessed mostly in terms of organic matter export and Chl-a distribution (Head et al., 1996; Neuer et al., 2002; Freudenthal et al., 2001, 2002; Arístegui and Harrison, 2002; García-Muñoz et al., 2005; Pelegrí et al., 2005a, 2005b). Most of these studies have been of very short duration and with little detail on the structure of the planktonic communities. In areas adjacent to C. Ghir, like the Canary Islands, the spatio-temporal variability in the structure of planktonic communities in the coastal upwelling and coastal transition zones has been addressed in several studies (Hagen et al., 1996; Barton et al., 1998; Arístegui et al., 2002, 2004, 2009; Arístegui and Montero, 2005; Baltar et al., 2009). These studies have shown that variations in the intensity of upwelling winds and in the water column stratification strongly influence the structure of phytoplankton communities as well as primary production. However, these results have focused only on one or two plankton size fractions within the range of the phytoplankton components (pico- to microplankton). The exception is a study focused in the area of a filament off C. Juby (Arístegui et al., 2004); however, its observational period was short (2 consecutive weeks) and did not include estimates of C-biomass for each size or functional group, nor a detailed taxonomic composition of the organisms.

Based on the available knowledge, the question posed here is whether the spatial and temporal variations in the coastal upwelling conditions off Cape Ghir produce significant changes in the structure of the planktonic communities in the coastal band and the adjacent coastal transition zone. In line with the results from other upwelling areas in the CCS (Arístegui et al., 2004, 2009; Arístegui and Montero, 2005; Baltar et al., 2009), and in other coastal upwelling systems (González et al., 2007; Kudela et al., 2010; Crespo et al., 2012; Espinoza-González et al., 2012), we expected to find that periods of intense upwelling would favour the dominance of diatoms in the nearshore area, where the maxima in nutrient concentrations is usually found. In contrast, periods of weak upwelling or cessation of upwelling would be associated with an increase of smaller autotrophic components, especially of nanoplanktonic flagellates, and with a more homogeneous cross-shore distribution of the planktonic abundance and biomass. In these terms, this study evaluates the effects of variations in upwelling conditions, in its spatial and temporal dimensions, on the structure of planktonic communities in the coastal upwelling and coastal transition zones off C. Ghir.

## 3.2. Methods

### 3.2.1. Study area, oceanographic samples, and complementary satellite data

A total of 5 cruises were conducted off Cape Ghir (December 2008, and February, June, August, and October 2009) on board the Moroccan R/V ‘‘Amir Moulay Abdellah (AMA)’’, from the Institut National de Recherche Halieutique (INRH; 4 cruises), and the Spanish R/V ‘‘Sarmiento de Gamboa’’ (August 2009), from the Spanish Research Council (CSIC), in the frame of the CAIBEX project. During each cruise, a transect perpendicular to the coast (31°N) was sampled, including 7 stations from the coast (9.8°W) to 150 km offshore (11.2°W). The most coastal station (E1) was located at ~2.3 km from the coast (30 m depth); the stations closer to the coast (E1–E5) were ~10–17 km apart whereas those located farther offshore (E5–E7) were ~30–34 km apart (Fig. 1a).

Hydrographic data were obtained with a CTD Sea Bird SBE-9-11 equipped with a fluorescence sensor (WetStar). Temperature and salinity data were used to estimate water density (as sigma-t) and stratification intensity (J $m^{-3}$) according to Bowden (1983). Discrete seawater samples were collected with Niskin bottles (5L) for the analyses of macro-nutrients ($PO_4$, $SiO_2$, $NO_2$, and $NO_3$) and Chl-a (total, and 2 size fractions: <20 µm and <3 µm). Five depth levels (0, 25, DCM (depth of Chl-a maximum fluorescence), 90 and 150 m depth) were considered, except in the shallowest stations (E1: 0, 10, and 25 m; and E2: 0, 10, 25, 50, 75 or 90 m). Chl-a samples were analyzed by the fluorometric method (Holm-Hansen et al., 1965), with a Turner Designs 10AU fluorometer; nutrients were analyzed with a Technicon-Bran Luebbe AAII analyzer, following JGOFS recommendations (UNESCO, 1994).

Satellite data on winds, sea level, sea surface temperatures (SST), and Chl-a were analyzed to provide a wider coverage of the spatial and temporal dimension during which the in situ observations took place. Daily wind data (1/4° x 1/4° resolution) were derived from the combined product CCMP (Cross-Calibrated Multi-Platform Ocean Surface Wind Vector) L3.0, from the NASA Jet Propulsion Laboratory – Physical Oceanography Distributed Active Archive Center (PO.DAAC: ftp://podaac-ftp.jpl.nasa.gov). Wind stress and the number of days favourable to upwelling prior to the cruises were estimated from these data. Daily SST data (2 x 2 km resolution) were obtained from the AVHRR Pathfinder V5.0 product at the NOAA-NODC website (ftp://ftp.data.nodc.-noaa.gov /pub/data.nodc /pathfinder). Sea level height data were obtained from the combined processing of TOPEX/JASON (1/4° x 1/4° resolution) from the ERS altimeter, distributed by AVISO (http://aviso.oceanobs.com); the geostrophic velocity field was estimated from these data. Daily satellite images of Chl-a were derived from the HERMES Data Portal, where a merged product of ESA and NASA sensors (MERIS, MODIS and SeaWiFS) is available through the GlobColour Archive data (http://hermes.acri.fr/).

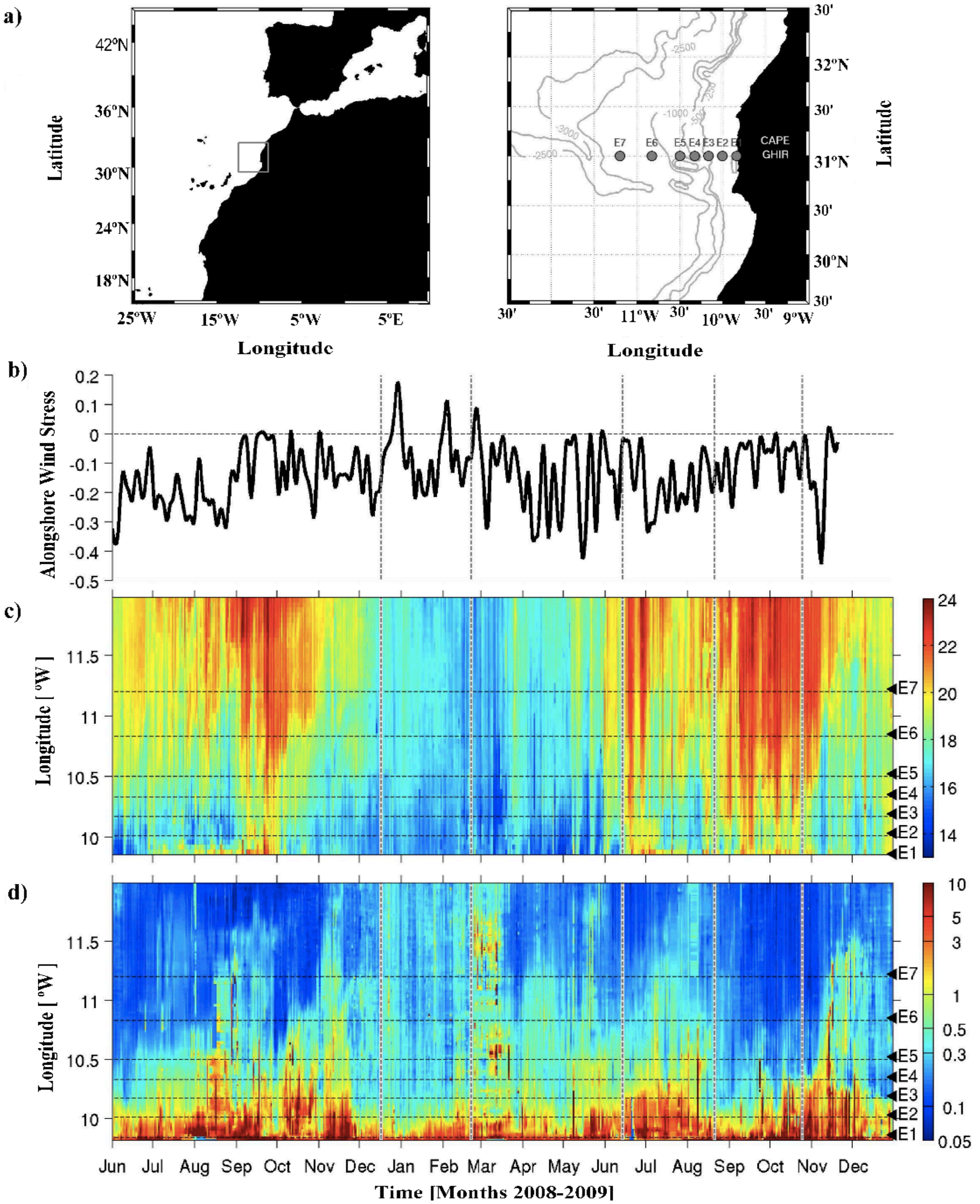


**Fig. 1.** (a) Region of study off Cape Ghir, NW Africa; bathymetry and location of the transect with the 7 stations (E1–E7) are shown; satellite time series data (June 2008– December 2009) on (b) daily mean wind stress (N m-$^{2}$), (c) Sea Surface Temperature (SST, in °C), and (d) Chlorophyll-a (Chl-a, in mg m-$^{3}$) in the area around the transect (30.5–31.5°N; 9.5–11.5°W). Vertical broken-lines indicate the dates of the cruises.

### 3.2.2. Plankton community structure: composition, abundance and biomass

Plankton samples at the same depth levels as for nutrients and Chl-a were obtained directly from the Niskin bottles, transferred to amber glass bottles (250 mL), and immediately preserved with an acid Lugol´s solution (2% final concentration), following the Utermöhl method (Villafañe and Reid, 1995). Nanoplankton (2–20 µm) and microplankton (20–200 µm) were analyzed with an inverted microscope (ZEISS AXIOVERT 35) with 1000x resolution. The enumeration lasted until at least 200 cells (nanoplankton) or 100 cells (microplankton) of the dominant taxa were registered in each sample. The following guides were used for taxonomic identification: Tomas, 1997; Ojeda, 1998; Anderson et al., 2002; Lynn and Small, 2002; Thompson, 2004.

Nanoplankton samples were also analyzed by epifluorescence microscopy to distinguish the cells according to their trophic function (autotrophs/mixotrophs or heterotrophs). Water samples were transferred to 50 mL tubes and immediately preserved with glutaraldehyde (1% final concentration; Gifford and Caron, 2000), and stored under cold (~4 °C) and dark conditions. Within 5 days after the sampling date (except in June 2009, when there was a delay of 3 months), subsamples of 20 mL (0–50 m depth) or 50 mL (90–150 m depth) were stained with a mixture of DAPI (4,6-diamidino-2-phenylindole) and Proflavine (3–6 diamino- acridine hemi-sulfate) at a final concentration of 5 µg mL$^{-1}$ (Verity and Sieracki, 1993), and then vacuum-filtered (<10 mmHg) onto black polycarbonate membrane filters (0.6 µm pore, 25 mm diameter). These filters were immediately mounted on glass slides and a drop of immersion oil was added before covering them with a glass cover slip; they were then stored at -20 °C in darkness until subsequent analysis (<8 months). Nanoplankton was enumerated (1000x magnification) with an epifluorescence microscope (ZEISS AXIOVERT 35) equipped with a digital camera plus UV (385–400 nm), blue (450–480 nm) and green (480–550 nm) filters. The enumeration included at least 100 cells of the most dominant taxa in each sample.

Picoplankton (0.2–2 µm) was enumerated by flow-cytometry (Becton–Dickinson FACScalibur with 488nm argon ion laser). Duplicate samples were collected in sterile cryovials (2 mL), immediately fixed with glutaraldehyde (0.1% final concentration), and frozen in liquid nitrogen (-196 °C) in darkness until analysis (Marie et al., 2000). For the enumeration of heterotrophic picoplankton (bacterioplankton), the samples were stained with SYTO-13 (Molecular Probes Inc.), using a dilution of the stock solution (1:10) to a final concentration of 2.5 µM; their signature was identified in a plot of side scatter (SSC) vs. the green fluorescence (FL1). The identification and enumeration of autotrophic picoplankton (*Prochlorococcus*, *Synechococcus*, and picoeukaryotes) in unstained samples was based on the analysis of multiple bivariate scatter plots of SSC, and red and orange fluorescence. The analyses were run at low speed for the bacterioplankton and at medium or high speed for the autotrophic picoplankton, until 10,000 events were acquired. A suspension of yellow-green 1 µm latex beads ($10^5$ and $10^6$ mL beads $mL^{-1}$ for autotrophs and bacterioplankton, respectively) was added as an internal standard (Polyscience Inc). The flow rate was determined volumetrically after every 10 samples run.

Plankton C-biomass was obtained from cell volume estimates for representative taxa in the different functional groups; volume measurements were taken during each of the cruises considering that cell size of a given taxa can display large variations (see Supplementary Table 1). For nano and microplanktonic cells, geometric models were applied (Balech, 1948; Chrzanowski and Simek, 1990; Alder, 1999; Sun and Lui, 2003). At least 20 cells of each type/taxa were randomly selected and measured using a micrometer grid as a reference; median values were obtained for each case. The following carbon/biovolume conversion factors in the literature were used after a preliminary evaluation which indicated that they provided the most conservative estimates: Menden-Deuer and Lessard (2000) for ciliates, dinoflagellates, and diatoms; Heinbokel (1978) for Tintinnids; and Børsheim and Bratbak (1987) for Flagellates. Also, a correction for biovolume estimates for the Lugol-fixed samples (microplankton) was applied, following Choi and Stoecker (1989). For the picoplankton, the following conversion factors were applied: 29 fg C cell$^{-1}$ for *Prochlorococcus* and 100 fg C cell$^{-1}$ for *Synechococcus* (Zubkov et al., 2000), and 1.5 pg C cell$^{-1}$ for picoeukaryotes (Zubkov et al., 1998). Bacterioplankton biomass was estimated assuming a conversion factor of 12 fg C cell$^{-1}$ (Fukuda et al., 1998).

The proportion between heterotrophic (H) and autotrophic (A) biomasses (H:A ratios), as an indicator of the trophic structure of communities in the oceans (Gasol et al., 1997), was also estimated. Flow-cytometry and epifluorescence microscopy allowed the distinction of the trophic function in the picoplankton and nanoplankton, respectively, but in the case of the microplankton this was derived from the literature and applied to specific taxa. Mixotrophy was not directly evaluated though it is common in dinoflagellates and ciliates (e.g. Stoecker et al., 1987; Bernard and Rassoulzadegan, 1994; Jacobson and Andersen, 1994; Kang et al., 2010; Jeong et al., 2010) but all cells with natural fluorescence were identified as autotrophs in the case of the pico and nanoplankton. In the case of microplanktonic dinoflagellates and ciliates which have been identified as mixotrophic species/genera in the literature, the approach of Stoecker et al. (1987, 1989, 1996) and Bernard and Rassoulzadegan (1994) was applied and by which 40% of the total biomass of mixotrophs is allocated to the autotrophic component. The H:A biomass ratios obtained with and without this correction were compared. Also, C:Chl-a were obtained from the estimates of C-biomass for autotrophs/ mixotrophs and of Chl-a, based on total and size fraction estimates.

### 3.2.3. Statistical analyses of data

All statistical analyses (either uni or multivariate) of the biological data were carried out using integrated values (see Table 2); depth has a strong influence on plankton distribution but the main focus of this study is on the horizontal and temporal variation (comparisons with non-integrated data were included in some cases as to evaluate the influence of depth). For the environmental variables, surface (temperature and salinity) and integrated (nutrients) data were used, in addition to the following data: wind stress (W), the number of days with winds favourable to upwelling prior to each cruise (WD), and the inshore–offshore SST gradient. Chl-a was not included in the multivariate analyses but its variation was analyzed separately with a non-parametric 2-way (spatial and temporal dimensions) ANOVA (Kruskal–Wallis), since the data displayed non-normality and/or non-homogeneity of variance (Kolmogorov–Smirnov and Browne Forsythe tests; Zar, 1984).

Multivariate analyses were performed with the PRIME software v.6 (Clarke and Warwick, 2001; Clarke and Gorley, 2006) to explore the spatial and temporal variations in the structure of the planktonic communities, as well as their association with the environmental conditions. Data were transformed in the environmental matrix (log n + 1) and the biological matrix (square root) to normalize them and to avoid asymmetry between the two matrices. In applying community similarity analyses, the Euclidean distance was used for the environmental variables and Bray–Curtis for the biological data. The spatial and temporal variations in the environmental and biological data were analyzed separately with he CLUSTER (hierarchical clustering) and MDS (non-metric multidimensional scaling) routines; the significance of the clusters was verified with the SIMPROF (similarity profile) routine. The ANOSIM (analysis of similarities) and SIMPER (species contributions) routines were used to assess the similarities and the dissimilarities between clusters with respect to the temporal and spatial variability in the biological matrix (at the level of functional groups and genera/morphological types). The associations between the biological data and the environmental variables were analyzed with the BIO-ENV and RELATE routines. In turn, the best combinations of variables determined by BIO-ENV were subjected to further analysis (LINKTREE) to determine the variable(s) which best represented the separation of the biological components into different groups/clusters.

## 3.3. Results

### 3.3.1. Variability in the meteorological and oceanographic conditions

satellite time series data (June 2008–December 2009) of wind stress, SST and Chl-a for the area around Cape Ghir (30.5–31.5°N, 9.5–11.5°W) are presented in Fig. 1. Wind upwelling favourable conditions were predominant during the whole period (Fig. 1b); favourable events during winter months (December–February) and relaxation episodes during the fall (September–October) appeared occasionally. SST (Fig. 1c) displayed a seasonal pattern, with colder waters in winter–spring (December to June) and warmer in summer–autumn (June to December); also, the cross-shore SST gradient was stronger during the latter. The highest Chl-a values (>2 mg $m^{-3}$) were concentrated near the coast (<25 km offshore) and persisted throughout the period; offshore extensions of such values were detected during the summer–autumn period and during short events in winter (Fig. 1d).

The satellite-derived distributions of winds, SST and Chl-a over a larger area around Cape Ghir (29.5–32.5°N, ~9.0–12.5°W) indicated that winds were upwelling favourable before and/or during the cruises, except in June-09 (Fig. 2, left panels). Average SST values had a nearly homogeneous horizontal distribution during the winter cruises whereas a strong thermal gradient, perpendicular to the coast, was evident during the summer–autumn cruises; in June-09, this gradient was mostly N–S in direction (Fig. 2, central panels). Mesoscale structures were also present during some of the cruises: a filament (sensu Van Camp et al., 1991; Pelegrí et al., 2005a, 2005b) during August-09 and October-09, and jets, meanders, and eddies in other cases (Fig. 2 central panels). The highest Chl-a values (≥1mg $m^{-3}$) were concentrated near the coast but intermediate values (0.5–1 mg $m^{-3}$) extended offshore during the winter cruises, mainly in February-09 (Fig. 2, right panels).

Water column temperatures (14–20 °C) and salinities (36.0–36.6) during the field observations off Cape Ghir were indicative of the presence of North Atlantic Central West Water (NACW). Water density, dominated by temperature variations, and temperature-salinity diagrams (Fig. 3) confirmed that the water column structure (0–200 m depth) was homogeneous during the winter cruises in comparison to the summer–autumn cruises, when stronger stratification occurred (Table 1). $NO_3$ and $NO_2$ concentrations (Table 1), as mean water column values (0–150 m, or shallower in E1 and E2), were highest during the winter cruises and lower during the summer–autumn cruises; the same pattern was observed for the integrated data (0–150 m), except that $NO_3$ was highest only during the December-08 cruise. In contrast, $PO_4$ and $SiO_2$ did not show a clear pattern of variation between winter and summer–autumn periods (as mean or integrated values) but maximum values were registered in December-08.

A preliminary analysis of wind direction and intensity (Fig. 2), the ascent of the 26.7 kg $m^{-3}$ isopycnal in the coastal zone (Fig. 3), and the SST gradient (Table 1) obtained from the field observations off Cape Ghir, allowed us to distinguish the following phases: weak upwelling (WEUP: December-08 and February-09), relaxation (RELAX: June-09), and moderate upwelling (MOUP: August-09 and October-09). A 2-way ANOSIM analysis of the environmental data (see specifications in Section 2.3) revealed significant variability between stations (coastal and coastal transition stations) and phases (correlation, r = 0.52, P = 0.001), except between RELAX and MOUP (r = 0.008, P = 0.41). In turn, CLUSTER and

MDS analyses identified the following clusters (Fig. 4): (A) the most coastal station (E1), and (B) the rest of the stations separated in two different phases, WEUP (C) and MOUP (D); RELAX was represented by a mixture of WEUP and MOUP conditions (SIMPROF, $P = 0.001$). The separation of station E1 from the rest does not represent a bias, due to its shallowness (25 m depth), since the same analysis using non-integrated data or an integration of only the top 25 m water column for all the stations/cruises displayed the same pattern. The variables that contributed most to the separation of these clusters (SIMPER analysis) were: (a) nutrient concentration ($SiO_2$, $PO_4$, $NO_3$): WEUP vs. E1 (similarity distance = 30), (b) nutrient concentration ($SiO_2$, $PO_4$) and SST: MOUP vs. E1 (s. distance = 30), and c) water density, SST and WD: WEUP vs. MOUP (s. distance = 15).

Total Chl-a in the water column (Fig. 5, left panels), which includes pigments from autotrophs and/or mixotrophs, showed a similar pattern of distribution as the satellite-derived data (Fig. 2). The distributions of Chl-a in the nano- and picoplankton (Fig. 5, right-central and right panels) were significantly different between the 3 clusters described above (Kruskal–Wallis, $n = 35$, $p < 0.05$) but not in the case of the microplankton (Fig. 5 left- central panels). The contribution of Chl-a in the nanoplankton size fraction to total Chl-a was from moderate to mostly high (30–93%) during the cruises, with a maximum at the coastal stations during RELAX and MOUP (October-09); their mean contribution (>50%), however, was the highest as a size fraction. Chl-a in the microplanktonic fraction was highly variable (2–85%), with maxima at the most coastal stations during contrasting phases (February-09 and October-09). The contribution of the picoplankton size fraction to total Chl-a was mostly in the low range (<25%), except during August-09 when it was 37% (Table 1).

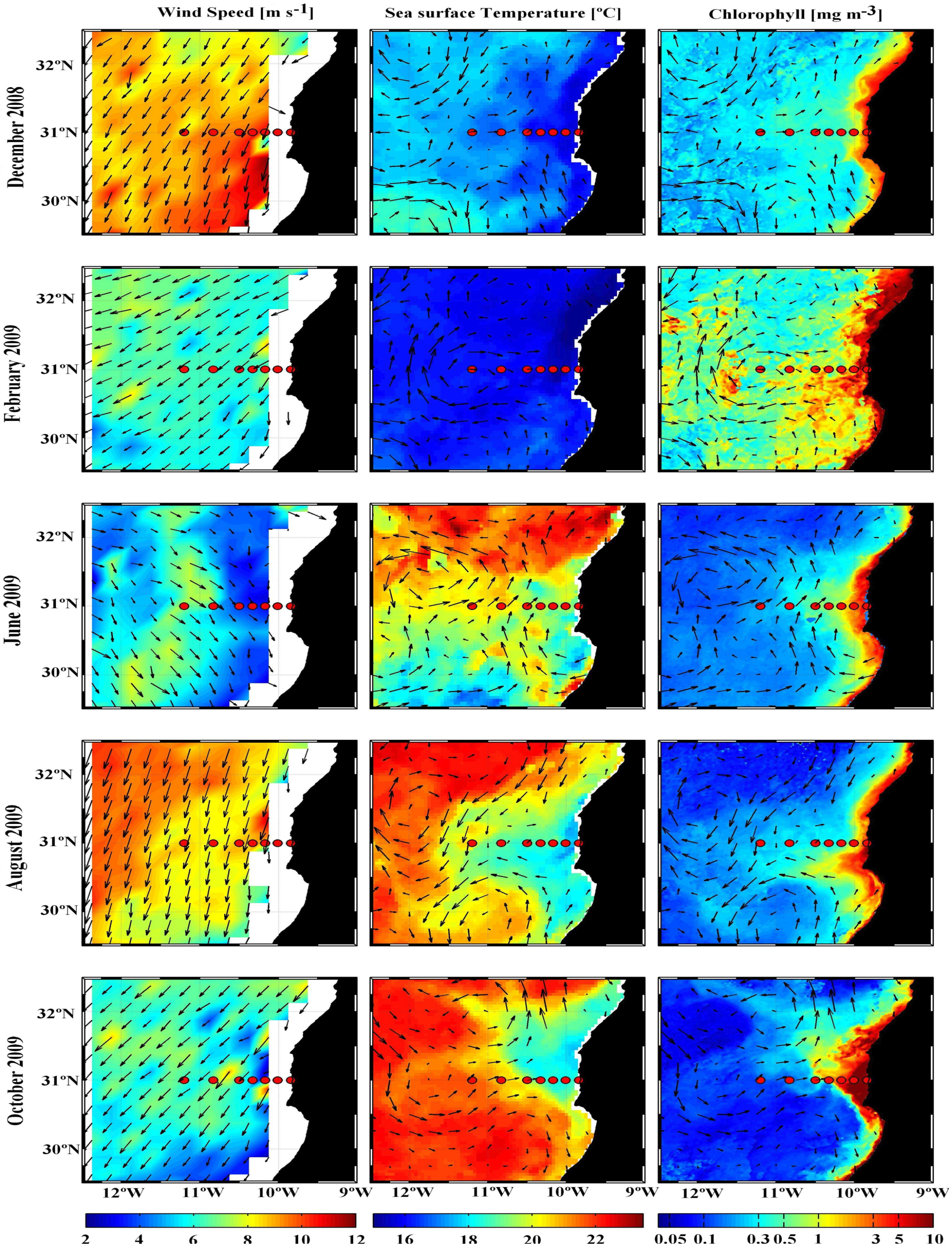
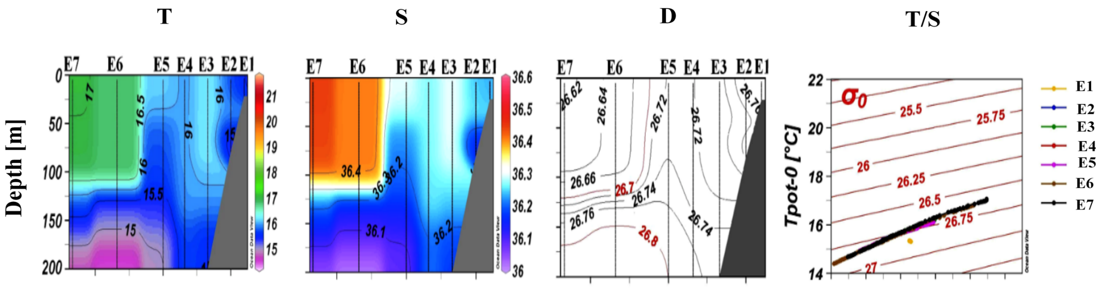


Fig. 2. Satellite data for the region around Cape Ghir (29.5–32.5°N; 9.0–12.5°W) during the in situ observations: wind velocity and direction (left panels), SST (central panels), and Chl-a (right panels). The data correspond to 5 days averages (3 d before and 2 d during each cruise). The geostrophic velocity field (cm $s^{-1}$) is also shown in the latter two.

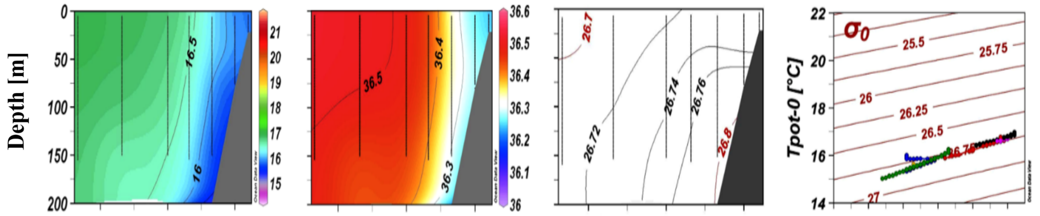
### 3,3,2, THE STRUCTURE OF PLANKTONIC COMMUNITIES UNDER VARYING OCEANOGRAPHIC CONDITIONS

The following nano and microplanktonic components (as functional groups, taxa and/or morphological types) were identified during the cruises off Cape Ghir: (a) 43 diatom (DIAT) genera (size range: 10–200 µm); (b) 27 dinoflagellate (DIN) genera (8–150 µm); (c) 32 ciliate (CIL) genera (15–150 µm); (d) 8 flagellate (FL) genera and 6 morphotypes, mostly in the nanoplanktonic size range, except for 4 colonial forms (20–80 µm); and (e) 2 silicoflagellate (SIL) genera (see Supplementary Table 1). A small number of coccolithophores were occasionally found but were not included in the analysis since the preservation technique applied was not appropriate for this group.

Cell abundance in the nanoplankton (Table 2; Fig. 6) was dominated by nanoflagellates (NFL) and, secondarily (an order of magnitude lower), by nanodinoflagellates (NDIN). The contribution of autotrophic/mixotrophic NFL represented >80% of all NFL, as was the case for NDIN, except in February-09 (<40%). Microplankton abundance (Table 2; Fig. 7) was dominated by microdiatoms (MDIAT), followed by colonial flagellates (MFL) and microdinoflagellates (MDIN). In both cases, the nano and microplankton, cells were mostly concentrated in the upper 50 m depth; nanoplankton accounted for the largest proportion (74–96%) of the total abundance during the cruises whereas the microplankton contributed most to the total biomass (69–82%).



December 2008



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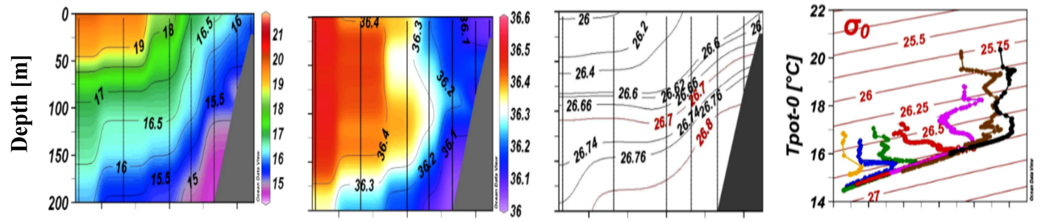

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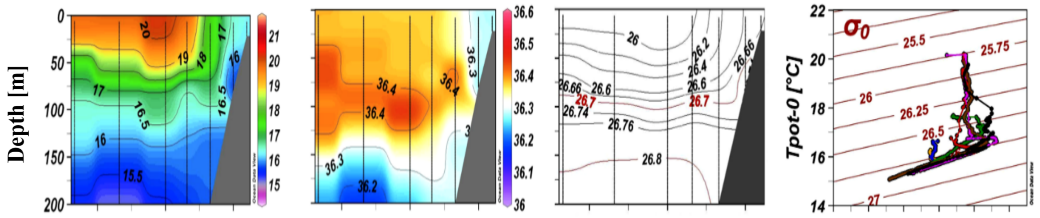

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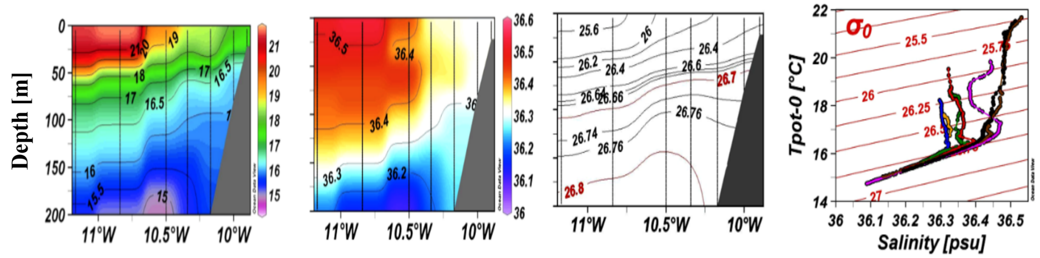

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**Fig. 3.** Distribution of oceanographic variables during the five cruises off Cape Ghir: temperature (T, °C; left panels), salinity (S, central-left panels), sigma-t (D, kg m$^{-3}$ central-right panels), and Temperature/Salinity (T/S) diagrams (right panels).

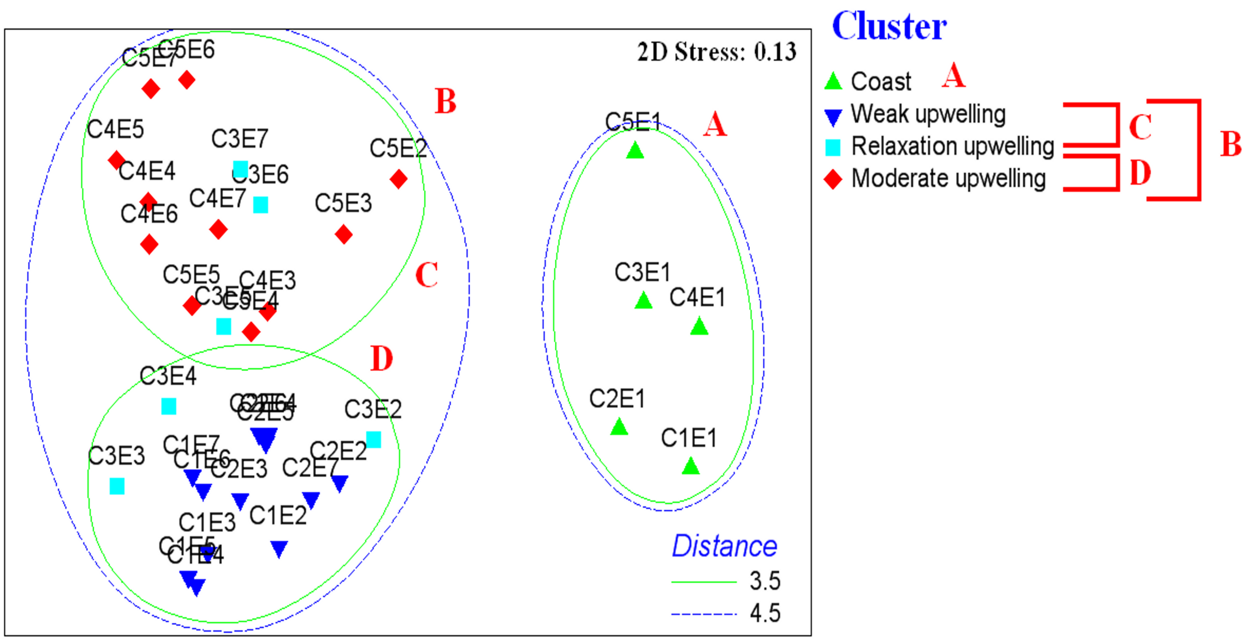


Fig. 4. Multidimensional scaling (MDS) and cluster analyses based on the environmental variables (meteorological and oceanographic) during the cruises off Cape Ghir. The nomenclature identifies the cruises (C1 to C5) and the stations (E1 to E7); for reference, see Table 1 and Fig. 3.

| Cruises | W | WD | SSTs | Ø | SST | SSTd | SS | $NO_3$ | $NO_2$ | $PO_4$ | $SiO_2$ | Chla T | Chl-a M | Chl-a N | Chl-a P |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Dec-08 (C1)<br>WEUP | -0.15 ±0.10 | 8 | 16.9 ±0.1 | 8±8 | 16.2±0.6 | 1.7 | 36.6 ±0.5 | 690 ±320<br>5.0 ±2.7 | 90 ±40<br>0.8 ±0.1 | 80 ±30<br>0.7 ±0.2 | 268 ±121<br>2.6 ± 1.4 | 53 ±20<br>0.5 ±0.2 | 15 ±9<br>0.1±0.1 | 31 ±15<br>0.3±0.1 | 6 ± 4<br>0.05± 0.03 |
| Feb-09 (C2)<br>WEUP | -0.06 ±0.04 | 1 | 16.7 ±0.2 | 6±4 | 16.5±0.5 | 1.3 | 36.4 ±0.1 | 310 ±140<br>2.6 ±1.4 | 90 ±50<br>0.7 ±0.2 | 50 ±20<br>0.5 ±0.1 | 280 ±110<br>2.1 ±0.8 | 56 ±25<br>0.7 ±0.8 | 20 ± 9<br>0.2 ±0.3 | 32 ±15<br>0.4 ±0.5 | 5 ± 4<br>0.04± 0.03 |
| Jun-09 (C3)<br>RELAX | -0.1 ±0.14 | -2 | 19.2 ±1.3 | 71±41 | 18±1.7 | 3.5 | 36.2 ±0.2 | 380 ±150<br>1.9 ±1.4 | 60 ±30<br>0.5 ±0.3 | 60 ±30<br>0.5 ±0.3 | 270 ±120<br>2.0 ±1.3 | 81 ±47<br>0.9 ±1.1 | 18 ±15<br>0.2 ±0.3 | 58 ±60<br>0.6 ±0.8 | 6 ± 3<br>0.06±0.06 |
| Aug-09(C4)<br>MOUP | -0.13 ±0.10 | 6 | 19.3 ±0.4 | 101±49 | 18.5±1.8 | 4 | 36.6 ±0.5 | 390 ±150<br>2.5 ± 1.8 | 60 ±30<br>0.5 ±0.3 | 70 ±30<br>0.7 ±0.2 | 250 ±90<br>2.0 ±0.7 | 35 ±15<br>0.4 ±0.3 | 4 ±4<br>0.05 ±0.1 | 18 ±9<br>0.2 ± 0.2 | 13 ± 6<br>0.14±0.11 |
| Oct-09 (C5)<br>MOUP | -0.13± 0.01 | 2 | 20.6 ±0.6 | 122±54 | 19.5±1.6 | 3.9 | 36.4 ±0.1 | 340 ±140<br>2.3 ± 1.7 | 30 ±30<br>0.2 ±0.2 | 50 ±20<br>0.6 ±0.2 | 280 ±110<br>2.4 ±1.3 | 76 ±48<br>0.9 ±1.4 | 26 ±21<br>0.4 ±1.0 | 44 ± 53<br>0.4 ± 0.5 | 5 ± 5<br>0.07±0.07 |

Table 1. Meteorological and oceanographic conditions during the cruises off Cape Ghir. Satellite-derived data include: wind stress (W, N $m^{-2}$), number of days favourable to upwelling before each cruise (WD), and Sea Surface Temperature (SSTs, °C); W and SSTs: mean values ± one standard deviation of 5 days (4 prior to and the day of each cruise) in the area between 30.5-31.5ºN and 9.5-11.5ºW. Water column data include mean values ± one standard deviation for all the stations in each cruise: a stability index (Ø, J $m^{-3}$) for the upper 150 m; ses surface temperature (SST, °C); the SST gradient (ºC) along the transect (SSTd); surface salinity (SS); nutrient concentrations in the upper 150 m depth (nitrate ($NO_3$), nitrite ($NO_2$), phosphate ($PO_4$), silicate (Si $O_2$)), as integrated (first row; mmol $m^{-2}$) and non-integrated (second row; mmol $m^{-3}$) values; and chlorophyll-a (Chl-a) in the upper 150 m depth (total and size fractions: micro (M), nano (N), and picoplankton (P)), as integrated (first row; mg $m^{-2}$) and non-integrated (second row; mg $m^{-3}$) values.

Cell abundance in the nanoplankton (Table 2; Fig. 6) was dominated by nanoflagellates (NFL) and, secondarily (an order of magnitude lower), by nanodinoflagellates (NDIN). The contribution of autotrophic/mixotrophic NFL represented >80% of all NFL, as was the case for NDIN, except in February-09 (<40%). Microplankton abundance (Table 2; Fig. 7) was dominated by microdiatoms (MDIAT), followed by colonial flagellates (MFL) and microdinoflagellates (MDIN). In both cases, the nano and microplankton, cells were mostly concentrated in the upper 50 m depth; nanoplankton accounted for the largest proportion (74–96%) of the total abundance during the cruises whereas the microplankton contributed most to the total biomass (69–82%).

Picoplankton data were only available for 3 cruises (December- 08, February-09, and August-09). Depth integrated abundance and biomass of the heterotrophic bacterioplankton (HB) and the autotrophic picoplankton (APP) are represented in Table 2. The HB accounted for the largest proportion of the total picoplankton abundance (91–99%) whereas their contribution to biomass was moderate to high (19–59%). The contribution of APP to picoplanktonic biomass was moderate to high (41–81%) despite its low relative abundance (1–9%). *Prochlorococcus* (PRO) and *Synechococcus* (SYN) contributed the most (65–84%) to total APP abundance whereas the picoeukaryotes (PEU) made similar or greater contributions to total APP biomass (54–89%). Biomass changes in the APP components (Table 2, Fig. 8) were well represented by Chl-a in that size fraction (Fig. 5, right panels).

Depth integrated abundance and biomass of the nano and microplanktonic components (as functional groups, taxa and/or morphological types) were significantly different between phases and sampling stations (2-way ANOSIM, correlation r = 0.70, P = 0.001; r = 0.37, P = 0.004, respectively), as reflected in the MDS and cluster analyses. In terms of abundance

(Fig. 9a), the main groups or clusters identified were coincident with those detected for the environmental variables: (A) the most coastal Station (E1), and (B) the rest of stations but differentiated by upwelling phases: WEUP (cluster C) and MOUP + RELAX (cluster D). For the biomass (Fig. 9b), the same 2 clusters were identified (A and B); in this case, B was subdivided in 3 clusters: WEUP (C), MOUP (D), and RELAX (E). The separation into these clusters was significant for both, abundance and biomass (SIMPROF, P = 0.001). In contrast to the hydrographic clusters, the formation of cluster A is a result of its shallowness since these clusters do not appear when integrated data from the top 25 m depth were analyzed for all the cruises; however, E1 station still remained as a separate subgroup in the latter case and, therefore, we kept it as a cluster in the interpretation of the results.

The analysis of dissimilarity (SIMPER) applied to the different phases identified above indicated that, in terms of abundance (Table 3), FL and DIN contributed the most to the separation between WEUP and MOUP (FL highest in WEUP and DIN in MOUP); DIAT was second in relevance (highest in MOUP). In terms of biomass, DIN contributed the most to the separation between WEUP and RELAX (highest in RELAX), and between WEUP and MOUP (highest in MOUP); CIL contribution was also important between WEUP and RELAX (highest in WEUP) whereas DIAT separated MOUP and RELAX (highest in RELAX), and WEUP and MOUP (highest in MOUP).

At a more specific level, the greatest contributions to dissimilarity in abundance between different phases were provided by NFL (20%) as a size fraction (mostly by NFL-1 type; 8%)and by DIN Gymnodiniaceae (19%; mostly by *Gymnodinium* spp.), followed by DIAT Bacillariaceae (9%).

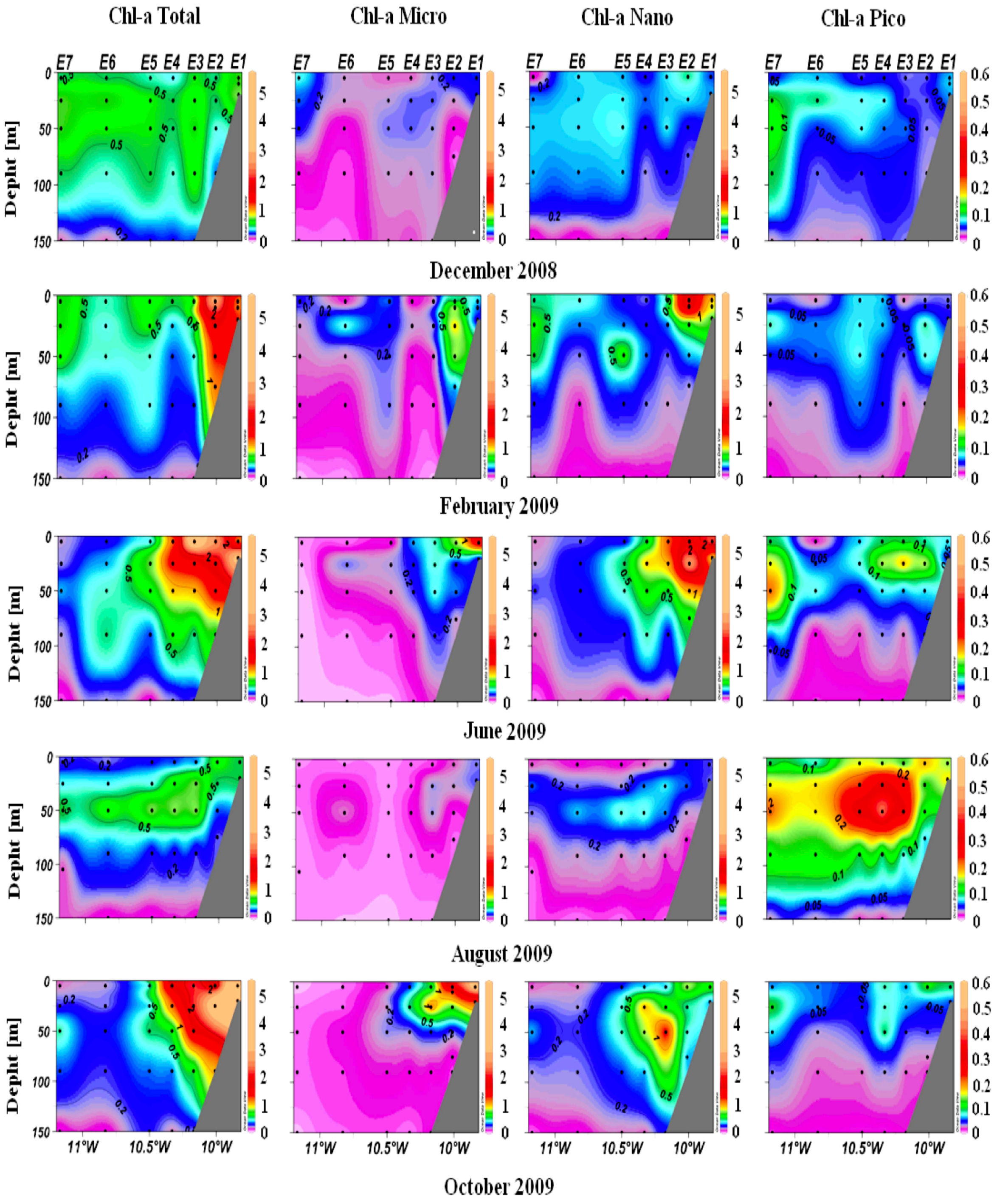


**Fig. 5.** Distribution of Chl-a concentration (mg $m^{-3}$) off Cape Ghir, as total and by size fractions: Micro- (<20 µm), Nanoplankton (>3 and <20 µm), and Picoplankton (<3 µm). Notice the different scale in the case of the picoplanktonic fraction.

In terms of biomass, the most important contributors to the differences between phases were DIN Gymmodiniaceae (12–16%), followed by DIN Ceratiaceae (11–14%) and CIL Strombidiidae (3– 7%). Among the DIAT, the Thalassiosiraceae, Rhizosoleniaceae and Coscinodiscaceae were also relevant (20%). Families identified during this study are described in Supplementary Table 1. SIMPER analysis for the abundance and biomass in the coastal stations (E2–E4) and coastal transition stations (E5–E7) revealed that DIAT contributed the most to this separation (31–37%), followed by FL (23–25%) and DIN (18–21%); in these cases, abundances and biomasses were highest in the coastal zone. When the picoplanktonic fraction was included (as HB and APP) in the SIMPER analysis, very similar results were obtained (data not shown); HB, but not APP, contributed to the separation between WEUP (higher) and MOUP (lower), and there were no across-shore differences in the abundance/biomass of these two functional groups.

The association between the planktonic communities (as integrated abundance and biomass of the nano and microplanktonic fractions) and the spatio-temporal variation in upwelling conditions off Cape Ghir was significant (RELATE, $r = 0.5$ (abundance) and 0.7 (biomass), $P < 0.001$). The environmental variables that best explained the changes in the planktonic communities (BIO-ENV) were a combination of SST and nutrients ($NO_3$, $SiO_2$, $PO_4$) for the abundance (correlation $r = 0.77$, $P < 0.001$), and WD, nutrients ($NO_3$, $PO_4$), and SS for the biomass ($r = 0.70$, $P < 0.001$). The variables that best defined the separation of the planktonic components into the clusters described above (Fig. 9) were identified with LINKTREE (Fig. 10; see Supplementary Table 2 for the values associated to each of the variables). The results indicate that cluster A (St. E1) was distinct from the rest of stations/cruises (cluster B) mainly due to differences in nutrient concentrations, the mean values per station being significantly higher in E1 compared with the rest (Supplementary Table 2).

In the case of the abundance of the planktonic components (Fig. 10a), SST was decisive in the subdivisions of B and C, leaving two coastal transition stations from October-09 (C5E6 and C5E7) separated from the rest. Further subdivisions resolved the different upwelling phases recognized in Fig. 9a (WEUP and MOUP) and were mainly explained by differences in SST. During WEUP, the two cruises were different mostly in terms of SS and WD whereas during MOUP, they were explained mostly by changes in SST; RELAX, however, was represented by a mixture of conditions. Spatial differences between stations (C2–C7) were not significant in this case. In terms of the planktonic C-biomass (Fig. 10b), WD best separated B into C and D; in turn, C and D clearly divided the rest of stations into the different phases. In this case, spatial differences during the phases were significant and were mainly attributed to nutrients, SST, SS, and WD. When the picoplankton data were included in the LINKTREE analyses (only 3 cruises), the patterns were very similar (RELATE, $r=0.8$ (abundance) and 0.7 (biomass), $P<0.001$), with WD (phases) and nutrients (coastal) best explaining the changes in abundance and biomass of the planktonic communities (BIO-ENV: $r = 0.9$; $P < 0.001$).

In terms of C-biomass (Fig. 10b), the most coastal station (E1) was separated between the WEUP+RELAX and MOUP phases and the environmental variables that best explained this separation were SS and nutrients. The DIN were the dominant functional group in both cases but the FL were clearly higher in the WEUP + RELAX phase. The rest of the RELAX stations were separated as coastal and coastal transition stations, the DIAT dominating in the former and the DIN in the latter. On the other hand, the rest of the WEUP stations were relatively homogenous in the cross-shore direction and the DIN and CIL were dominant. During MOUP, the stations were separated but several environmental variables explained this; however, SS, SST and $NO_3$ contributed to the separation of coastal and coastal transition stations during these surveys. In this case, the DIN were dominant and the DIAT were more important in the coastal zone.

### 3.3.3. TROPHIC FUNCTION, AND H:A AND C:CHL-A RATIOS DURING DIFFERENT OCEANOGRAPHIC CONDITIONS

The contribution of different functional groups to total autotrophic biomass (A) during each cruise off Cape Ghir were analyzed but the contribution of the picoplankton was assessed only in three of them (Table 4). In addition, this comparison includes data corrected and non-corrected for mixotrophy for specific taxa in the microplanktonic DIN and CIL (Table 4 and Supplementary Table 2). The relative contribution of APP (December-08, February-09, and August-09) ranged between 19% and 34% (maximum in December-08), most of which was provided by PEU (15–31%); after correction for mixotrophy, total APP contribution diminished slightly (15–26%). The contribution of autotrophic FL (AFL, including NFL, SIL and MFL) during the cruises (11–37%) was also highest in December-08 and October-09; after correction for mixotrophy, the percentages also diminished slightly (5–26%). The average contribution of the DIAT was lowest during December-08 (20%) and

| Cruises | HB | APP | NFL | MFL | MSIL | MCIL | NCIL | MDIN | NDIN | MDIAT | NDIAT |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Abundance | | | | | |
| Dec-08 (C1) WEUP | 47508 ± 17560 | 1756±874 | 55.6 ± 30.5 | 2.22 ± 1.83 | 0.04 ± 0.02 | 0.29 ± 0.15 | 0.15 ± 0.07 | 0.68 ± 0.52 | 1.16 ± 1.07 | 0.37 ± 0.11 | 0.13 ± 0.08 |
| Feb-09 (C2) WEUP | 29071 ± 11435 | 1326 ±744 | 25.7 ± 10.5 | 0.90 ± 0.39 | 0.06 ± 0.04 | 0.39 ± 0.19 | 0.23 ± 0.16 | 1.05 ± 0.29 | 2.80 ± 1.52 | 3.71 ± 2.77 | 0.71 ± 0.60 |
| Jun-09 (C3) RELAX | | | 30.7 ± 14.2 | 0.38 ± 0.40 | 0.27 ± 0.34 | 0.09 ± 0.05 | 0.05 ± 0.03 | 1.70 ± 1.23 | 5.49 ± 3.11 | 4.90 ± 5.00 | 0.79 ± 0.54 |
| Aug-09 (C4) MOUP | 24707 ± 9346 | 2112 ± 1578 | 21.5 ± 7.90 | 0.48 ± 0.55 | 0.03 ± 0.02 | 0.35 ± 0.42 | 0.34 ± 0.22 | 2.82 ± 1.40 | 2.83 ± 1.61 | 1.47 ± 1.04 | 0.25 ± 0.12 |
| Oct-09 (C5) MOUP | | | 11.8 ± 5.90 | 1.84 ± 1.96 | 0.02 ± 0.03 | 0.41± 0.33 | 0.21 ± 0.14 | 1.48 ± 0.63 | 5.31 ± 2.89 | 3.55 ± 3.98 | 0.49 ± 0.42 |
| | | | | | | Biomass | | | | | |
| Dec-08 (C1) WEUP | 756 ± 276 | 911 ± 428 | 971 ± 526 | 144 ± 21 | 22 ± 11 | 1424 ± 778 | 14 ± 8 | 1287 ± 780 | 179 ± 154 | 207 ± 140 | 8 ± 2 |
| Feb-09 (C2) WEUP | 480 ± 207 | 787 ± 475 | 745 ± 300 | 161 ± 98 | 38 ± 27 | 1852 ± 949 | 18 ± 15 | 2039 ± 799 | 347 ± 168 | 1490 ± 821 | 22 ± 11 |
| Jun-09 (C3) RELAX | | | 800 ± 422 | 60 ± 71 | 162 ± 200 | 643 ± 366 | 3 ± 2 | 4286 ± 3112 | 777 ± 476 | 4002 ± 3949 | 36 ± 26 |
| Aug-09 (C4) MOUP | 386 ± 170 | 838± 675 | 412 ± 204 | 65 ± 111 | 20 ± 18 | 1896 ± 2190 | 23 ± 14 | 3573 ± 1657 | 515 ± 289 | 917 ± 345 | 15 ± 10 |
| Oct-09 (C5) MOUP | | | 297 ± 167 | 112 ± 195 | 11 ± 15 | 2797 ± 2207 | 20 ± 11 | 2603 ± 1167 | 829 ± 561 | 1139 ± 667 | 20 ± 19 |

Table 2. Integrated abundance (10 $^{9}$ cells m$^{-2}$) and biomass (mg C m$^{-2}$) of planktonic components (as size and functional groups) in the water column (0-150 m depth) during the cruises off Cape Ghir. Mean and standard deviation values for all the stations in each cruise: HB= heterotrophic bacterioplankton, APP= autotrophic Picoplankton, NFL= Nano-flagellates, MFL= Micro-flagellates, MSIL= Micro-silicoflagellates, MCIL= Micro-ciliates, NCIL= Nano-ciliates, MDIN= Micro-dinoflagellates, NDIN= Nano-dinoflagellates, MDIAT= Micro-diatoms, NDIAT= Nano-diatoms.

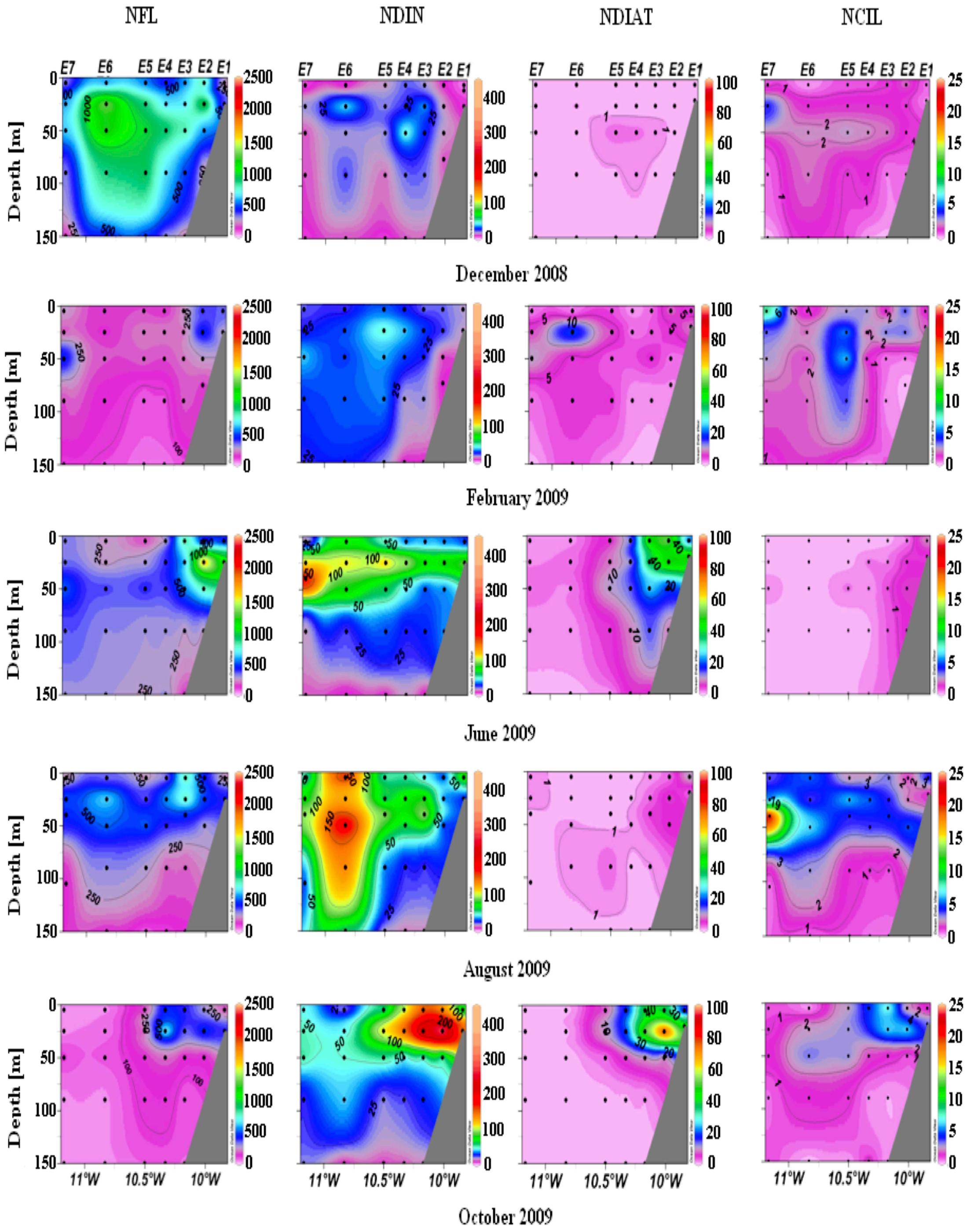
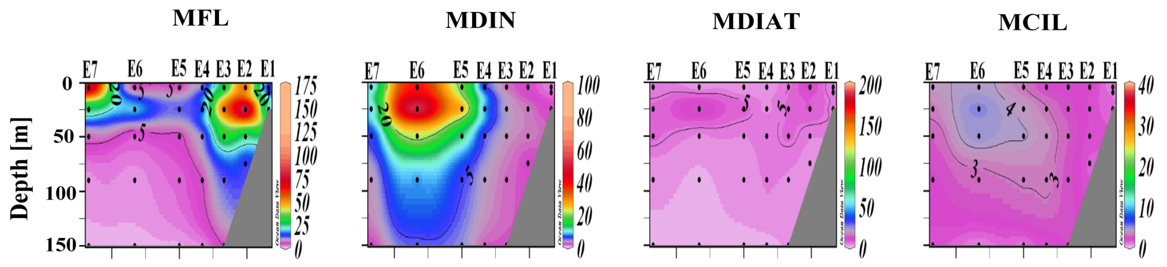


**Fig. 6.** Distribution of nanoplankton abundance (cells mL$^{-1}$) off Cape Ghir. Panels from left to right, respectively: NFL (nano-flagellates), NDIN (nano-dinoflagellates), NDIAT (nano-diatoms), and NCIL (nano-ciliates). Notice the change in scale for different groups.

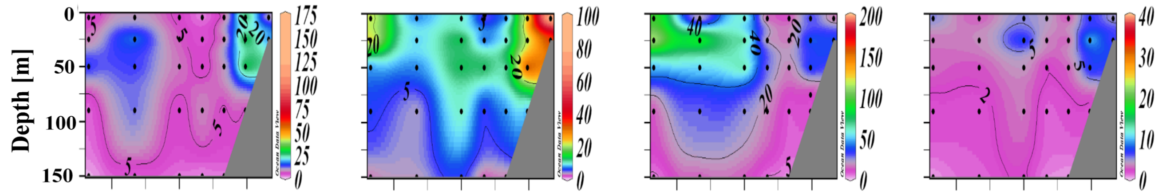
august-09 (39%) but higher during the rest of the cruises (58–68%); after correction for mixotrophy, the percentages diminished too (15–42%). The percentages of autotrophic dinoflagellates (ADIN) ranged between 2 and 29% (maximum in August-09 and October-09) whereas those of autotrophic CIL (ACIL) were low during all the cruises (<3%). After the inclusion of mixotrophy to total autotrophic biomass, their contribution increased in these two functional groups (22–36% and 10–25%, respectively).

In terms of the heterotrophic C-biomass, the contributions of HB were low to moderate (9–24%) in the three cruises when picoplankton was included whereas the heterotrophic FL (HFL) were represented by a very small proportion (<1%) during all the cruises (Table 4). The heterotrophic DIN (HDIN) and CIL (HCIL) made the largest contributions (35–77% and 22–47%, respectively). After the correction for mixotrophy for specific taxa in the microplanktonic DIN and CIL, they still remained as dominant components (29–86% and 13–41%, respectively). The H:A biomass ratios (H:A) for the three cruises during which the whole planktonic community (pico to microplankton) was considered were >1.5 when no correction for mixotrophy was applied but after correction (for MDIN and MCIL), these ratios (H:A) diminished to 61.0 (Table 4).

The ratios between total autotrophic C-biomass and Chl-a were estimated for each of the cruises (mean values per cruise), including total and size-fractioned estimates (Table 5). As total C:Chl-a ratios (weight:weight), the mean values ranged between 49 and 71 and the correction for mixotrophy elevated them to 62 and 92. The C:Chl-a mean ratios for the nanoplankton displayed similar values (20–75) as those for the total C:Chl-a whereas those of the picoplankton ranged between 29 and 175. In the case of the microplankton, the mean C:Chl-a ratios varied an order of magnitude (30–330) between cruises and the correction for



December 2008 (Weak)



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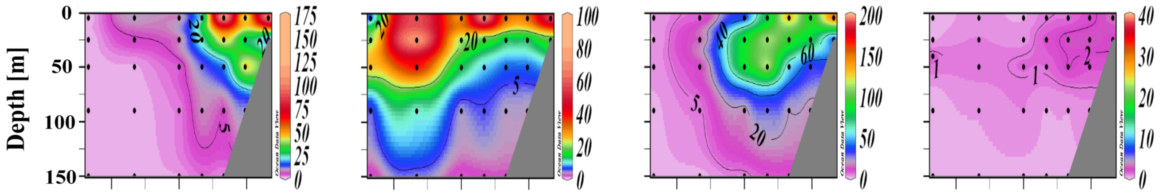
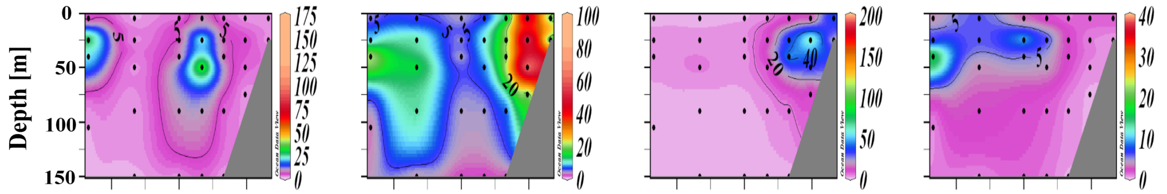
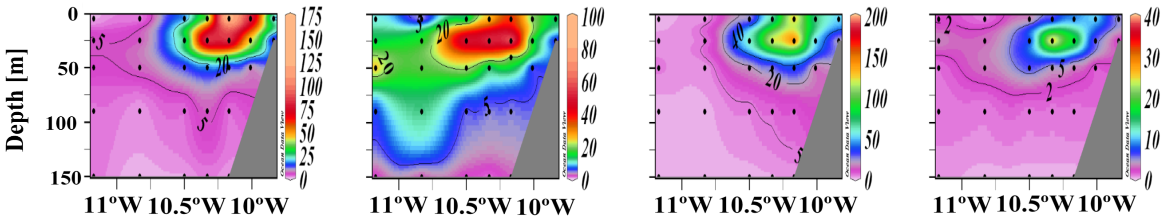


June 2009 (Relax)



August 2009 (Moup)



October 2009 (Moup)

**Fig. 7.** Distribution of microplankton abundance (cells $mL^{-1}$) off Cape Ghir: MFL (micro-flagellates), MDIN (micro-dinoflagellates), MDIAT (micro-diatoms), and MCIL (micro-ciliates). Notice the change in scale for different groups.

mixotrophy elevated these ratios to different extents (74–452); the highest values were observed during the June-09 (RELAX) and August-09 (MOUP). On the other hand, the relationship between C-biomass and Chl-a was analyzed by linear regression; as total and by size fractions, the relationships were significant, except for the microplanktonic autotrophs when no correction for mixotrophy was applied (Table 5).

## 3.4. DISCUSSION

### 3.4.1. OCEANOGRAPHIC AND CHL-A VARIABILITY IN THE AREA OFF CAPE GHIR

During this study, wind conditions and the SST distribution around Cape Ghir (Fig. 1b and c), derived from time series satellite data, were similar to those described previously for this area, with NE winds favourable to upwelling during most of the year and a strong seasonality in the cross-shelf SST gradient (Barton et al., 1998; Pelegrí et al., 2005a; Lauthuilière et al., 2008; Arístegui et al., 2009). They also agree with time series results on winds and SST in the NW African coastal zone which indicated that the region between 20 and 33°N is characterized by persistent upwelling, being more intense during summer and autumn in the area between 25 and 33°N (Marcello et al., 2011). Despite the recurrence of upwelling in this region, as well as in similar coastal upwelling systems located in subtropical regions (Mackas et al., 2006), the results of our study indicated that there are significant changes in the oceanographic conditions. We distinguished at least two phases, WEUP and MOUP, represented by variations in: (a) the direction, duration, and intensity of the upwelling favourable winds, (b) the strength of the cross-shore SST gradient, (c) nutrient concentrations, and (d) water column stratification. Strong upwelling conditions (highly

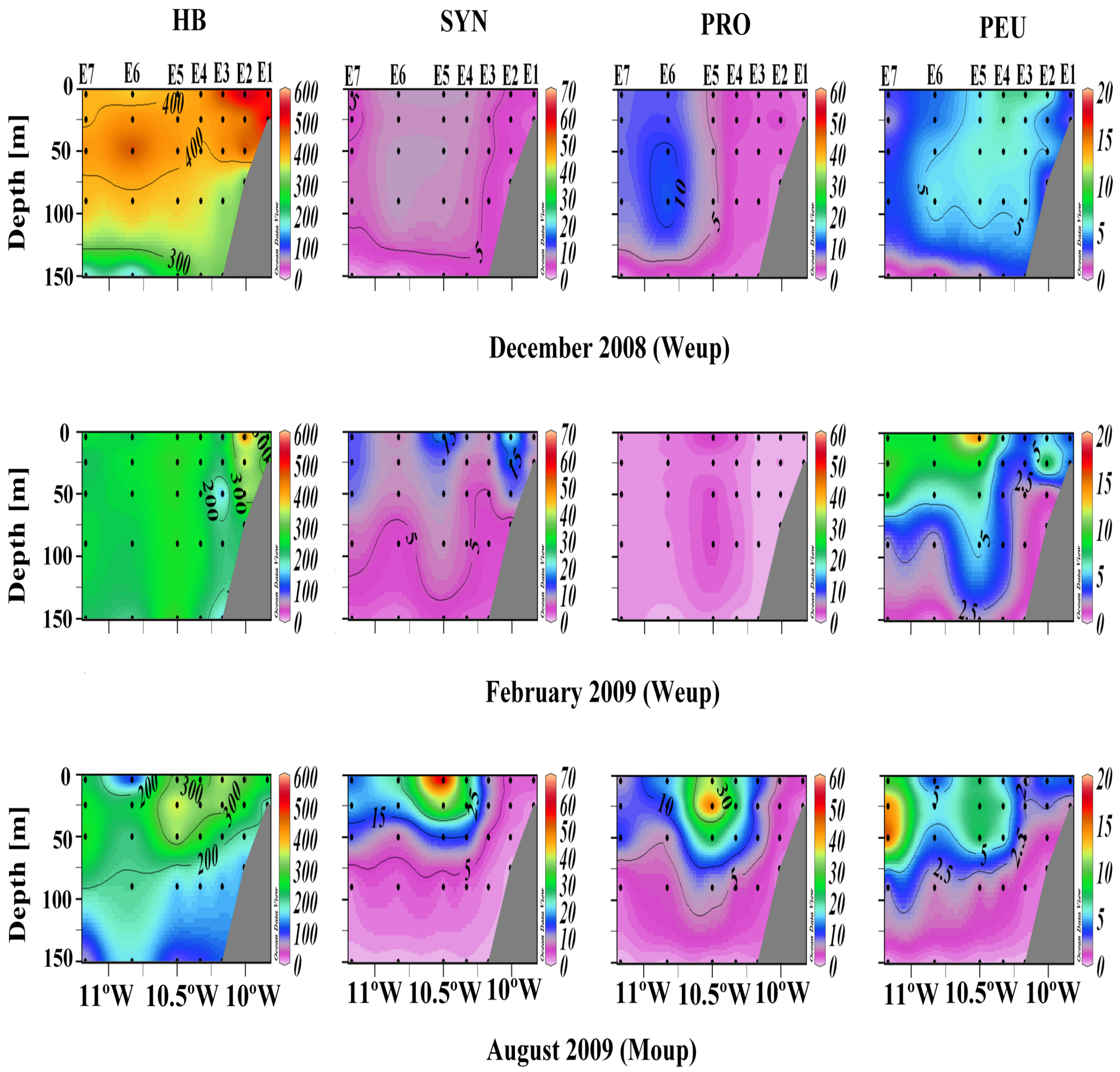


**Fig. 8.** Distribution of picoplankton abundance (cells mL$^{-1}$) off Cape Ghir (only 3 cruises): HB (heterotrophic bacterioplankton), SYN (*Synechococcus*), PRO (*Prochlorococcus*), and PEU (Picophytoeukaryotes). Notice the change in scale for different groups.

negative, monthly mean alongshore wind stress) were not registered during our cruises but they were present at other times, mainly during April and July 2009 (Fig. 1b). The two phases recognized in this study were associated with different seasons (e.g. winter and spring–summer) but wind stress was highly variable at the synoptical scale (~5–10 days; Fig. 1b); it could be that these short-term changes in wind forcing also elicit a rapid response of the planktonic communities, an aspect that needs to be tackled in future investigations.

The distribution of satellite Chl-a in the area around Cape Ghir (Fig. 1d) showed the highest concentrations and undetectable seasonal variability in the coastal zone whereas, in the coastal transition zone immediately adjacent to it, seasonal and higher frequency variability were evident. Overall, however, the mean concentrations of in situ total Chl-a (Table 1) varied within a narrow range of relatively low values (35–81 mg $m^{-2}$) but the differences between stations were of one order of magnitude (8–232 mg $m^{-2}$), without significant differences between the identified upwelling phases. Previous studies off C. Ghir and C. Juby (Arístegui et al., 2004; García-Muñoz et al., 2005; Pelegrí et al., 2005b) have reported a similarly narrow range of variation (11–90 mg $m^{-2}$) of relatively low values. In agreement with this, satellite Chl-a time series data for the NW African upwelling system have shown that the region between 24 and 33°N is characterized by a weak seasonality and that the highest Chl-a values are confined to a narrow band in the coastal zone, probably in response to nutrient limitation (Lauthuilière et al., 2008). In fact, low productivity and low Chl-a concentration values associated with low nutrient concentrations (especially of silicates), have been reported for the region between Cape Sim and C. Ghir (Minas et al., 1982).

In comparison with other coastal upwelling regions within the Canary Current System or other coastal upwelling regions (Herrera and Escribano, 2006; Lachkar and Gruber, 2012; Morales and Anabalón, 2012; Kim et al., 2009), the region around C. Ghir contains lower nutrient concentrations in the upwelled waters, according to previous studies (Codispoti et al., 1982; Arístegui et al., 2006; Chavez and Messié, 2009) and this study (Table 1). Part of the explanation can be attributed to differences in the circulation pattern and water mass composition along the NW African System (Codispoti et al., 1982; Lauthuilière et al., 2008), to the presence of a relatively narrow shelf between C. Ghir and Casablanca (~31–33.5°N), implying a smaller residence time of upwelled waters compared with areas having a wider shelf, and to comparatively higher mesoscale activity (Lachkar and Gruber, 2012). Our results also indicate that weak to moderate intensities of the upwelling favourable winds (Table 1) might also be involved in the lower nutrient content of the upwelled waters compared to other systems.

### 3.4.2. PLANKTONIC COMMUNITY STRUCTURE UNDER CHANGING OCEANOGRAPHIC CONDITIONS OFF CAPE GHIR

The contribution of diatoms to total autotrophic C-biomass during this study ranged from low to moderate (20–68%); a correction for mixotrophy in specific taxa of microplanktonic dinoflagellates and ciliates further lowered their contribution (15–42%; Table 4). A lack of strong dominance of diatoms in this system can be explained by time–space variations in the upwelling conditions (e.g. WD, SST, SS) and, most directly, by the levels of nutrient content in the upwelled waters. Considering that Si:N ratios <1 and Si:P

| Functional groups | Abundance | | Biomass | | | |
|---|---|---|---|---|---|---|
| Clusters: | E1/rest<br>A-B | WEUP/MOUP<br>BC-BD | E1/rest<br>A-B | WEUP/ RELAX<br>BC-BD | WEUP/MOUP<br>BC-BE | RELAX/MOUP<br>BE-BD |
| FL | 40 | 39 | 11 | 8 | 12 | 10 |
| DIN | 23 | 33 | 43 | 38 | 37 | 22 |
| DIAT | 26 | 20 | 21 | 20 | 34 | 34 |
| CIL | 6 | 10 | 21 | 32 | 10 | 24 |
| SIL | 2 | 1 | 4 | 3 | 7 | 8 |
| Average: | 54 | 43 | 66 | 48 | 54 | 25 |

**Table 3** Contribution (%) of different functional groups to the dissimilarity between the clusters formed by the biological data, in terms of abundance and biomass of the nanoplankton and microplankton size fractions (see Fig. 9a and b). SIMPER analysis, cut off at 75% accumulated frequency. Abbreviations: WEUP: weak upwelling (December-08 and February- 09), RELAX: relaxation (June-09), MOUP: moderate upwelling (August-09 and October-09); E1: the most coastal station, rest: stations E2 to E7; Clusters: A, B, C, D, and E. Functional groups: FL = Flagellates, DIN = Dinoflagellates, DIAT = Diatoms, CIL = Ciliates, SIL = Silicoflagellates.

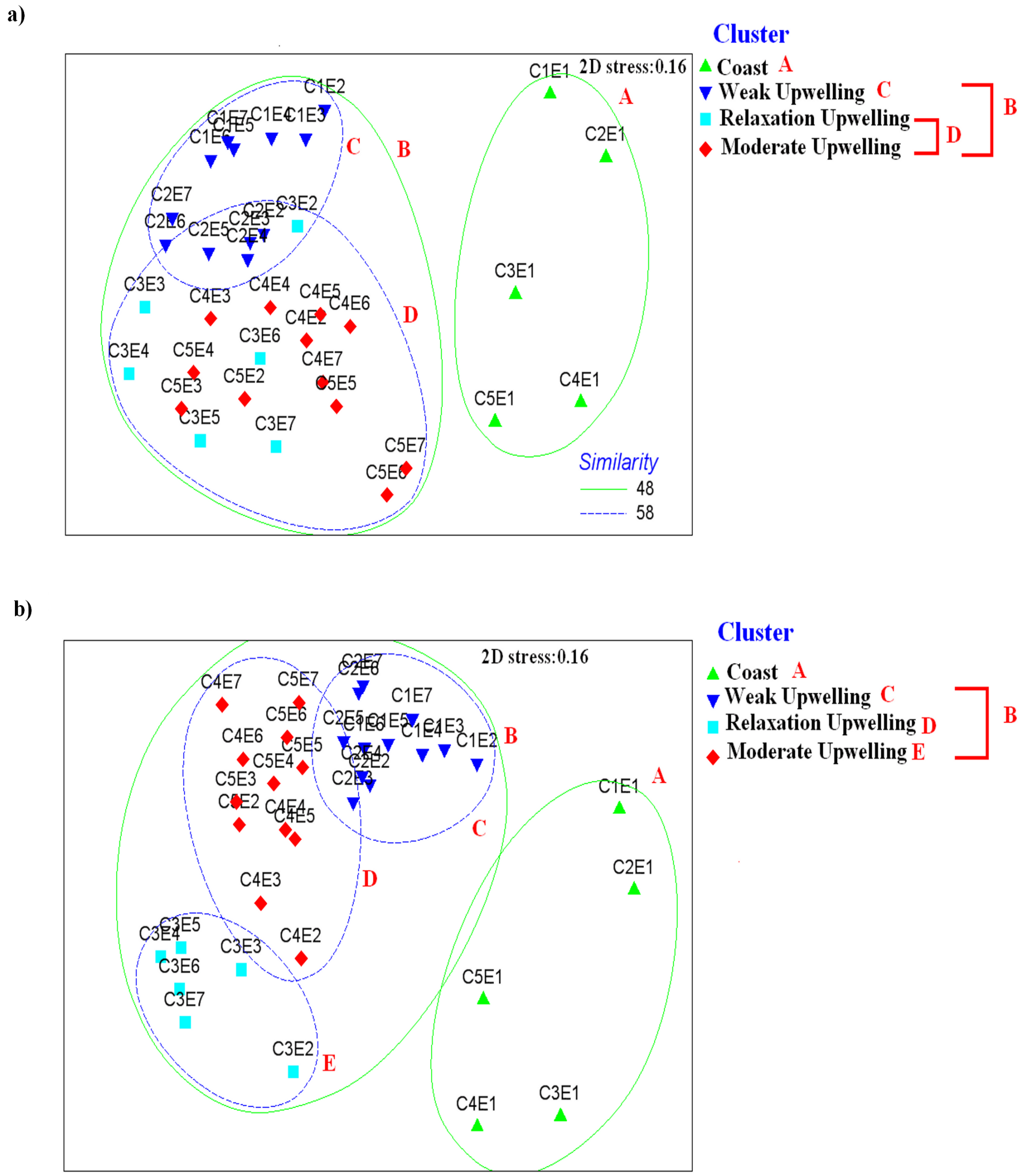


**Fig. 9.** MDS and cluster analyses based on the biological variables (nano and microplanktonic components; integrated 0–150 m) during the cruises off Cape Ghir: (a) Abundance, and (b) Carbon-biomass. The nomenclature identifies the cruises (C1 to C5) and the stations (E1 to E7); for reference, see Table 1 and Fig. 3.

ratios ≤3 are indicative of potential Si-limitation (Harrison et al., 1977; Levasseur and Therriault, 1987), such a condition was present during the surveys in December-08 and August-09 (Si:N = 0.4 and 0.6, Si:P = 3.0 and 2.9, respectively). Associated with this, the contribution of diatoms was lowest during these surveys (Table 4). Si-limitation in diatom assemblages has been previously described for this area (Treguer and Le Corre, 1978; Fanning, 1992), as well as for surrounding areas (Romero et al., 2002). In contrast to all other surveys, the autotrophic C-biomass in December-08 was characterized by the dominance of pico-eukaryotes and nanoflagellates; in August-09, diatoms and dinoflagellates made the highest contributions (Table 4) but Chl-a biomass was the lowest (Table 1) and the C:Chl-a ratio one of the highest (Table 5) of the surveys.

Potential Si-limitation by itself, however, does not explain the observed differences in mean diatom biomass between December-08 and August-09, which were three times lower in the former (Table 4). This may be explained by changes in species composition with different Si-requirements. During August-09, large diatoms (range: 40–300 lm) were present and *Coscinodiscus wailesii* and *Thalassiosira* ssp. made the highest contribution to total diatom biomass (58% and 20%, respectively). *C. wailesii* survives as vegetative cells in sediments for prolonged periods and is resuspended in the water column during upwelling events (Van Ruth et al., 2012). Both genera, *Coscinodiscus* and *Thalassiosira*, are more sensitive to low N concentration and are able to store it in vacuoles; under Si-limitation, they prioritize basic cell functions and low Si concentrations affect *Thalassiosira* more than *Coscinodiscus* but, in both cases, cell abundances diminish under this condition (Van Ruth et al., 2012). In turn, this suboptimal condition directly influences the intracellular Chl-a concentration and the C:Chl-a ratios (Harrison et al., 1977; Gilpina et al., 2004) and this can be associated with the low Chl-a and high C:Chl-a detected during this survey (Table 5). In addition, high abundances of *Pseudo-nitzschia* and *Cylindrotheca* were observed in August-09 (26% and 16% of total diatom abundance, respectively). In both cases, some of the species are capable of withstanding Si-limitation (Staats et al., 2000; Anderson et al., 2010).

During December-08, diatoms were of smaller size (6–110 lm) and *Guinardia* ssp. (in the coastal band) and *Coscinodiscus argus* (in the coastal transition zone) were dominant in terms of total diatom C-biomass (30% and 38%, respectively). *Guinardia* ssp. has similar Si-requirements to *Thalassiosira* but, in addition, is favoured by higher turbulence and lower temperatures (Alpine and Cloern, 1992), conditions that were present during this survey (Table 1). A species present in December-08, *G. flaccida*, presents poorly silicified frustules under a condition of Si-depletion after a bloom, probably as a strategy to sustain population growth under suboptimal conditions (Reid et al., 1990). In addition, turbulence contributes to the resuspension of small benthic species (Alpine and Cloern, 1992), such as *Navicula* (Troccoli, 1989), which was dominant in abundance, but not in biomass, during this survey. On the other hand, relatively similar contributions of diatoms and pigmented dinoflagellates to total autotrophic biomass were observed during August-09 (MOUP). After the correction for mixotrophy in specific taxa of dinoflagellates and ciliates, the contribution of auto/mixotrophic dinoflagellates was similar to that of diatoms during October-09 (MOUP) and it was relatively high during June-09 (RELAX), when diatoms were the most dominant component (Table 4). During these three cruises, ratios of N:P < 6 were observed, potential N-limitation for phytoplankton (Moore et al., 2013); in addition, Si:N P 1 were detected in

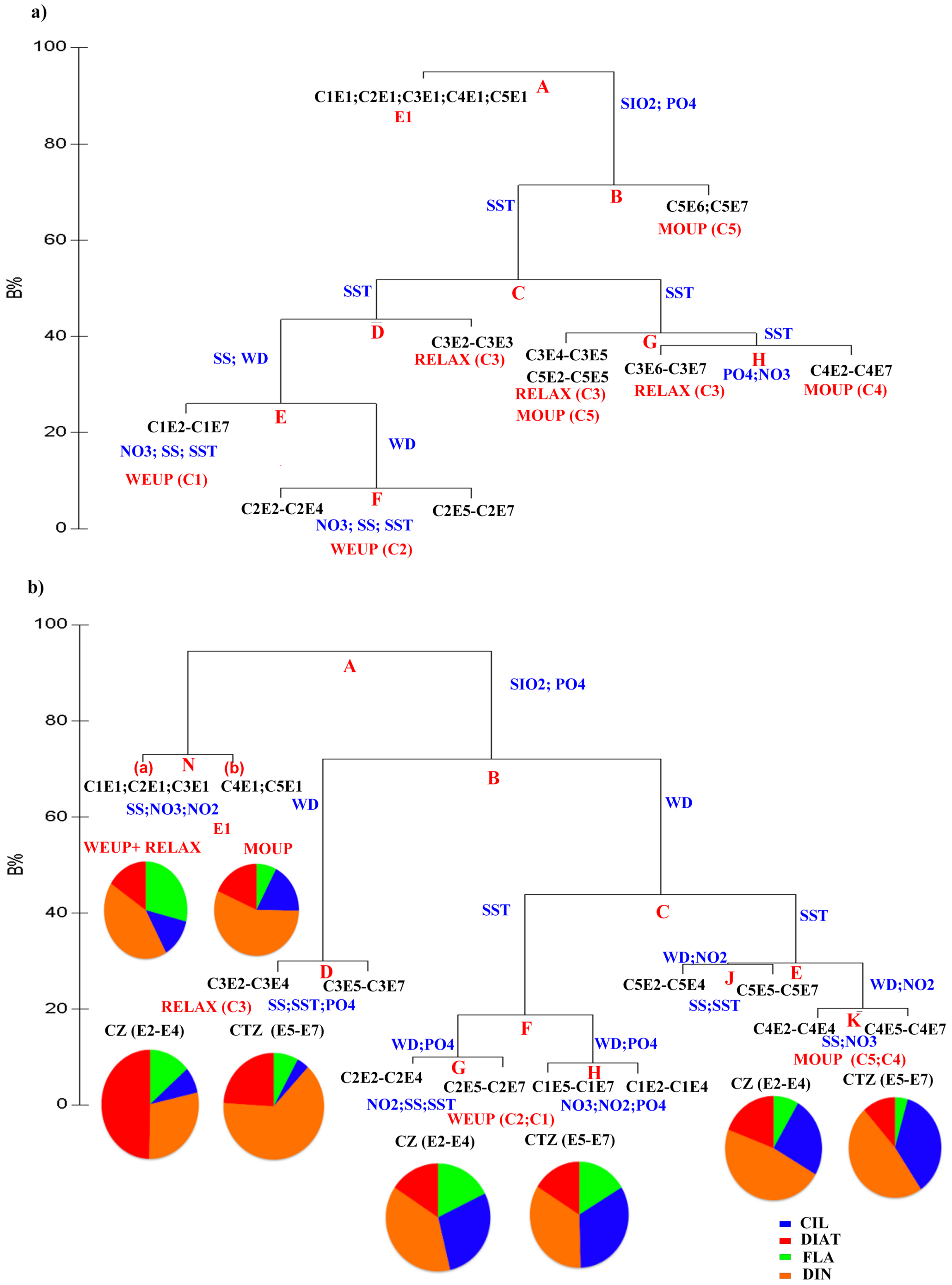


**Fig. 10.** Environmental variables that best explain the clusters identified for the biological variables (see Fig. 9), along an axis of Bray–Curtis similarity (B%) and using LINKTREE analysis: (a) Abundance, and (b) Carbon-biomass.

June-09 and October-09. Slightly higher N:P values were observed during the WEUP phase (~7–9) but the Si:N ratios were different in these two cruises (0.4 in December-08 and 1.1 in February-09). N-limitation or N-deficient waters (not including $NH_4$) may partially explain the prevalence of mixed assemblages of autotrophic/mixotrophic functional groups in the upwelling area off C. Ghir, especially during RELAX and MOUP phases; Si and N co-limitation may explain the lowest total Chl-a values during the August-09 cruise (Table 1). However, nutrient ratios in the water column probably cannot account alone for actual phytoplankton nutrient limitation in coastal ecosystems as organisms can strongly influence nutrient availability and nutrient requirements are taxa-specific within the different functional groups (Quigg et al., 2003; Trommer et al., 2013).

Nanophytoflagellates and picophytoplankton are also expected to make important contributions to the autotrophic C-biomass when N concentrations (mostly as $NO_3$) are lower compared to the values usually found during active upwelling events which favour diatom growth in coastal upwelling systems. The contribution of AFL (excluding nanodinoflagellates) to total autotrophic C-biomass was mostly low during the cruises (Table 4), except during RELAX (N-limitation) and WEUP in December-08 (Si-limitation). In the case of the picophytoplankton, the biomass of APP was relatively similar during the three cruises in which estimates were available but their relative contribution was highest during WEUP in December-08 (Table 4). In concordance with previous studies (Sherr et al., 2005; Crespo et al., 2012; Morales and Anabalón, 2012), our results suggest that the smaller autotrophic components are a typical component of coastal upwelling systems and become more important when upwelling conditions become weaker or upwelling ceases.

During this study, the nanoplanktonic autotrophs (mostly flagellates and dinoflagellates) were dominant in terms of Chl-a biomass whereas microplanktonic autotrophs/mixotrophs were dominant in terms of C-biomass. An order of magnitude variation in the C:Chl-a ratios was detected in the case of the microplanktonic autotrophs but not for the nanoplanktonic autotrophs (Table 5). This range of variation has been previously reported for microplanktonic diatoms and dinoflagellates, including species which were present in our samples (Harrison et al., 1977; De Jonge, 1980; Moal et al., 1987). The picoplanktonic autotrophs also displayed a large change in C:Chl-a ratios (Table 5) and these values are within the range of annual variation reported by Calvo-Díaz et al. (2008) in a coastal time series, one of the few studies available on this matter. In general terms, environmental changes (e.g. light, nutrients, temperature, turbulence) but also changes in the relative biomass contribution of different functional groups or taxa, in the size composition within a functional group, or even a specific taxa, can also influence the variations in C:Chl-a ratios in planktonic components (Geider et al., 1997). Mixotrophy also contributes to increase C:Chl-a ratios in planktonic assemblages (Skovgaard et al., 2000; Crespo et al., 2011), and this appeared to be the case during the June-09 and August-09 and cruises but not in October-09, when the contribution to C-biomass of autotrophic dinoflagellates plus autotrophic ciliates was lower compared to the other two cruises (Table 5).

| Cruises | Autotrophs (A) | | | | | | Heterotrophs (H) | | | | H:A ratios |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | CIAN | PEU | AFL | DIAT | ADIN | ACIL | HB | HFL | HDIN | HCIL | |
| Dec-08 (C1) | 77 ± 46 | 776 ± 402 | 950 ± 676 | 366 ± 181 | 322 ± 231 | 19 ± 27 | 756 ± 276 | 10 ± 5 | 1299 ± 850 | 1425 ± 1425 | 1.5 ± 0.6 |
| WEUP | | | | | 683 ± 348 | 356 ± 187 | | | 783 ± 453 | 1082 ± 588 | 0.9 ± 0.2 |
| Feb-09 (C2) | 78 ± 46 | 598 ± 499 | 340 ± 213 | 1735 ± 870 | 38 ± 35 | 2 ± 5 | 480 ± 207 | 35 ± 18 | 2034 ± 759 | 1801 ± 909 | 1.7 ± 0.5 |
| WEUP | | | | | 981 ± 302 | 694 ± 351 | | | 1406 ± 471 | 1175 ± 557 | 0.7 ± 0.1 |
| Jun-09 (C3) | | | 1258 ± 593 | 4073 ± 3985 | 37 ± 46 | 802 ± 170 | | 31 ± 15 | 4306 ± 3116 | 732 ± 369 | |
| RELAX | | | | | 1878 ± 1410 | 1053 ± 170 | | | 3185 ± 2029 | 219 ± 84 | |
| Aug-09 (C4) | 140 ± 159 | 606 ± 362 | 396 ± 228 | 1139 ± 444 | 1079 ± 824 | 9 ± 7 | 386 ± 156 | 50 ± 32 | 3507 ± 1920 | 1920 ± 1936 | 2 ± 0.9 |
| MOUP | | | | | 1391 ± 801 | 678 ± 719 | | | 2697 ± 1308 | 1242 ± 1218 | 1 ± 0.1 |
| Oct-09 (C5) | | | 231 ± 345 | 1395 ± 865 | 290 ± 217 | 25 ± 34 | | 22 ± 12 | 2587 ± 1244 | 2777 ± 2093 | |
| MOUP | | | | | 1296 ± 498 | 1118 ± 827 | | | 2137 ± 923 | 1699 ± 1263 | |

**Table 4.** Biomass (mg C $m^{-2}$) of Autotrophs (A) and Heterotrophs (H), and the H:A ratios, of the functional groups in the water column (0-150 m depth) during the cruises off Cape Ghir. Mean and standard deviation values for all the stations in each cruise; in the case of Dinoflagellates and Ciliates, the second row corresponds to the values corrected for mixotrophy in specific taxa of the microplanktonic components. CIAN= *Synechococcus* and *Prochlorococcus*; PEU= Picophytoeukaryotes, AFL= autotrophic nanoflagellates, DIAT= Diatoms, ADIN= autotrophic/mixotrophic Dinoflagellates, ACIL= autotrophic/mixotrophic Ciliates; HB= heterotrophic bacterioplankton; HFL= heterotrophic Flagellates; HDIN= heterotrophic Dinoflagellates; and HCIL= heterotrophic Ciliates

### 3.4.3. H:A RATIOS IN THE AREA OFF CAPE GHIR: IMPLICATIONS FOR ECOSYSTEM FUNCTIONING

The average H:A biomass ratios in the area off Cape Ghir during this study were estimated to be >1 during the surveys in which pico to microplanktonic communities were included (Table 4). According to Gasol et al. (1997), these values are representative of relatively straight to inverse trophic pyramids; in contrast, these authors proposed that a normal pyramid (H:A < 1) was representative of productive systems, such as coastal upwelling areas. One of the critical aspects in the calculation of H:A ratios has been recognized to be the inclusion of mixotrophy (Gasol et al., 1997), however, the assessment of the contribution of mixotrophs in the analyses of the trophic modes of planktonic components is still a big challenge (Flynn et al., 2013). The contribution of mixotrophs is usually hidden in the direct assessments of the abundance of photo-autotrophs by autofluorescence (e.g. flow-cytometry and epifluorescence) because the two trophic modes are undistinguishable with these techniques and, therefore, mixotrophs are assigned to the autotrophic mode. In the case of the microplankton, the trophic modes cannot be directly assessed by observation of lugols fixed cell and they have to be based on previous knowledge on the prevalent mode in functional groups or in specific taxa (e.g. as functional group, diatoms are assumed to all be autotrophs; the dinoflagellate Heterocapsa is known to be autotrophic or mixotrophic).

The application of a correction factor for mixotrophy in the microplanktonic fraction (only to selected dinoflagellate and ciliate taxa), based on literature information, resulted in a significant decrease in the original H:A values obtained in this study (Table 4). After this

| Cruises | Total | | Microplankton | | Nanoplankton | Picoplankton |
|---|---|---|---|---|---|---|
| | aC:Chl-a | aCm:Chl-a | aC:Chl-a | aCm:Chl-a | aC:Chl-a | aC:Chl-a |
| Dec-08 (C1) | 49 | 62 | 30 | 74 | 39 | 168 |
| Feb-09 (C2) | 50 | 59 | 104 | 140 | 20 | 175 |
| Jun-09 (C3) | 78* | 104* | 310 | 394 | 49 | |
| Aug-09 (C4) | 71 | 92 | 330 | 452 | 75 | 30 |
| Oct-09 (C5) | 30* | 47* | 90 | 168 | 22 | |
| All cruises: Y: | 34.8X + 926 | 44.0X + 1122 | 61.3X + 528 | 92.5X + 1127 | 44.9X - 172 | 89.9X + 311 |
| $R^2$: | 0.49 | 0.58 | 0.35 | 0.51 | 0.60 | 0.59 |
| P: | 0.001 | 0.0007 | 0.1 | 0.05 | 0.0001 | 0.0001 |

**Table 5** Autotrophic Carbon (aC) to Chlorophyll-a (Chl-a) ratios (as total and by size fractions), and the linear regression between them, for the planktonic components in the water column (0–150 m depth) during the cruises off Cape Ghir. Mean ratios for all the stations in each cruise are based on integrated values (mg $m^{-2}$); corrections for mixotrophic taxa in the microplanktonic Dinoflagellates and Cilates are also included (aCm). Y = C-biomass, X = Chl-a, $R^2$ = coefficient of determination, P = significance level.

correction, a normal pyramid was representative of the WEUP phase (2 surveys) and a straight pyramid in one of the MOUP surveys (August-09). The latter can be explained by environmental factors, such as nutrient limitation (this study) or an increase in the concentration of detritus in the water column (Cho and Azam, 1990; Roman et al., 1995; Gasol et al., 1997). In summary, mixotrophy can largely influence the calculations of H:A in the upwelling region around C. Ghir, a result that differs from the conclusion of Gasol et al. (1997) that its inclusion was not relevant.

A critical point in the calculation of H:A biomass ratios relates to the diverse methodologies which are currently used for making estimates of cellular volume and C-content in planktonic components (Menden-Deuer and Lessard, 2000; Leblanc et al., 2012). In terms of biovolume, the estimates are usually based on one or two linear dimension measurements and, based on cell shape, they are transformed to volume (Børsheim and Bratbak (1987); Putt and Stoecker, 1989; Lessard, 1991; Montagnes et al., 1994; Menden-

Deuer and Lessard, 2000). This calculation can have a bias if cell shape is more complex than the standard geometric forms used in the calculations (Chrzanowski and Simek, 1990; Sun and Lui, 2003) or/and by a distortion of cell volume caused by the fixative used (Choi and Stoecker, 1989). In our study, volume estimates which have been previously standardized for pico to microplanktonic components in the region of study were used (Ojeda, 1998; Zubkov et al., 1998, 2000; Fukuda et al., 1998). Moreover, most of the components were taxonomically identified and measured in great detail as to accurately estimate their C-content (Table 4). In addition, variability in cell size of the different plankton species or functional groups is common (Tomas, 1997) and this would strongly affect the estimates if average C-values are used. For example, we applied an intermediate value for C-biomass in the case of autotrophic PEU but their volume can vary between 1.2 $\mu m^3$ and 2.5 $\mu m^3$ per cell (Calvo-Díaz et al., 2008); therefore, their contribution (Tables 2 and 3) could have been 10 times lower or higher than that estimated value if size variation during the surveys had been considered.

In estimating H:A biomass ratios in different marine systems, Gasol et al. (1997) included a wide range of sizes (pico to mesoplankton) whereas existing estimates for the CCS have included only the pico and nanoplanktonic fractions (combining flagellates and dinoflagellates), the resulting H:A ratios in this case ranging between 0.9 and 4.1 in the CCS (Arístegui et al., 2004; Arístegui and Montero, 2005; Baltar et al., 2009). When calculating H:A ratios with these two fractions (pico and nanoflagellates, including NFL and NDIN) for our data, the values obtained decreased slightly (0.6–0.8) in comparison with using pico- to microplanktonic fractions, with or without correction for mixotrophy (Table 4). No doubt, the contribution of the microplankton fraction to C-biomass is important in upwelling systems but that of mixotrophic components has been overlooked, mostly because it is usually assumed that these systems are dominated by diatoms.

## 3.5. CONCLUSIONS

In the coastal and coastal transition zones of Cape Ghir, a region of permanent upwelling, spatial and temporal changes in upwelling conditions were strongly associated with time–space variations in planktonic community structure. As autotrophic biomass, total Chl-a was dominated by the nanoplanktonic fraction but mixed assemblages of microplanktonic diatoms and auto/mixotrophic dinoflagellates usually made the highest contributions to C-biomass. In terms of H:A biomass ratios in the community (pico to microplankton), mean values <1 (normal pyramid = productive system) were obtained when mixotrophs were included but changed to >1 (= unproductive systems) when they were excluded. The presence of mixed assemblages of photoautotrophs/mixotrophs in this area is probably the result of lower nutrient contents in the upwelled waters compared to other coastal upwelling systems, in combination with a relatively narrow shelf, higher levels of mesoscale activity, and/or weaker to moderate wind intensities for most part of the year. These results strongly imply that, besides functional or size groups, mixotrophy and a detailed account of taxa composition of the planktonic are essential for improving our understanding of the response of planktonic components/communities to environmental fluctuations and to ongoing climate change in this and other upwelling systems. In addition, these results call for caution in the use of fixed C:Chl-a ratios to indirectly assess primary production and/or carbon flux in the oceans, or to derive the relative dominance of functional or size groups of autotrophic components based only on size-fractionated Chl-a estimates.

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## 3.7 APPENDIX A. SUPPLEMENTARY MATERIAL

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pocean.201 3.10.015.

## 3.8 REFERENCES

Alder, V.A., 1999. Tintinnoinea. In: Boltovskoy, D. (Ed.), South Atlantic Zooplankton. Backhuys, Leiden, pp. 321–384.

Alpine, A.E., Cloern, J.E., 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. Limnol. Oceanogr. 37, 946–955.

Anderson, O.R., Nigrini, N., Boltovskoy, D., Takahashi, K., Swanberg, N., 2002. Class Polycystinea. In: Lee, J. (Ed.), An Illustrated Guide to the Protozoa, 2nd Protozoologists. Lawrence, Kansas, pp. 371–656.

Anderson, C.R., Sapiano, M.R.P., Bala Krishna Prasad, M., Long, W., Tango, P.J., Brown, C.W., Murtugudde, R., 2010. Predicting potentially toxigenic Pseudo-nitzschia blooms in the Chesapeake Bay. J. Marine Syst. 83, 127–140.

Arístegui, J., Harrison, W.G., 2002. Decoupling of primary production and community respiration in the ocean: implications for regional carbon studies. Aquat. Microb. Ecol. 29, 199–209.

Arístegui, J., Barton, E.D., Tett, P., Montero, M.F., García-Muñoz, M., Basterretxea, G., Cussatlegras, A.S., Ojeda, A., de Armas, D., 2004. Variability in plankton community structure, metabolism, and vertical carbon fluxes along an upwelling filament (Cape Juby, NW Africa). Prog. Oceanogr. 62, 95– 113.

Arístegui, J., Montero, M.F., 2005. Temporal and spatial changes in microplankton respiration and biomass in the Canary Islands: the effect of mesoscale variability. J. Marine Syst. 4, 65–82.

Arístegui, J., Álvarez-Salgado, X.A., Barton, E.D., Figueiras, F.G., Hernández-León, S., Roy, C., Santos, A.M.P., 2006. Oceanography and fisheries of the Canary Current Iberian region of the Eastern North Atlantic. In: Robinson, A., Brink, K.H. (Eds.), The Global Coastal Ocean: Interdisciplinary Regional Studies and Syntheses, The Sea: Ideas and Observations on Progress in the Study of the Seas, vol. 14. Harvard University Press, pp. 877–931.

Arístegui, J., Barton, E.D., Álvarez-Salgado, X.A., Santos, A.M.P., Figueiras, F.G., Kifani, S., Hernández-León, S., van Mason, E., Machú, E., Demarcq, H., 2009. Sub- regional ecosystem variability in the Canary Current upwelling. Prog. Oceanogr. 83, 33–48.

Balech, E., 1948. Tintinnoinea de Atlántida (R. O. del Uruguay). Comunicaciones del Museo Argentino de Ciencias Naturales ‘‘Bernardino Rivadavia’’. Ciencias Zoológicas 7, 1–23.

Baltar, F., Arístegui, J., Montero, M.F., Espino, M., Gasol, J.M., Herndl, G.J., 2009. Mesoscale variability modulates seasonal changes in the trophic structure of nano- and picoplankton communities across the NW Africa–Canary Islands transition zone. Prog. Oceanogr. 83, 180–188.

Barton, E.D., Arístegui, J., Tett, P., Cantón, M., García-Braun, J., Hernández-León, S., Nykjaer, L., Almeida, C., Almunia, J., Ballesteros, S., Basterretxea, G., Escánez, J., García-Weill, L., Hernández-Guerra, A., López-Laatzen, F., Molina, R., Montero, M.F., Navarro-Pérez, E., Rodríguez, J.M., van Lenning, K., Vélez, H., Wild, K., 1998. The transition zone of the Canary Current upwelling region. Prog. Oceanogr. 41, 455–504.

Bernard, C., Rassoulzadegan, F., 1994. Seasonal variations of mixotrophic ciliates in the northwestern Mediterranean Sea. Mar. Ecol. Progr. Ser. 108, 295– 301.

Børsheim, K.Y., Bratbak, G., 1987. Cell volume to cell carbon conversion factor for a bacterivorous Monas sp. enriched from seawater. Mar. Ecol. Progr. Ser. 36, 171–175.

Bowden, K.F., 1983. Physical oceanography of coastal waters. In: Ellis Horwood Series on Marine Science. John Wiley and Sons, NewYork, 302 pp.

De Jonge, V.N., 1980. Fluctuations in the organic carbon to chlorophyll-a ratios for estuarine benthic diatom populations. Mar. Ecol. Progr. Ser. 2, 345– 353.

Calvo-Díaz, A., Morán, X.A.G., Suárez, L.A., 2008. Seasonality of picophytoplankton chlorophyll-a and biomass in the central Cantabrian Sea, southern Bay of Biscay. J. Marine Syst. 72, 271–281.

Chavez, F.P., Messié, M., 2009. A comparison of eastern boundary upwelling systems. Prog. Oceanogr. 83, 80–96.

Cho, B.C., Azam, F., 1990. Biogeochemical significance of bacterial biomass in the ocean's euphotic zone. Mar. Ecol. Progr. Ser. 63, 253–259.

Choi, J.W., Stoecker, D.K., 1989. Effects of fixation on cell volume of marine planktonic Protozoa. Applied and Environmental Microbiology 55, 1761–1765. Chrzanowski, T.H., Simek, K., 1990. Prey-size selection by freshwater flagellated Protozoa. Limnol. Oceanogr. 35 (7), 1429–1436.

Clarke, K.R., Warwick, R.M., 2001. Change in marine communities: an approach to statistical analysis and interpretation, second ed. Plymouth, PRIMER-E, 172 pp. Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual/Tutorial. Plymouth, PRIMER-E.

Codispoti, L.A., Dugdale, R.C., Minas, H.J., 1982. A comparison of the nutrient regimes off North-west Africa, Peru and Baja California. Rapports et Proces- verbaux des Réunions. Conseil International pour l'Éxploration de la Mer 180, 184–201.

Crespo, B.G., Espinoza-González, O., Teixeira, I.G., Castro, C.G., Figueiras, F.G., 2011. Possible mixotrophy of pigmented nanoflagellates: microbial plankton biomass, primary production and phytoplankton growth at the NW Iberian upwelling in spring. Estuarine Coastal Shelf Science 94, 172–181.

Crespo, B.G., Espinoza-González, I.O., Teixeira, I.G., Castro, C.G., Figueiras, F.G., 2012. Structure of the microbial plankton community in the NW Iberian margin at the end of the upwelling season. J. Marine Syst. 95, 50–60.

Espinoza-González, I.O., Figueiras, F.G., Crespo, B.G., Teixeira, I.G., Castro, C.G., 2012. Autotrophic and heterotrophic microbial plankton biomass in the NW Iberian upwelling: seasonal assessment of metabolic balance. Aquat. Microb. Ecol. 67, 77–89.

Fanning, K.A., 1992. Nutrient provinces in the sea: concentration ratios, reaction rate ratios, and ideal covariation. J. Geophys. Res . 97 (C4), 5693–5712.

Flynn, K.J., Stoecker, D.K., Mitra, A., Raven, J.A., Glibert, P.M., Hansen, P.J., Granèli, D., Burkholder, J.M., 2013. Misuse of the phytoplankton–zooplankton dichotomy: the need to assign organisms as mixotrophs within plankton functional types. J. Plankton Res. 35, 3–11.

Freudenthal, T., Neuer, S., Meggers, H., Davenport, R., Wefer, G., 2001. Influence of lateral particle advection and organic matter degradation on sediment accumulation and stable nitrogen isotope ratios along a productivity gradient in the Canary Islands region. Marine Geology 177, 93–109.

Freudenthal, T., Meggers, H., Henderiks, J., Kuhlmann, H., Moreno, A., Wefer, G., 2002. Upwelling intensity and filament activity off Morocco during the last 250,000 years. Deep-Sea Research I 49, 3655–3674.

Fukuda, R., Ogawa, H., Nagata, T., Koike, I., 1998. Direct determination of carbon and nitrogen content of natural bacteria assemblages in marine environments. Applied Environmental Microbiology 64, 3352–3358.

García-Muñoz, M., Arístegui, J., Pelegrí, J.L., Antoranz, A., Ojeda, A., Torres, M., 2005. Exchange of carbon by an upwelling filament off Cape Guir (NW Africa). J. Marine Syst. 54, 83–95.

Gasol, J.M., del Giorgio, P.A., Duarte, C.M., 1997. Biomass distribution in marine planktonic communities. Limnol. Oceanogr. 42, 1353–1363.

Geider, R.J., MacIntyre, H.L., Kana, T.M., 1997. Dynamic model of phytoplankton growth and acclimation: responses of the balanced growth rate and the chlorophyll-a:carbon ratio to light, nutrient-limitation and temperature. Mar. Ecol. Progr. Series 148, 187–200.

Gifford, D.J., Caron, D.A., 2000. Sampling, preservation, enumeration and biomass of marine protozooplankton. In: Harris, R.P., Wiebe, P., Lenz, J., Skjoldal, H.R., Huntley, M. (Eds.), ICES Zooplankton Methodology Manual. Academic Press, London, pp. 193–221.

Gilpina, L.C., Davidson, K., Roberts, E., 2004. The influence of changes in nitrogen:silicon ratios on diatom growth dynamics. J. Sea Res. 51, 21–35.

González, H.E., Menschel, E., Aparicio, C., Barría, C., 2007. Spatial and temporal variability of microplankton and detritus, and their export to the shelf sediments in the upwelling area off Concepción, Chile (□36°S), during 2002– 2005. Prog. Oceanogr. 75, 435–451.

Hagen, E., Zulicke, C., Feistel, R., 1996. Near-surface structures in the Cape Ghir filament off Morocco. Oceanologica Acta 19, 577–598.

Harrison, P.J., Conway, H.L., Holmes, R.W., Davis, C.O., 1977. Marine diatoms grown in chemostats under silicate or ammonium limitation. III. Cellular chemical composition and morphology of Chaetoceros debilis, Skeletonema costatum, and Thalassiosira gravida. Marine Biology 43, 19– 31.

Head, E.J.H., Harrison, W.G., Irwin, B.I., Horne, E.P.W., Li, W.K.W., 1996. Plankton dynamics and carbon flux in an area of upwelling off the coast of Morocco. Deep-Sea Research I 43, 1713–1738.

Heinbokel, J.F., 1978. Studies on the functional role of tintinnids in the southern California Bight. I and II. J. Phys. Oceanogr. 47, 177–197.

Hernández-Guerra, A., Nykjaer, L., 1997. Sea surface temperature variability off north-west Africa: 1981–1989. Int. J. Rem. Sens. 18, 2539–2558.

Herrera, L., Escribano, R., 2006. Factors structuring the phytoplankton community in the upwelling site off El Loa River in northern Chile. J. Marine Syst. 61, 13–38.

Holm-Hansen, O., Lorenzen, C.J., Holmes, R.W., Strickland, J.D.H., 1965. Fluorometric determination of chlorophyll. Journal du Conseil International pour l'Exploration de la Mer 30, 3–15.

Jacobson, D.M., Andersen, R.A., 1994. The discovery of mixotrophy in photosynthetic species of Dinophysis (Dinophyceae): light and electron microscopical observations of food vacuoles in Dinophysis acuminata, D. norvegica and two heterotrophic dinophysoid dinoflagellates. Phycologia 33, 97–110.

Jeong, H.J., Yoo, Y.D., Kang, N.S., Rho, J.R., Seong, K.A., Park, J.W., Nam, G.S., Yih, W.H., 2010. Ecology of Gymnodinium aureolum. I. Feeding in western Korean water. Aquat. Microb. Ecol. 59, 239–240.

Kang, N.S., Jeong, H.J., Moestrup, Ø., Shin, W.G., Nam, S.W., Park, J.Y., de Salas, M.F., Kim, K.W., Noh, J.H., 2010. Description of a new planktonic mixotrophic dinoflagellate Paragymnodinium shiwhaense n. gen., n. sp. from the coastal waters off western Korea: morphology, pigments, and ribosomal DNA gene sequence. J. Eukaryot. Microbiol. 57, 121–144.

Kim, H.J., Miller, A.J., McGowan, J., Carter, M.L., 2009. Coastal phytoplankton blooms in the Southern California Bight. Prog. Oceanogr. 82, 137– 147.

Kudela, R.M., Seeyave, S., Cochlan, W.P., 2010. The role of nutrients in regulation and promotion of harmful algal blooms in upwelling systems. Prog. Oceanogr. 85, 122–135.

Lachkar, Z., Gruber, N., 2012. A comparative study of biological production in eastern boundary upwelling systems using an artificial neural network. Biogeosciences 9, 293–308.

Lauthuilière, C., Echevin, V., Lévy, M., 2008. Seasonal and intraseasonal surface chlorophyll-a variability along the northwest African coast. J. Geophys. Res. 113, C05007. http://dx.doi.org/10.1029/2007JC004433.

Leblanc, K., Arístegui, J., Armand, L., Assmy, P., Beker, B., Bode, A., Breton, E., Cornet, V., Gibson, J., Gosselin, M.P., Kopczynska, E., Marshall, H., Peloquin, J., Piontkovski, S., Poulton, A.J., Quéguiner, B., Schiebel, R., Shipe, R., Stefels, J., van Leeuwe, M.A., Varela, M., Widdicombe, C., Yallop, M., 2012. A global diatom database – abundance, biovolume and biomass in the world ocean. Earth System Science Data 4, 149–165.

Lessard, E.J., 1991. The trophic role of heterotrophic dinoflagellates in diverse marine environments. Marine Microbial Food Webs 5, 49–58.

Levasseur, M.E., Therriault, J.C., 1987. Phytoplankton biomass and nutrient dynamics in a tidally induced upwelling: the role of the NO3:SiO4 ratio. Mar. Ecol. Progr. Ser. 39, 87–97.

Lynn, D.H., Small, E.B., 2002. Phylum Ciliophora. In: Lee, J.J., Bradbury, P.C., Leedale, G.F. (Eds.), An Illustrated Guide to the Protozoa. Society of Protozoologists, Lawrence, KS, pp. 994–1022.

Mackas, D., Strub, P.T., Thomas, A.C., Montecino, V., 2006. Eastern ocean boundaries pan-regional view. In: Robinson, A.R., Brink, K.H. (Eds.), The Sea. Harvard Press Ltd., Boston, pp. 21–60, Chapter 2.

Marcello, J., Hernandez-Guerra, A., Eugenio, F., Fonte, A., 2011. Seasonal and temporal study of the northwest African upwelling system. Int. J. Rem. Sens. 32, 1843–1859.

Marie, D., Partensky, F., Simon, N., Guillou, L., and Vaulot, D., 2000. Flow cytometry analysis of marine picoplankton. In: Diamond, R.A., DeMaggio, S. (Eds.), Living Colors: Protocols in Flow Cytometry and Cell sorting, pp. 421–454.

Menden-Deuer, S., Lessard, E.J., 2000. Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. Limnol. Oceanogr. 45, 569–579.

Minas, H.J., Codispoti, L.A., Dugdale, R.C., 1982. Nutrients and primary production in the upwelling region off Northwest Africa. Rapports et Proces-verbaux des Réunions. Conseil International pour l'Éxploration de la Mer 180, 148–183.

Moal, J., Martin-Jezequel, V., Harris, R.P., Samain, J.F., Poulet, S.A., 1987. Interspecific and intraspecific variability of the chemical composition of marine phytoplankton. Oceanologica Acta 10 (3), 339–346.

Montagnes, D.J., Berges, J.A., Harrison, P.J., Taylor, F.J., 1994. Estimating carbon, nitrogen, protein and chlorophyll-a from volume in marine phytoplankton. Limnol. Oceanogr. 39, 1044–1060.

Moore, C.M., Mills, M.M., Arrigo, K.R., Berman-Frank, I., Bopp, L., Boyd, P.W., Galbraith, E.D., Geider, R.J., Guieu, C., Jaccard, S.L., Jickells, T.D., La Roche, J., Lenton, T.M., Mahowald, N.M., Marañón, E., Marinov, I., Moore, J.K., Nakatsuka, T., Oschlies, A., Saito, M.A., Thingstad, T.F., Tsuda, A., Ulloa, O., 2013. Processes and patterns of oceanic nutrient limitation. Nature Geoscience 6, 701–710.

Morales, C.E., Anabalón, V., 2012. Phytoplankton biomass and microbial abundances during the spring upwelling season in the coastal area off Concepción, central- southern Chile: Variability around a time series station. Prog. Oceanogr. 92, 81–91.

Neuer, S., Freudenthal, T., Davenport, R., Llinás, O., Rueda, M.J., 2002. Seasonality of surface water properties and particle flux along productivity gradient off NW Africa. Deep Sea Research II 49, 3561–3567.

Nieto, N., Demarcq, H., McClatchie, S., 2012. Mesoscale frontal structures in the Canary Upwelling System: new front and filament detection algorithms applied to spatial and temporal patterns. Remote Sens. Environ. 123, 339– 346.

Nykjaer, L., Van Camp, L., 1994. Seasonal and interannual variability of coastal upwelling along Northwest Africa and Portugal from 1981 to 1991. J. Geophys. Res. 99 (C7), 14197–14207.

Ojeda, R.A., 1998. Dinoflagelados de Canarias: estudio taxonómico y ecológico. Ph.D. thesis, Universidad de Las Palmas de Gran Canaria, Las Palmas de Gran Canaria, Spain, 438 pp.

Pelegrí, J.L., Arístegui, J., Cana, L., González-Dávila, M., Hernández-Guerra, A., Hernández-León, S., Marrero-Díaz, A., Montero, M.F., Sangrá, P., Santana- Casiano, M., 2005a. Coupling between the open ocean and the coastal upwelling region off northwest Africa: water recirculation and offshore pumping of organic matter. J. Marine Syst. 54, 3–37.

Pelegrí, J.L., Marreno-Díaz, A., Ratsimandresy, A., Antoranz, A., Cisneros-Aguirre, J., Gordo, C., Grisolía, D., Hernández-Guerra, A., Láiz, I., Martínez, A., Parrilla, G., Pérez-Rodríguez, P., Rodríguez-Santana, A., Sangrá, P., 2005b. Hydrographic cruises off northwest Africa: the Canary Current and the Cape Ghir region. J. Marine Syst. 54, 39–63.

Putt, M., Stoecker, D.K., 1989. An experimental determined carbon: volume ratio for marine ‘‘oligotrichous’’ ciliates from estuarine and coastal waters. Limnol. Oceanogr. 34, 1097–1103.

Quigg, A., Zoe, V., Finkel, Z.V., Irwin, A.J., Rosenthal, Y., Ho, Tung-Yuan, Reinfelder, J.R., Schofield, O., Morel, F.M.M., Falkowski, P.G., 2003. The evolutionary inheritance of elemental stoichiometry in marine phytoplankton. Nature 425, 291–294.

Reid, P.C., Lancelot, C., Gieskes, W.C., Hagmeier, E., Weichart, G., 1990. Phytoplankton of the North Sea and its dynamics: a review. Netherlands J. Sea Res. 26, 295–331.

Roman, M.R., Caron, D.A., Kremer, P., Lessard, E.J., Madin, L.P., Malone, T.C., Napp, J.M., Peele, E.R., Youngbluth, M.J., 1995. Spatial and temporal changes in the partitioning of organic carbon in the plankton community of the Sargasso Sea off Bermuda. Deep-Sea Research 42, 973–992.

Romero, O.E., Lange, C.B., Wefer, G., 2002. Interannual variability (1988–1991) of siliceous phytoplankton fluxes off northwest Africa. J. Plankton Res. 24, 1035–1046.

Sherr, E.B., Sherr, B.F., Wheeler, P.A., 2005. Distribution of coccoid cyanobacteria and small eukaryotic phytoplankton in the upwelling ecosystem off Oregon coast during 2001 and 2002. Deep-Sea Resarch II 52, 317–330.

Sicre, M.A., Ternois, Y., Paterne, M., Martinez, P., Bertrand, P., 2001. Climatic changes in the upwelling region off Cap Blanc NW Africa over the last 70 k year: a multi-biomarker approach. Organic Geochemistry 32, 981–990.

Skovgaard, A., Hansen, P.J., Stoecker, D.K., 2000. Physiology of the mixotrophic dinoflagellate Fragilidium subglobosum. I. Effects of phagotrophy and irradiance on photosynthesis and carbon content. Mar. Ecol. Progr. Ser. 201, 129–136.

Staats, N., Stalb, L.J., Mur, L.R., 2000. Exopolysaccharide production by the epipelic diatom Cylindrotheca closterium: effects of nutrient conditions. J. Exp. Mar. Biol. Ecol. 249, 13–27.

Stoecker, D.K., Michaels, A.E., Davis, L.H., 1987. A large fraction of marine planktonic ciliates can contain functional chloroplasts. Nature 326, 790–792.

Stoecker, D.K., Taniguchi, A., Michaels, A.E., 1989. Abundance of autotrophic, rnixotrophic and heterotrophic planktonic ciliates in shelf and slope waters. Mar. Ecol. Progr. Ser. 50, 241–254.

Stoecker, D.K., Gustafson, D.E., Verity, P.G., 1996. Micro and mesoprotozooplankton at 140° W in the equatorial Pacific: heterotrophs and mixotrophs. Aquat. Microb. Ecol. 10, 273–282.

Sun, J., Lui, D., 2003. Geometric models for calculating cell biovolume and surface area for phytoplankton. J. Plankton Res. 25, 1331–1346.

Thompson, G.A., 2004. Tintinnid diversity trends in the southwestern Atlantic Ocean (29 to 60° S). Aquat. Microb. Ecol. 35, 93–130.

Tomas, C., 1997. Identifying Marine Phytoplankton. Academic Press, 858 pp.

Treguer, P.,Le Corre, P., 1978. The ratios of nitrate, phosphate, and silicate during uptake and regeneration phases of the Moroccan upwelling regime. Deep-Sea Research 26A, 163–184.

Troccoli, L. 1989. Análisis Cualitativo y Cuantitativo del Fitoplancton de la Bahía de Charagato, Isla de Cubagua, Venezuela. M.Sc. thesis, Universidad de Oriente, Cumaná, Venezuela, 71 pp.

Trommer, G., Leynaert, A., Klein, C., Naegelen, A., Beker, B., 2013. Phytoplankton phosphorus limitation in a North Atlantic coastal ecosystem not predicted by nutrient load. J. Plankton Res. 1–13.

UNESCO, 1994. Protocols for the Joint Global Ocean Flux Study (JGOFS) Core Measurement. Intergovernmental Oceanographic Commission. Manual and Guides 29, pp. 169.

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

Van Ruth, P.D., Qin, J.G., Branford, A.J., 2012. Size dependent competition in centric diatoms as a function of nitrogen and silicon availability. Open J. Marine Sci. 2, 33–42.

Verity, P., Sieracki, M., 1993. Use of color image analysis and epifluorescence microscopy to measure plankton biomass. In: Kemp, P., Sherr, E., Cole, J. (Eds.), Handbook of Methods in Aquat. Microb. Ecol.. Lewis Publisher, Boca Raton, pp. 327–338.

Villafañe, V., Reid, F., 1995. Métodos de microscopía para la cuantificación del fitoplancton. In: Alveal, K., Ferrario, M.E., Oliveira, E.C., Sar, E. (Eds.), Manual de métodos ecólogicos. Universidad de Concepción, Chile, Editorial Aníbal Pinto, pp. 169–185.

Zar, J.H., 1984. Biostatistical Analysis. Prentice-Hall International Inc., New Jersey, 718 pp.

Zubkov, M.V., Sleigh, M., Tarran, G.A., Burkill, P.H., Leakey, R.J.G., 1998. Picoplankton community structure on an Atlantic transect from 50°N to 50°S. Deep Sea Research I 45, 1339–1355.

Zubkov, M.V., Sleigh, M.A., Burkill, P.H., 2000. Assaying picoplankton distribution by flow cytometry of underway samples collected along a meridional transect across the Atlantic Ocean. Aquat. Microb. Ecol. 21, 13–20.

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  ***one in its nets of wonder forever.***
*El mar, una vez que lanza su hechizo, te*
 *sostiene en su red de maravillas para siempre*
***Cousteau***

# CHAPTER 2

## Phytoplankton biomass and microbial abundances during the spring upwelling season in the coastal area off Concepción, central-southern Chile: Variability around a time series station

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# CHAPTER

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## Abstract

In the coastal system off Concepción, time series observations at a fixed station (St. 18) have shown strong seasonal changes in the oceanographic environment of the upper layer (<35 m depth), accompanied by large increases in phytoplankton biomass during the spring-summer upwelling season. These blooms, dominated by microplanktonic diatoms, have usually overshadowed the relevance of the smaller microbial components during upwelling. This study focuses on the variability of oceanographic conditions and their association with the structure of the planktonic community (size fractionated chlorophyll-a and microbial abundances) in the upper layer during the upwelling season, examining the extent to which

St. 18 is representative of the coastal system off Concepción during springtime. For this purpose, data from three consecutive springs (2004, 2005, 2006) were compared, which included cruises for all years (8 stations around St. 18) as well as monthly sampling at St. 18. Most of the spatial (submesoscale) variability in chlorophyll-a and the microbial components was not significant, but data dispersion around mean values was high. Water column structure (temperature and salinity) in the upper layer explained a significant fraction (25–65%) of the spatial variability in most of the planktonic components; their responses to oceanographic variability were linear in some cases and non-linear in others. For the most part, St. 18 appears to adequately represent mean oceanographic conditions and the structure of planktonic communities in the coastal waters off Concepción during springtime, however spatial variability needs to be taken into account in the interpretations of temporal changes at this fixed station as well as in assessments of carbon flow within, and exportation processes from, this upwelling system.

## 4.1. Introduction

In the Humboldt Current System (HCS), the oceanographic environment of the coastal region off central southern Chile (30–40°S) is characterized by high temporal variability on daily to interannual scales (Strub et al., 1998), with seasonal upwelling being one of the most well studied modes (e.g. Avaria et al., 1989; Shaffer et al., 1999; Sobarzo et al., 2007; Correa-Ramírez et al., this volume). Off Concepción (~36.5°S), the upwelling season starts in the austral spring and reaches maximum intensity during summer. Upwelled water is mostly Equatorial Subsurface Waters (ESSW) in origin, associated with low dissolved oxygen ($O_2$) concentrations and higher salinities than the surface waters (Sobarzo et al., 2007). The spatial manifestation of upwelling over the shelf area is highly heterogeneous due to changes in bottom topography (e.g. presence of canyons, offshore extension of the shelf) and to coastline orientation (e.g. bays, capes); river inputs in winter and spring also affect water column properties (Faúndez et al., 2001; Narváez et al., 2004; Sobarzo and Djurfeldt, 2004; Sobarzo et al., 2007). Phytoplankton biomass, in terms of chlorophyll-a (Chl-a) concentration, displays a strong seasonal pattern in the shelf area, with maxima during the upwelling season (Böttjer and Morales, 2007; González et al., 2007).

The coastal region off central southern Chile is also subject to intra-seasonal and interannual variability in the oceanographic environment; part of this is remotely forced and linked to the El Niño Southern Oscillation (ENSO) cycle and part is driven by local winds (Hormazabal et al., 2001, 2002). Although winds usually remain upwelling favorable along the coast of the HCS during El Niño events, nutrient inputs into the upper layer can be reduced, thereby affecting phytoplanktonic biomass, species composition and/or primary production (e.g. Carr et al., 2002). Off central southern Chile, the upwelling favorable wind intensity appears to be weaker during El Niño years (Shaffer et al., 1999). In this region, ENSO related interannual variability in the onset of the upwelling season and in the intensity of upwelling favorable winds (represented by the extent of offshore Ekman transport) has been linked to significant changes in Chl-a concentration within the coastal band (Gómez, 2008).

Time series observations in the coastal system off Concepción (St. 18) have shown that the strong seasonal changes in the oceanographic environment and Chl-a are accompanied by several alterations in the structure of planktonic communities within the upper layer. Among the smaller size components, microplanktonic diatoms dominate during the upwelling season, with about 70% of their abundance concentrated within the upper 10 m. A summer maximum in diatoms is accompanied by increases in microplanktonic tintinnids and dinoflagellates (González et al., 2007). In the nanoplankton, auto (including mixo-) and heterotrophic nanoflagellates are numerically dominant and, at times, contribute most of the total carbon biomass in the upper layer. The seasonality of this size fraction is low but data dispersion around the mean abundance values is high during the upwelling period, with maximum values tending to co-occur with those of total Chl-a (Anabalón et al., 2007; Böttjer and Morales, 2007). Among the picoplankton, the abundance of heterotrophic bacterioplankton is highest in summer and lowest in winter; autotrophs, mostly dominated by cyanobacteria (*Synechococcus* sp.), peak in autumn and are concentrated within the upper layer. In both cases, data dispersion around mean values is high within each seasonal period (Alarcón, 2008). Although the St. 18 time series data span over almost 8 years, interannual changes in the abundances and biomasses of the smaller planktonic components remain to be explored.

The dominance of microplanktonic phytoplankton blooms in coastal waters during the upwelling season has usually overshadowed the relevance of the smaller microbial components in the coastal system off Concepción (but see Böttjer and Morales, 2007; Vargas et al., 2007; Eissler et al., 2010) and in other eastern boundary systems (but see Sherr et al., 2005, Baltar et al., 2009). In assessing the extent to which these blooms regulate the carbon flow in the coastal system or contribute to the exportation of carbon away from the coast, the spatial variance in the structure of planktonic communities becomes relevant. However, studies of the spatial variability of pico and nanoplanktonic assemblages in the coastal upwelling system off Concepción are very limited (Cuevas et al., 2004), even for microplankton assemblages (Gonzalez et al., 2007). On the other hand, the spatial distribution of surface Chl-a in this system, as detected by satellite, is usually of high heterogeneity at submesoscale (tens of km) and mesoscale (>80 km up to a few hundred km) levels, (Morales et al., 2007, 2010; Correa-Ramírez et al., 2007, this volume). Within this context, the present study focuses on the variability of oceanographic conditions and their association with the structure of the planktonic community (size fractionated Chl-a and microbial abundances) within the upper layer during the upwelling season, examining the extent to which St. 18 is representative of the coastal system off Concepción during springtime.

## 4.2. METHODS

### 4.2.1. STUDY AREA, SAMPLING, AND SAMPLE ANALYSES

The continental shelf off Concepción – the Itata Terrace – is bound by the Itata Canyon (north) and the Biobío Canyon (south). Bathymetry, coastline morphology, river inputs and the presence of a main upwelling center on the southern border (Pta. Lavapié), as well as a secondary center farther north (Peninsula Tumbes), all influence the dynamics of the Concepción coastal upwelling system (Fig. 1a). This study includes data from St. 18 (36°30'S, 73°08'W, 90 m depth) collected during monthly sampling in the springs of 2004, 2005 and 2006 (Fig. 1a); these data are part of the COPAS database (www.copas.cl). It also includes data obtained during three spring cruises (SPC) in November 2004, December 2005 and October 2006. During each cruise, eight stations located on the shelf and shelf break, in the area around St. 18, were repeatedly sampled; half the stations were located over the inner shelf and half over the outer shelf or shelf edge (~10 and 40 km from the coast, respectively).

Continuous vertical profiles (0–100 m or to the maximum depth if shallower) of hydrographic variables were obtained with a CTD-O (Sea Bird SBE-25 + $O_2$ sensor). Discrete water samples (8 L Niskin bottles) were used to determine $O_2$ , macro-nutrients ($PO^{-3}$ , $SiO_4^{-2}$ , $NO^{=}_2$ , $NO^{-}_3$ ), Chl-a as total (Chl-aT) and within two size fractions: <20 (Chl-a < 20) and < 3 μm (Chl-a < 3), and to estimate nano and picoplankton abundances. In this study, only the samples from the top layer (SPC: 0, 10, 20, and 35 m depth: St. 18: 0, 5, 10, 15, 20, 30, and 40 m depth) have been analyzed since previous studies during the upwelling season have shown that smaller planktonic components are mostly concentrated in this strata (Böttjer and Morales, 2007; González et al., 2007; Morales et al., 2007; Alarcón, 2008).

The methods used for the sampling and analysis of $O_2$, nutrients and Chl-a followed those applied to the St. 18 time series studies (e.g. Anabalón et al., 2007). Chl-a fractions were obtained as follows: for Chl-aT, subsamples were vacuum filtered using glass-fiber GFF filters (0.7 μm); for the Chl-a < 20 fraction, subsamples were gravitationally filtered through a 20 μm Nytex mesh mounted on a 47 mm filtration device and the water collected was filtered as above; for the Chl-a < 3 fraction, subsamples were filtered through a 3 μm membrane filter and the water collected was then filtered as for Chl-aT. Each Chl-a size fraction was then obtained from the differences between fractions: microplankton (Chl-aT - Chl-a < 20 = Chl-aT-20), nanoplankton (Chl-a < 20 - Chl-a < 3 = Chl-a 20-3), and picoplankton (Chl-a < 3).

For nanoplankton, duplicate samples were collected in centrifuge tubes (50 mL) and immediately preserved with glutaraldehyde (2% final concentration), and stored under dark low temperature (~5 °C) conditions until subsequent analysis within 3 months following sampling. For picoplankton, duplicate samples were collected in sterile cryovials (2 mL), immediately fixed with glutaraldehyde (1% final concentration) and, after 10 min at room temperature, were initially stored in liquid nitrogen, and then subsequently stored in the dark at -80°C until analysis within 6 months following sampling.

Nanoplankton abundances were obtained by epifluorescence microscopy (Nikon TE2000S) following Porter and Feig (1980). Subsamples (20 mL) were taken from each collection tube and stained with a fluorochrome (final concentration: 0.01%); the SPC samples were stained with Proflavine (3–6 diamine-acridine hemi-sulfate; Hass, 1982) and the St. 18 samples with DAPI (40,6-diamidino-2-phenylindole; Porter and Feig, 1980). A comparison of these methods showed no significant differences in cell counts when using a multiple filter (V. Anabalón, unpublished data). The stained samples were then filtered onto black polycarbonate membrane filters (0.8 μm pore size) supported by 0.45 μm membrane filters. These filters were mounted on glass slides and stored at -20 °C in the dark until later analysis. Filters were examined with 1000x magnification and at least 100 nanoplanktonic cells (3–20 μm) were counted per sample.

Picoplankton estimates of abundance were obtained via flow cytometry (Becton–Dickinson FACScalibur with a 488 nm Ion-Argon Laser), following Marie et al. (2000). Subsamples for counting autotrophic and heterotrophic cells were taken from different cryovials and analyzed separately; only cells <3 μm in size were included. The samples for counting heterotrophs were stained with fluorochrome SYBR Green I (Molecular Probes). Further details of sample analysis are given in Alarcón, 2008.

### 4.2.2. DATA ANALYSES

All the data were tested for normality and homogeneity of variance (Kolmogorov–Smirnov and Browne–Forsythe tests, respectively); results suggested that parametric analyses of the raw data were not appropriate (Zar, 1984). Oceanographic and planktonic variability in spatial (between sampling stations during the SPC) and temporal (between different years) dimensions, and between the SPC and St. 18 during the same year, were analyzed with two-way ANOVA using ranked data (Zar, 1984); in all cases, depth was used as the second factor. Differences between observations were further analyzed with post hoc multiple comparisons (Tukey test), except in the case of depth differences.

Associations between oceanographic and planktonic variables in the upper layer were explored with non-parametric simple correlation analyses (Spearman), but since most variables were strongly linked to depth variation, partial correlations with ranked data were applied (STATISTICA® v. 6.0). Furthermore, linearity in the responses of biological components (such as size and functional groups) to environmental factors and the potential interactions among multiple factors was explored with habitat modeling using a non-parametric multiple regression (NPMR; HYPERNICHE® v. 1.12). A Gaussian weighting function with a local linear regression model was used in all cases, with a free exhaustive search method included in the software. The settings used were the following: a minimum average neighborhood size ($N^*$) for an acceptable model of 5% of the sample size (measure of flexibility); an improvement criterion of 10 (measure of parsimony); data/predictor ratios according to each data set; minimum neighborhood size equal to 5; and maximum allowable missing estimates equal to 5% (McCune and Mefford, 2004). The best models obtained were assessed for fit with a cross-validated $R^2$ (x $R^2$) and for statistical significance with the Monte Carlo permutation test (250 runs, 99% confidence level).

### 4.2.3. CLIMATOLOGICAL AND SATELLITE BACKGROUND INFORMATION

Information on the climatological and environmental conditions in the study area was derived from remote (satellite) sources so as to provide a wider perspective of the results from in situ sampling. The processed data were kindly provided by Dr. S. Hormazabal (UdeC). ENSO-like variability during the study period was assessed using climatological indices, the multivariate ENSO index (MEI; Wolter and Timlin, 1998) and the SST anomaly in the El Niño 3.4 region. These data (2003–2007) were obtained from the National Oceanographic and Atmospheric Administration (NOAA) website (http:// www.cdc.noaa.gov/people/klaus.wolter/MEI/table.html).

Local wind time series satellite data were used to evaluate general upwelling conditions. Daily sea surface wind stress based on QuikSCAT L3 daily gridded ocean wind vectors (JPLSeaWinds Project, http://podaac.jpl.nasa.gov/quikscat) were obtained for 0.25° x 0.25° grids and then averaged across the 1° x 1° grid closest to the coast (centered on 73.5°W–36.5°S). Data gaps of a few days were linearly interpolated and low-pass filtered with a 91- day cosine-Lanczos filter and a half amplitude point at 21 days to remove synoptic

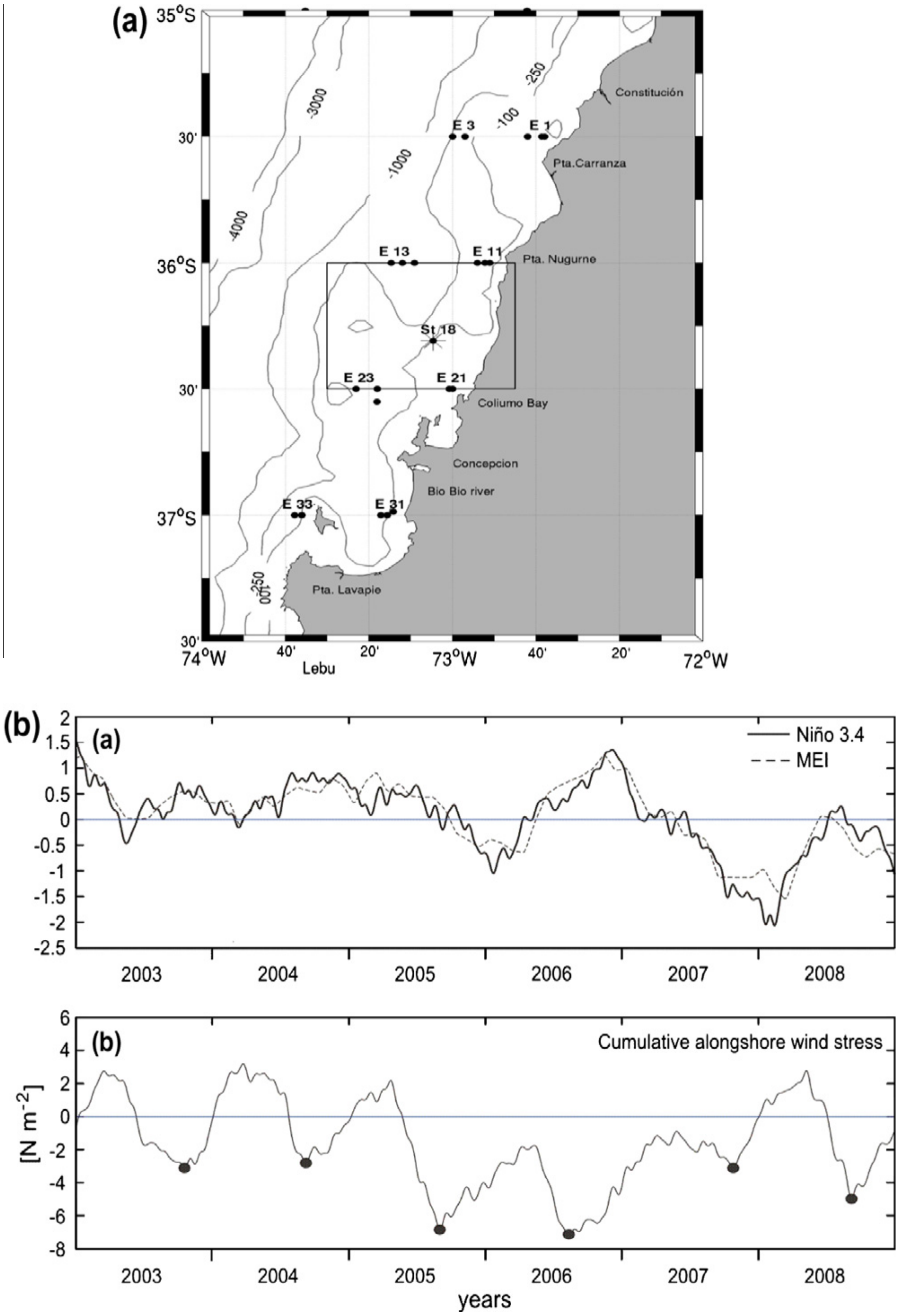

**Fig. 1.** Study area and geographic location of the spring cruise stations and the fixed time series station (St. 18) on the shelf (Itata Terrace) off Concepción, Chile (a); climatological indices for the ENSO cycle: MEI and El Niño 3.4 (b, upper panel) and, cumulative offshore Ekman transport series (b, lower panel).

variability. Alongshore wind stress was calculated for the 1° x 1° QuikSCAT data using the orientation of the coastline found by fitting a straight line to the 2' resolution coastline obtainned from Sandwell/Smith bathymetry (Sandwell and Smith, 1997), a drag coefficient of 1.3 x $10^{-3}$ and an air density of 1.2 kg $m^{-3}$ (Bakun and Nelson, 1991).

To assess the degree to which the in situ fluctuations in oceanographic conditions and phytoplankton biomass during this study reflected those of the entire coastal area, satellite sea surface temperature (SST) and Chl-a data for the period of study were included. For this purpose, time series data (January 2004 through to December 2007) were obtained for the coastal waters around St. 18 (36–36.5°S; 72.75–73.5°W); daily (night) SST data were derived from the NOAA database in AVHRR Pathfinder V5.0 (ftp://data.nodc.noaa.gov/pub/data.nodc/pathfinder), whereas Chl-a daily images were gathered from the HERMES multi-sensor combined product (MODIS, MERIS, SeaWiFS) obtained from GlobColor (http://www.globcolour.info < http://oceancolor.gsfc.nasa.gov). The spatial resolution of the images obtained is 4 km.

## 4.3. RESULTS

The evolution of two ENSO indices (MEI and El Niño 3.4) from 2003 to 2007 (Fig. 1b, upper panel) indicates that the in situ sampling of the present study (2004–2006) encompassed different stages of the ENSO cycle, including a weak warm event (late 2006–early 2007), preceded by a weak La Niña (first half of 2006) and succeeded by a similar cold event (second half of 2007). During the study period, the cumulative offshore transport off Concepción (Fig. 1b, lower panel) shows that the start of the spring upwelling-favorable season (i.e. the transition from poleward to equatorward (positive) alongshore wind stress) fell slightly earlier in 2006 (14 August) than in 2004 and 2005 (7 and 5 September, respectively). Mean daily Ekman offshore transport values (not shown) were however similar for the three springs (2004: 648 ± 772, 2005: 772 ± 878, and 2006: 721 ± 882 m $s^{-1}$ x 1000 m coastline).

### 4.3.1. VARIABILITY IN THE OCEANOGRAPHIC CONDITIONS

The water properties of the upper layer, from SPC and St. 18 samplings (Table 1), differed slightly between the three spring periods, mostly in terms of salinity (lower in 2006); nutrient and $O_2$ concentrations were mostly similar during the three SPC, whereas St. 18 values were significantly different in 2004 from the other two springs. A comparison of the oceanographic conditions between St. 18 and SPC (only the central stations surrounding St. 18) for each year showed that, for the most part, the differences were not significant; the exceptions were salinity and $SiO_4^{-2}$ in 2005 ($p < 0.001$). These similarities and differences are reflected in the mean values included in Table 1.

The extent of the spatial variability in the coastal waters off Concepción during the SPC was assessed in terms of inshore (E1, E11, E21, E31) versus shelf edge (E3, E13, E23, E33) stations, and central (surrounding St. 18: E11, E13, E21, E23) versus border stations (E1, E3, E31, E33); for this purpose, data from the three cruises were pooled in each of those categories. The central and border stations had relatively similar upper layer oceanographic conditions, whereas the inshore stations were significantly colder and more saline, with lower $O_2$ and higher nutrient concentrations, than the shelf edge stations (Table 2). Depth differences for each of these variables within the upper layer were significant, except for $NO^{=}_{2}$ (Tables 1 and 2).

To complement the comparisons between springs, the vertical distributions of temperature, salinity and $O_2$ during the SPC (0–100 m) and at St. 18 (0–80 m), were graphically analyzed. For the SPC, the transect parallel to the coast within the shelf edge area (Fig. 1a: stations E3, E13, E23, E33) confirmed that the patterns described for the upper layer were maintained (Fig. 2), with higher salinities (>34.2 close to the surface) in 2004 and 2005 compared with 2006, and lower $O_2$ (<1 mL $L^{-1}$); both are characteristic of the upwelling source – ESSW – found deeper in 2006 compared to the other two years. At St. 18 (Fig. 3), the evolution of oceanographic conditions in the water column during spring (including September and January for proper interpolation at seasonal boundaries), also confirms the presence of fresher waters in 2006 compared with the other two years. In early September of 2006, however, waters indicative of upwelling (34.5 isohaline and low $O_2$) were present at this station, appearing slightly later in the two other years.

### 4.3.2 VARIABILITY IN SIZE FRACTIONATED CHL-A AND ABUNDANCES OF MICROBIAL COMPONENTS

The concentrations of Chl-a in the upper layer were highly variable during the three springs, during the SPC and at St. 18, but, for the most part, differences were not significant (Table 3). During the SPC, the microplankton (Chl-aT-20) biomass was lower and the nanoplankton (Chl-a20-3) higher in 2006 compared with 2004; at St. 18, these differences

| Year | Temperature [ºc] | Salinity | $O_2$ [mL $L^{-1}$] | $PO_4^-$ [μM] | $NO_2^-$ [μM] | $NO_3$ [μM] | $SiO_4^{-2}$ [μM] | year comparison |
|---|---|---|---|---|---|---|---|---|
| Cruises | | | | | | | | |
| 2004 | 11.8±1.0 | 34.3±0.2* | 3.5±2.2 | 1.8±0.8 | 0.3±0.2 | 18.2±8.3 | 16.3±9.3 | 06 vs. 04 |
| 2005 | 11.4±1.2* | 34.2±0.4 | 3.0±2.4 | 2.0±0.8 | 1.1±1.3* | 18.4±9.9 | 17.1±8.4 | 06 vs. 05 |
| 2006 | 12.0±0.9 | 34.0±0.5 | 3.6±2.1 | 1.6±0.8 | 0.3±0.2** | 17.5±8.6 | 11.7±7.0** | 04 vs. 05 |
| St. 18 | | | | | | | | |
| 2004 | 11.6±1.2 | 34.4±0.2** | 2.4±2.3** | 2.1±0.8** | 0.5±0.5 | 19.7±9.8** | 17.2±9.0** | 06 vs. 04 |
| 2005 | 11.5 ±1.5* | 34.4±0.1** | 4.4±3.1 | 1.5±1.0 | 0.3±0.5 | 13.1±10.9 | 8.3±7.9 | 06 vs. 05 |
| 2006 | 12.4±1.6 | 34.1±0.4 | 4.4±2.4* | 1.4±0.8* | 0.2±0.1 | 13.3±8.9* | 7.1±6.4** | 04 vs. 05 |

**Table 1**. Temporal variability in oceanographic conditions in the upper layer during spring, from SPC (0–35 m) and St. 18 (0–30 m) samplings, in the upwelling area off Concepción (Chile). Mean ± standard deviation values and 2-way ANOVA comparisons (factors: years and depth; SPC n = 95, St. 18 n = 54); probability values: $^{*}p < 0.01$, $^{**}p < 0.001$, others are not significant. Differences in depth were all significant except for $NO_{-2}$.

| Variables | Border/Central | P | Inshore/shelf-edge | P |
|---|---|---|---|---|
| Temperature [ºc] | 11.6 ± 1.0/11.8 ± 1.1 | - | 11.4 ± 1.0/12.0 ± 1.1 | * |
| Salinity | 34.2 ± 0.4/34.1 ± 0.4 | - | 34.3 ± 0.4/34.0 ± 0.4 | ** |
| $O_2$ [mL L-1] | 3.2 ± 2.2/3.5 ± 2.3 | - | 2.5 ± 2.3/4.3 ± 1.7 | ** |
| $PO_4$- [µM] | 2.0 ± 0.8/1.7 ± 0.8 | - | 2.2 ± 0.8/1.5 ± 0.7 | ** |
| $NO_2$- [µM] | 0.7 ± 1.1/0.4 ± 0.4 | - | 0.8 ± 1.1/0.4 ± 0.3 | ** |
| $NO_3$- [µM] | 18.3 ± 8.8/17.7 ± 8.9 | - | 20.1 ± 8.6/16.0 ± 8.7 | - |
| $SiO_4$-$^2$ [µM] | 14.6 ± 8.5/15.2 ± 9.1 | - | 17.8 ± 9.7/12.1 ± 6.8 | * |
| Chl-aT | 3.3 ± 3.7/2.5 ± 4.2 | - | 3.8 ± 4.9/2.0 ± 2.5 | - |
| Chl-aT-20 | 2.5 ± 3.4/1.6 ± 4.0 | - | 2.9 ± 4.6/1.2 ± 2.3 | - |
| Chl-aT 20-3 | 0.7 ± 0.7/0.8 ± 0.5 | - | 0.7 ± 0.6/0.7 ± 0.6 | - |
| Chl-aT < 3 | 0.1 ± 0.1/0.1 ± 0.2 | - | 0.1 ± 0.1/0.2 ± 0.2 | - |
| HNF x 103 | 0.42 ± 0.31/0.50 ± 0.69 | - | 0.56 ± 0.69/0.36 ± 0.31 | - |
| ANF x 103 | 0.65 ± 0.75/0.46 ± 0.37 | - | 0.63 ± 0.75/0.48 ± 0.39 | - |
| APP x 106 | 0.05 ± 0.09/0.35 ± 0.88 | - | 0.03 ± 0.06/0.37 ± 0.87 | ** |
| HPP x 106 | 1.12 ± 0.86/1.37 ± 0.90 | - | 1.15 ± 0.63/1.35 ± 1.08 | - |

**Table 2** Spatial variability in oceanographic conditions and planktonic components in the upper layer (0–35 m) during the SPC (2004–2006 combined data) in the upwelling area off Concepción. Location of the stations (Fig. 1a): central (E11, E13, E21, E23), border (E1, E3, E31, E33), inshore (E1, E11, E21, E31), and shelf-edge (E3, E13, E23, E33). Mean ± standard deviation values and 2-way ANOVA comparisons (factors: location and depth); probability values (p) shown only for location differences: $^{*}$< 0.01, $^{**}$< 0.001; – = not significant. Depth differences were all significant except for $NO_{-2}$ , Chl-a in the microplankton fraction, and HPP. Chl-a values in mg $m^{-3}$ and abundance of nano- and picoplankton in cells $mL^{-1}$ (see Section 2 for abbreviations)

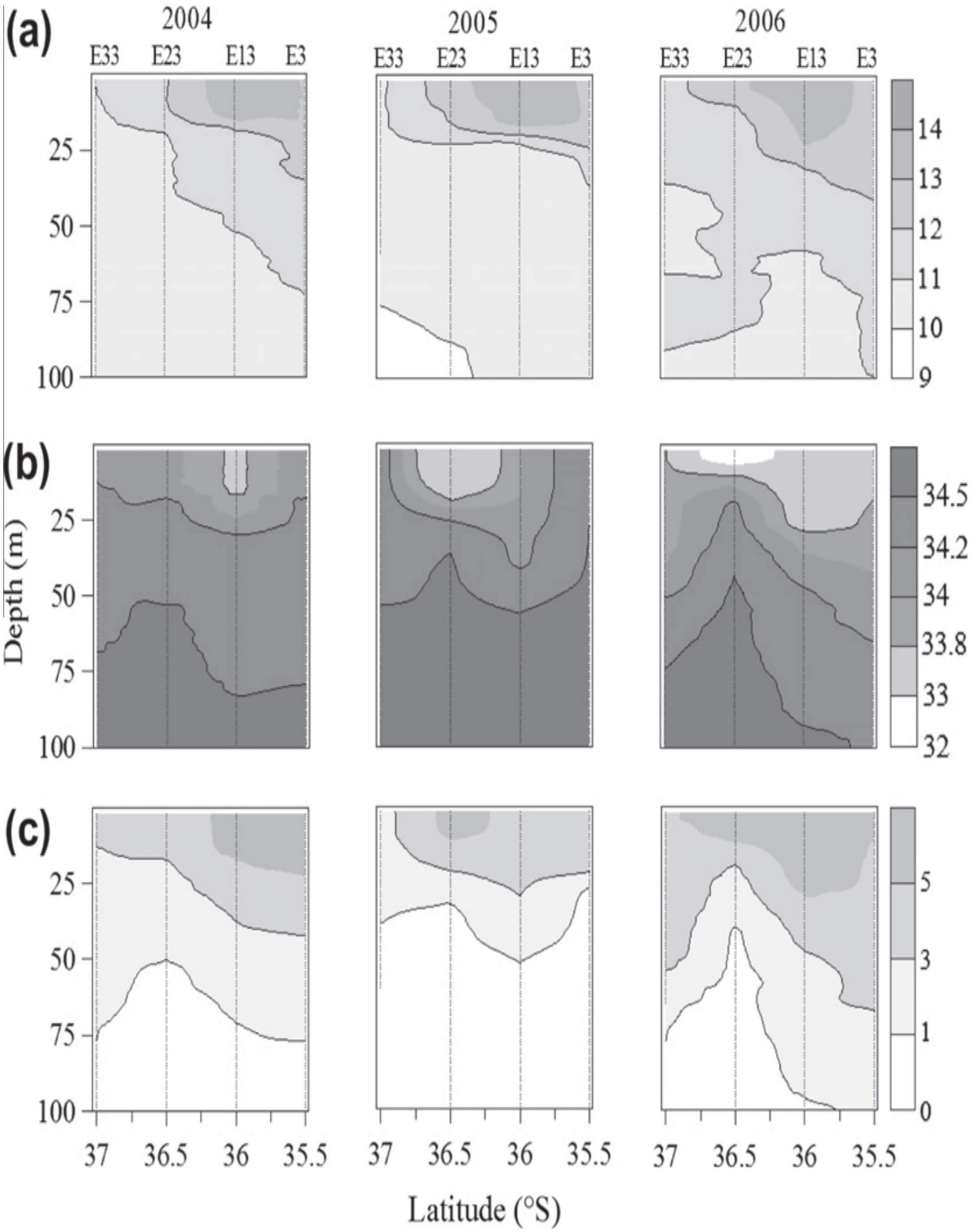

**Fig. 2.** Vertical distribution (0–100 m) of the oceanographic variables along a N–S transect over the shelf-edge stations (see Fig. 1a) during the 3 SPC off Concepción: temperature in ºC (a), salinity (b), and dissolved oxygen in mL $L^{-1}$ (c).

were not significant. In comparing the two sampling modes: SPC (only the central stations) and St. 18, the total and size fractionated Chl-a concentrations were relatively similar for both modes during 2004 and 2006, whereas all the values were significantly higher ($p < 0.001$) in 2005 at St. 18 than during the SPC (Table 3).

In terms of the spatial distribution during the SPC (data grouped as for the oceanographic variables), Chl-a concentrations were similar at different locations but data dispersion around mean values was high; specifically, the mean values of Chl-aT and Chl-aT-20 were almost double at inshore stations (Table 2). In addition, variations in Chl-a values with depth during the SPC were highly significant ($p < 0.001$) except for the microplankton fraction (Tables 2 and 3), which displayed surface and subsurface maxima; at St. 18, this exception also applied to Chl-aT (Table 3).

The abundances of the microbial components in the upper layer were also highly variable during the three springs at both the SPC stations and St. 18 (Table 3). The nanoplankton was dominated by nanoflagellates; autotrophic (and mixotrophic) nanoflagellates (ANF) abundances were similar during the different periods, whereas heterotrophic nanoflagellates (HNF) abundances were lower in 2006 for the SPC, and lower in 2004 at St. 18. Among the picoplankton, autotroph (APP) abundances, dominated by the cyanobacterium *Synechococcus*, were lower in 2005 compared with 2006 for the SPC, whereas at St. 18 they were similar during all the three springs; heterotrophic picoplankton (HPP), or bacterioplankton, abundance was relatively similar during the three spring periods. In comparing the two sampling modes (as for Chl-a), ANF and HNF abundances were similar at St. 18 and during the SPC for all springs, except for the HNF in 2004, which were very low at St. 18 compared with the SPC ($p < 0.01$). In the picoplankton, the APP mean values were one order of magnitude higher for the SPC during 2004 and 2006 ($p < 0.001$) compared with St. 18 whereas HPP values were similar for both.

With regards to the spatial distribution during the SPC (data grouped as for Chl-a), the abundances of ANF, HNF and HPP were similar between the locations (Table 2). The mean abundance of APP, however, was one order of magnitude higher at the shelf edge than at the inshore stations; this was also true for the central versus the border stations, but the differences were not statistically significant. Depth differences in distribution in the upper layer were significant at the SPC stations for all components except for the HPP (Tables 2 and 3), whereas at St. 18 only the APP showed a depth dependent distribution (Table 3).

### 4.3.3 INFLUENCE OF THE OCEANOGRAPHIC VARIABILITY UPON THE PLANKTONIC COMPONENTS

The responses of planktonic assemblages to oceanographic variability in the upper layer during the springtime were explored separately for the SPC and the St. 18 data to reduce the sources of variability. As a preliminary approach, simple correlation analyses showed that the associations between the oceanographic variables themselves were all highly significant ($p < 0.001$) during both sampling modes (except for $NO^{=}_2$ ). In particular, temperature and $O_2$ were negatively correlated with depth, whereas salinity and nutrient concentrations were positively correlated with depth. Most of the planktonic components (except Chl-aT-20 and HNF) were also significantly correlated with depth and thus, with most of the oceanographic variables during the SPC, but less so at St. 18 (data not shown). In controlling for depth with a partial correlation analysis (Table 4), the above associations persisted for the SPC in only two cases (Chl-a < 3 and APP) whereas in others they became weak or disappeared; also, a positive correlation between Chl-aT-20 and salinity emerged. In contrast, at St. 18 most of the partial correlations were weak or non-significant, with the exception of HNF (Table 4).

The associations between microbial abundances and Chl-a concentrations (simple correlation) were stronger during the SPC compared with St. 18 (Table 5). Among the autotrophs, APP were well represented by Chl-a < 3 and ANF by Chl-a20-3 in both sampling modes; also, abundances of ANF and APP were correlated with each other. HNF and HPP abundances were correlated with each other only at St. 18, and, for the most part, these components were correlated with the smaller Chl-a fractions for both sampling modes.

The spatial variability of the planktonic components in association with the changes in oceanographic conditions and Chl-a concentration during springtime was further evaluated with NPMR analysis using the SPC data (n ~ 100). Based on the correlation results, six environmental factors (predictors) were selected for this analysis: temperature, salinity, $O_2$, and the three macro-nutrient concentrations (no data transformations). Because of the dependency between the autotrophic components and Chl-a, the latter data were included as factors in a separate analysis. Chl-a data (no data transformations) were considered both as absolute and relative values when analyzed as responses (dependant variables); microbial abundance data were log transformed since, for the most part, they spanned several orders of magnitude.

NPMR results (Table 6) indicated that the variability of the Chl-a size fractions was mostly represented by the combined variations of temperature and salinity (i.e. water column structure); the responses were linear in some cases and non-linear in others, as exemplified

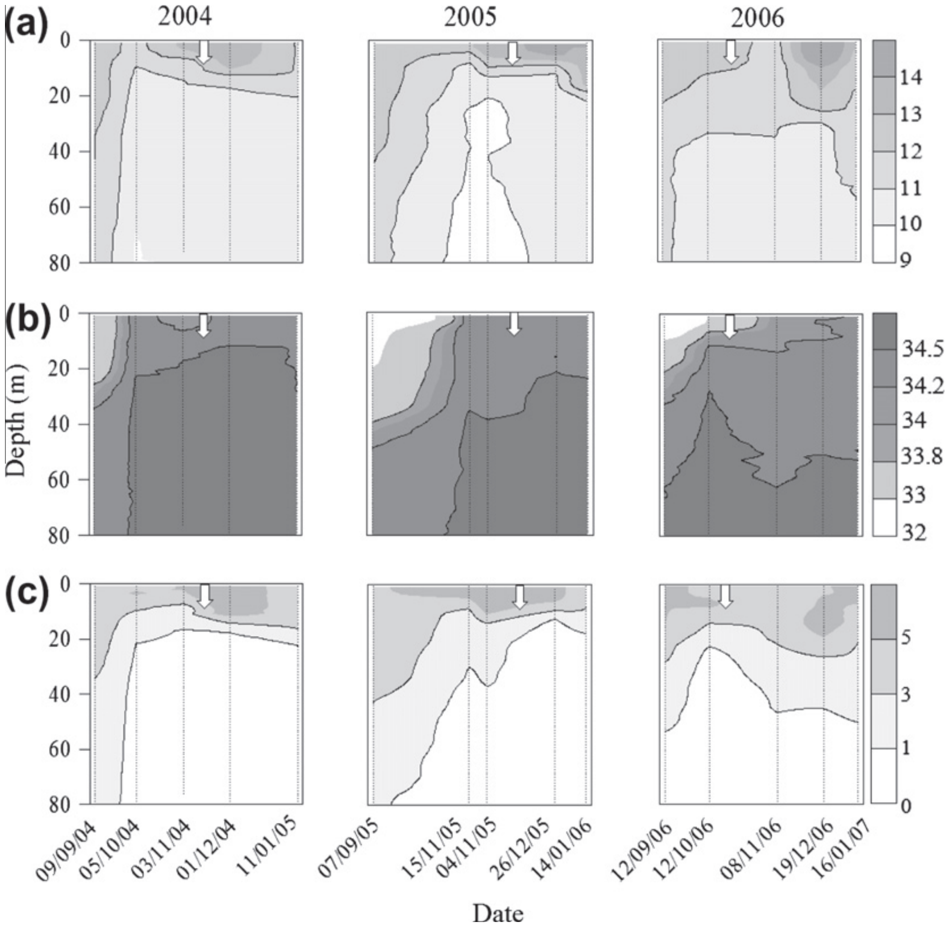

**Fig. 3.** Vertical distribution (0–80 m) of the oceanographic variables during the spring upwelling period (October, November, December) at the time series station St. 18 off Concepción: temperature in ºC (a), salinity (b), and dissolved oxygen in mL $L^{-1}$ (c).

| Year | Chl-aT | Chl-aT-20 | Chl-a 20-3 | Chl-a <3 | HNFx$10^3$ | ANFx$10^3$ | APPx$10^6$ | HPPx$10^6$ | Y comparison |
|---|---|---|---|---|---|---|---|---|---|
| Cruises | | | | | | | | | |
| 2004 | 3.6 ± 4.5 | 3.0 ± 4.2 * | 0.5 ± 0.4* | 0.1 ± 0.1 | 0.55 ± 0.36** | 0.49 ± 0.32 | 0.15 ± 0.28 | 0.82 ± 0.72 | 06 vs. 04 |
| 2005 | 3.5 ± 4.9 | 2.6 ± 4.5 | 0.8 ± 0.7 | 0.1 ± 0.1 | 0.59 ± 0.81* | 0.66 ± 0.71 | 0.06 ± 0.12 * | 1.30 ± 0.88 | 06 vs. 05 |
| 2006 | 2.6 ± 1.2** | 0.5 ± 1.0 | 0.9 ± 0.6** | 0.1 ± 0.1** | 0.23 ± 0.18 | 0.51 ± 0.68** | 0.37 ± 0.97 | 1.41 ± 0.91 | 04 vs. 05 |
| | | | | | | | | | Z Differences |
| St. 18 | | | | | | | | | |
| 2004 | 4.2 ± 6.3 | 3.4 ± 5.8 | 0.7 ± 0.7 | 0.1 ± 0.1 | 0.08 ± 0.10** | 0.35 ± 0.34 | 0.02 ± 0.04 | 1.10 ± 0.93 | 06 vs. 04 |
| 2005 | 5.9 ± 4.8 | 4.6 ± 4.3 | 1.2 ± 0.9 | 0.1 ± 0.1* | 0.73 ± 0.36 | 0.41 ± 0.41 | 0.02 ± 0.04 | 2.28 ± 1.51 | 06 vs. 05 |
| 2006 | 3.9 ± 3.6 | 2.8 ± 3.0 | 1.0 ± 1.2 | 0.1 ± 0.2 ** | 0.51 ± 0.38** | 0.62 ± 0.47 | 0.01 ± 0.02* | 1.72 ± 1.28 | 04 vs. 05 |
| | | | | | | | | | Z Differences |

**Table 3**. Temporal variability in Chl-a concentrations (mg $m^{-3}$) and in the abundances (cells $mL^{-1}$) of nanoplankton (HNF-ANF) and picoplankton (HPP-APP) in the upper layer during spring, from SPC (0–35 m) and St. 18 (0–30 m) samplings, in the upwelling area off Concepción (Chile). Mean ± standard deviation values and 2-way ANOVA comparisons (factors: years (Y) and depth (Z)); probability values: $*p < 0.01$, $**p < 0.001$, others are not significant.

| Variables | Temperature | Salinity | $O_2$ | $PO_4^-$ | $NO_3^-$ | $SIO_4^{-2}$ |
|---|---|---|---|---|---|---|
| Cruises | | | | | | |
| Chl-aT | 0.29 | | | | -0.26 | |
| Chl-aT-20 | | 0.33 | | | | |
| Chl-a 20-3 | 0.5 | | 0.28 | -0.31 | -0.44 | -0.37 |
| Chl-a <3 | 0.66 | -0.36 | 0.62 | -0.59 | -0.56 | -0.49 |
| HNF | 0.24 | | | | -0.25 | |
| ANF | 0.28 | | | -0.31 | -0.47 | -0.33 |
| HPP | 0.48 | | | | -0.3 | -0.26 |
| APP | 0.70 | -0.62 | 0.69 | -0.58 | -0.43 | -0.48 |
| | | | | | | |
| Station 18 | | | | | | |
| Chl-aT | | | | | | |
| Chl-aT-20 | | | | | | |
| Chl-a 20-3 | | | | | | |
| Chl-a <3 | | | | | | |
| HNF | 0.29 | | 0.53 | -0.55 | -0.63 | -0.68 |
| ANF | 0.39 | -0.28 | | | | -0.34 |
| HPP | 0.22 | | | | -0.37 | |
| APP | | -0.34 | | | | |

**Table 4** Partial correlations between the oceanographic variables and the planktonic compo- nents in the upper layer during the SPC (0–35 m; n = 92–95) and at St. 18 (0–30 m; n = 51–54) in the upwelling area off Concepción. The controlled variable was depth in all the cases; bold = $p < 0.001$; non-bold = $p < 0.01$; italics = $p < 0.05$; others were not significant.

| Variables | n | Chl-aT | Chl-a -20 | Chl-a 20-3 | Chl-a < 3 | HNF | HPP | APP |
|---|---|---|---|---|---|---|---|---|
| Cruises | | | | | | | | |
| HNF | 95 | 0.47 | 0.42 | 0.29 | 0.40 | | | |
| ANF | 95 | 0.47 | | 0.49 | 0.47 | 0.64 | 0.35 | 30 |
| HPP | 77 | | | 0.56 | 0.42 | | | |
| APP | 79 | | | 0.46 | 0.55 | | 0.51 | |
| | | | | | | | | |
| Station 18 | | | | | | | | |
| HNF | 54 | | | 0.37 | 0.29 | | 0.41 | |
| ANF | 54 | | | 0.30 | | 0.32 | | 0.39 |
| HPP | 52 | | | 0.43 | 0.29 | 0.41 | | |
| APP | 52 | | | 0.45 | 0.50 | | | |

**Table 5** Associations between the planktonic components in the upper layer (0–35 m) during the SPC and at St. 18 in the upwelling area off Concepción. Correlation values are shown; bold: $p < 0.001$; non-bold: $p < 0.01$; italics = $p < 0.05$ other are not significant.

| Variable | n | Best predictors | x $R^2$ | Tolerance | Sensitivity 1 | N* |
|---|---|---|---|---|---|---|
| ChlT-20 | 93 | T-S-02 | 0.49 | 0.4-0.5-5.6 | 0.7-2.1-1.5 | 20 |
| Chl-a 20-3 | 93 | T-S | 0.30 | 3.3-0.6 | 0.5-0.3 | 66 |
| Chl < 3 | 93 | 02-NO3 | 0.46 | 0.7-24 | 0.7-0.6 | 20 |
| RA Chl-a-20 | 93 | T-S-O2 | 0.47 | 0.9-0.2-1.5 | 0.7-3.0-1.6 | 17 |
| RA Chl-a-20-3 | 93 | T-S-O2 | 0.46 | 0.4-1.4-1.1 | 0.8-2.6-1.5 | 13 |
| RA Chl-a <3 | 93 | T-PO4 | 0.21 | 0.4-0.7 | 1.2-0.6 | 17 |
| ANF | 93 | S-NO3 | 0.26 | 1.0-4.7 | 0.6-0.9 | 29 |
| HNF | 93 | S-O2 | 0.28 | 0.2-1.5 | 2.5-1.1 | 24 |
| APP | 75 | T-S | 0.65 | 0.9-0.4 | 0.8-1.1 | 24 |
| HPP | 75 | T-O2 | 0.33 | 0.4-5.5 | 1.8-0.9 | 20 |
| ANF | 95 | Chl-a20-3 | 0.24 | 2.3 | 1.0 | 88 |
| HNF | 95 | Chl-aT | 0.20 | 17 | 1.0 | 90 |
| APP | 77 | Chl-a < 3 | 0.33 | 0.2 | 1.1 | 62 |
| HPP | 77 | Chl-a20-3 | 0.25 | 0.7 | 1.8 | 50 |

**Table 6** Model results from NPMR analysis (local linear model – LLM) based on the responses of Chl-a concentrations (absolute and relative (RA)) and of microbial abundances during the SPC. Definitions: $R^2$ = cross-validated $R^2$ (model evaluation; maximum = 1); Tolerance = the extent to which the estimate for a given point is based on the surrounding sample space (in LLM, a small value implies a strong non-linear response); Sensitivity1 = relative importance of a parameter within the model (greater values = higher influence). The values for these two descriptors are displayed in the same order as the predictors; T = temperature, S = Salinity, n = number of data, other abbreviations in Section 2); $N^*$ = average neighborhood size. All models were statistically significant ($p < 0.01$; Monte Carlo permutation test; runs = 250).

in Fig. 4. In the smaller Chl-a fractions (<20 μm), the variations in concentration were almost linear with temperature (positive) and salinity (negative), whereas in the microplankton fraction they were hump shaped for temperature and bimodal for salinity. Also, all the Chl-a size fractions displayed a negative trend in variation with increasing nutrient concentrations, but this was only significant in the picoplankton fraction.

The NPMR analysis also confirmed that ANF and APP were linearly related to variations in Chl-a20-3 and Chl-a < 3, respectively (Table 6). Variation of HNF was a linear function of the Chl-aT concentration, whereas variation of HPP displayed a weak association with Chl-a. In terms of the influence of oceanographic variations upon microbial compone (Table 6), APP abundances exhibited the highest significance (i.e. best fit); temperature (positive and linear) and salinity (negative and linear, with a maximum at ~33.6) were the most relevant factors (Fig. 4). To a lesser extent, the variations in ANF were mostly explained by salinity (negative and linear, with a maximum at <33.0; Fig. 4), as was the case for the HNF but with the opposite response (positive and linear; not shown). In contrast, changes in HPP were best represented by temperature using a non-linear model.

## 4.4. DISCUSSION

During the study period, the central and eastern equatorial Pacific regions displayed positive anomalies in SST that have been associated with the development of a weak to moderate El Niño event from late 2006 to February 2007 (Arguez et al., 2007; Levinson and Lawrimore, 2008). In the HCS, unusually warmer and higher salinity waters were registered in August 2006 off Peru (Criales-Hernández et al., 2008). In our study, slight changes in temperatures (higher) and salinities (lower) were recorded during 2006, compared with the two previous spring periods, and these changes were coherent with both, the SPC and St. 18 sampling modes (Table 1; Figs. 2 and 3). This implies that, instead of an intrusion of warmer and saltier equatorial waters towards the coast (typical of El Niño events), oceanic waters (off the shelf and shelf break area) invaded the coastal area or upwelling activity diminished during most of the spring in 2006. Recently, Ochoa et al. (2010) have suggested that, during warm periods (e.g. El Niño events), a decrease in offshore transport or the intrusion of offshore waters (e.g. from beyond the shelf) to the coast is possible in the upwelling area off Peru.

The variations in Chl-a concentration and microbial abundances during the three spring periods were mostly not significant, both during SPC and at St. 18, although mean values for Chl-aT and Chl-aT-20 were slightly lower in 2006 (Table 3). We further analyzed the latter result by estimating the relative importance of the microphytoplankton biomass in each period; its mean contribution was higher in the springs of 2004 and 2005 (72% and 59% of Chl-aT, respectively), compared with 2006 (31%). In contrast, the contribution of the nanoplankton fraction to total Chl-a increased from 23–33% in 2004–2005 to 62% in 2006. In addition, integrated (0–35 m) Chl-aT concentrations at St. 18 were unusually low (<20 mg $m^{-2}$) between February and April 2007 (summer to autumn) compared with the data for other years of the 2003–2009 time series (C.E. Morales, unpublished data). These differences suggest that the microphytoplankton blooms might have been infrequent or even suppressed in the spring of 2006 and in early 2007. On the other hand, the abundances of the microbial components did not vary significantly between the three springs (Table 3), except for HNF which displayed differences between springs but they were not consistent in the two sampling modes. This suggests that, unlike the estimates of microphytoplankton Chl-a biomass, the abundances of microbial components remained relatively unaffected by the oceanographic event occurring during the spring of 2006.

The above results could be biased by some or all the following aspects: limited frequency of sampling at St. 18, small number of sampling stations during the SPC, and/or

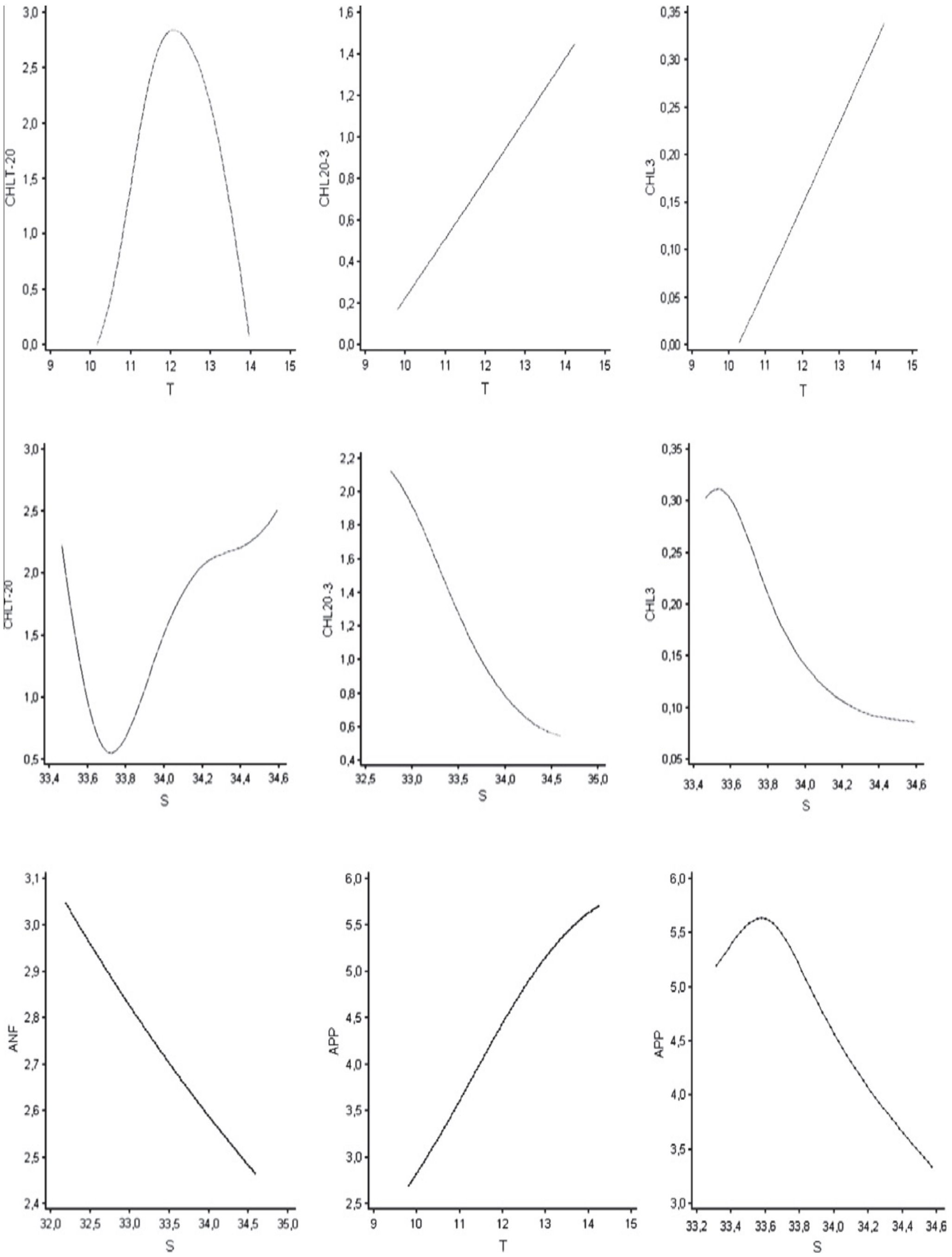

**Fig. 4.** Results of the NPMR analysis: examples of the responses of the Chl-a size fractions and the microbial components (ANF, HNF, APP and HPP) to oceanographic variability. Chl-a data were not transformed (mg $m^{-3}$) whereas the microbial abundances (cells $mL^{-1}$) were $log_{10}$ transformed.

differences in the timing of each SPC (1–2 months). For this purpose, we compared the in situ observations with satellite time series data on the distributions of SST and Chl-a in an area centered around St. 18 (Fig. 5). During the 2004–2006 period, SST varied to a similar extent throughout the annual cycle; however, values were slightly lower at the beginning of the spring in 2005 (~Julian day 600–700) whereas a warm event of ~30–50 days occurred in October 2006 (~Julian day 1050), when the maximum positive MEI value was recorded (http://www.cdc.noaa.gov/people/klaus.wolter/MEI/ index.html). After this event, the values fell before they increased again, suggesting that this variation was probably the result of an intra-seasonal process, such as the passage of a coastally trapped wave or other local or remote forcing. Events of this duration have been previously reported during El Niño periods off Peru and northern Chile (Carr et al., 2002; Ulloa et al., 2001). Also, satellite Chl-a concentration varied to a similar extent during the annual cycle, although maximum values in the spring of 2006 and summer of 2007 were slightly lower when viewed as seasonal (3 month) averages. Overall, the satellite data provided a similar picture of temporal variation (between the springs) as the in situ observations but they set a limit to the time period over which the changes took place (i.e. the warm event in spring 2006).

Within the spatial context, a sharp decline in Chl-a concentration with distance from the coast during the upwelling season is reported for most eastern boundary current systems (review in Chavez and Messié, 2009). The decrease in Chl-a is usually accompanied by a change in community structure, with smaller size fractions dominating offshore oligotrophic waters along with increasing abundances of nano and pico-autotrophs (Hutchings et al., 1995; Sherr et al., 2005; Lassiter et al., 2006). Under this scheme, we expected St. 18 to be most representative of the inshore conditions on the shelf off Concepción, considering that the autotrophic microplankton (mostly diatoms) shows a tendency to concentrate there and to dominate in abundance and biomass at this station during the upwelling season (González et al., 2007). Our results indicate that there was a tendency for total Chl-a and the microplankton fraction to be higher at inshore stations during the SPC, but the only significant variation with distance from the coast was for APP abundance (Table 2). In concordance with this, Cuevas et al. (2004) did not find large differences in the across-shore distributions of bacterioplankton and nanoplankton abundances during springtime in the same area.

These results suggest that the scheme of changes in community structure with distance from the coast in eastern boundary upwelling systems only represents a one dimensional perspective (advection due to upwelling), but a more comprehensive view should include the mesoscale and submesoscale processes occurring within the area affected by upwelling activity and beyond in the coastal transition zone (Baltar et al., 2009). Off Concepción, mesoscale and submesoscale processes and features are associated with a relatively high eddy kinetic energy, which, in turn, extends the influence of the upwelling activity further offshore into a coastal transition zone (Hormazabal et al., 2004). These process are associated, among others, with changes in the local circulation or water column structure due to river inputs, abrupt variations in bathymetry (e.g. canyons, terraces) and in coastline orientation or shape (e.g. capes, bays), and differences in wind forcing both along-shore and across-shore (Hormazabal et al., 2004). In fact, satellite data show that, in the upwelling area off central-southern Chile, the distributions of SST, salinity and Chl-a concentration in the upper layer are highly heterogeneous (Wieters et al., 2003; Morales et al., 2007, 2010). In the present study, this heterogeneity is represented by the high dispersion of the data around the mean

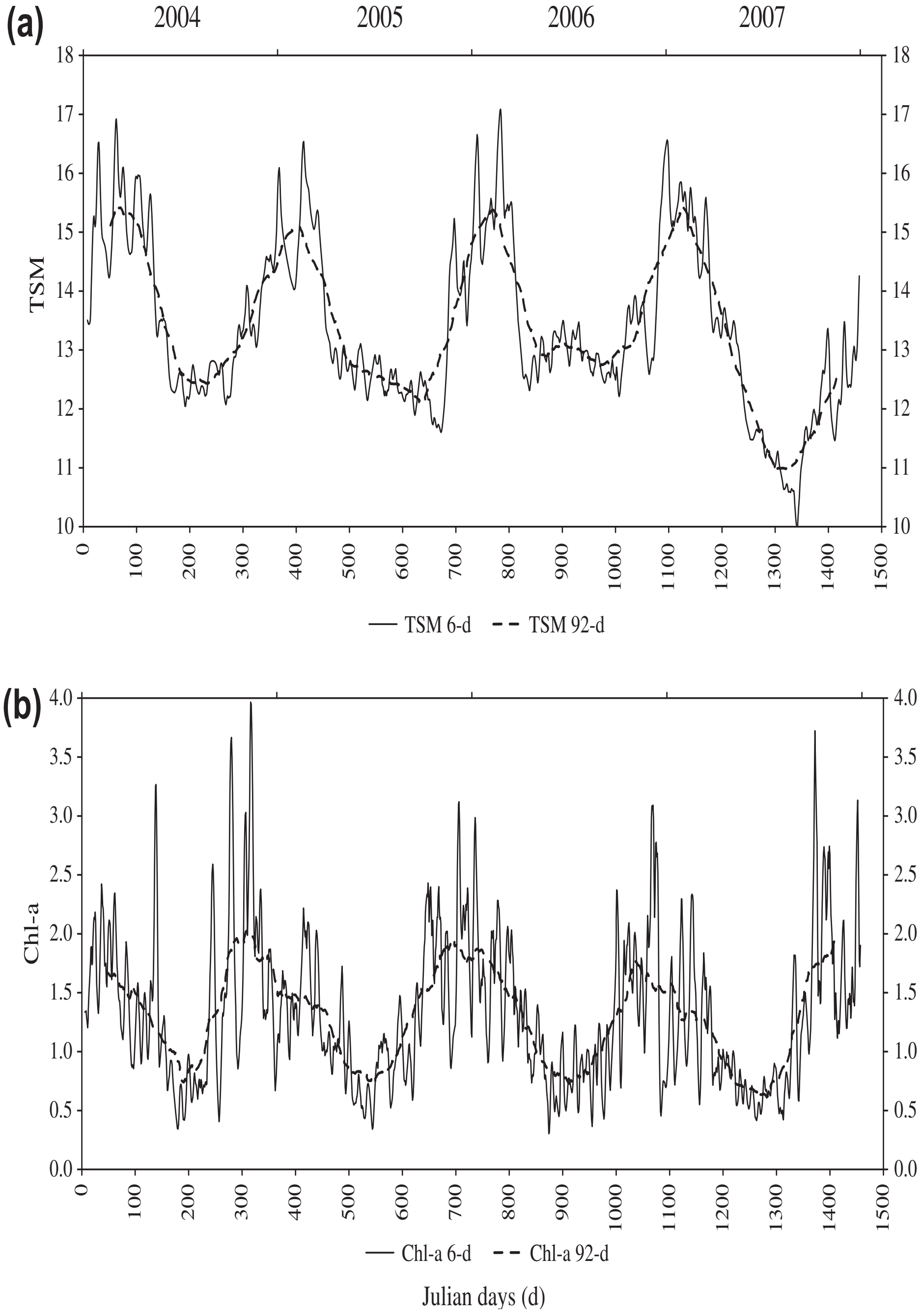

**Fig. 5.** Satellite time series data (from January 2004 through to December 2007) on SST (a) and Chl-a concentration (b) for an area centered around St. 18 (36–36.5ºS and 72.75–73.5ºW). Data were averaged over 6 d (continuous lines) and 92 d (broken lines) in order to remove the lowest frequency changes.

values, which, in turn, imply that St. 18 is probably representative of the mean oceanographic conditions and planktonic communities over the shelf and shelf break waters.

The clear exception to the above was, according to our results, APP abundance, mostly dominated by *Synechoccocus*. At St. 18, the abundance of this cyanobacterium in the upper layer shows a seasonal variation (Alarcón, 2008), with a maximum in autumn (mean of 0.1 x$10^6$ cells mL$^{-1}$) and a minimum in spring (0.03 x $10^6$ cells mL$^{-1}$). Our results indicate that during the spring- time APP display maximum values at the shelf edge stations (Table 2), which suggests that the seasonal pattern described above might be explained by an offshore displacement of *Synechococcus*. In this case, and probably for the picophytoplankton in general, the variance in both the spatial and temporal dimensions becomes highly relevant in understanding the mechanisms by which the abundances of these assemblages are controlled in this coastal system. For example, Baltar et al. (2009) found that mesoscale features in the upwelling system off NW Africa were associated with large variations in the nano and picoplankton distributions, and that these differences were at times comparable to the average seasonal variability.

Previous studies of the variability of planktonic communities in the coastal upwelling area off Concepción have explored the influence of oceanographic and ecological factors, mainly in terms of simple correlation analyses (e.g. González et al., 2007 Böttjer and Morales, 2007; Escribano et al., 2007; Alarcón, 2008). In the present study, the use of this traditional approach is contrasted with an advanced statistical method, NPMR analysis, which requires no assumptions of data distribution or of independence between factors. This approach is most relevant when the responses of the plankton to environmental variability, including biotic and abiotic, are likely to be non-linear (e.g. Planque et al., 2007; Zarauz et al., 2008) and/or are the result of multiple interacting factors which might be operating on the same or on different spatial and temporal scales (e.g. Rutllant and Montecino, 2002; Cloern and Dufford, 2005).

Both linear correlation and NPMR analyses produced similar results in this study when the plankton responses to environmental variability approached linearity, except that NPMR also identified the range over which the relationship applies. However, when NPMR identified a non-linear response, the results were different and the linear correlation approach failed to show a significant relationship. The best example of this is the case of the usually dominant autotrophic component (in terms of Chl-a biomass), the microplanktonic fraction: the NPMR showed that combined temperature and salinity explained ~50% of spatial variability during springtime (Table 6), whereas the fit with a partial correlation was poorer and was only related to salinity (Table 4). The bimodal response to salinity (Fig. 4) suggests that there are probably two microplanktonic assemblages dominating the shelf area during the spring upwelling season, one of oceanic origin (lower salinity) and the other of inshore origin (higher salinity). This, in turn, might be the result of coastal-oceanic exchange processes taking place during the upwelling cycle (e.g. river or upwelling plumes, fronts, eddies, filaments) in this region (Strub et al., 1998; Sobarzo et al., 2007; Morales et al., 2010). The NPMR analysis also indicates that the spatial variations in the nano and picoplankton Chl-a fractions were related almost linearly to temperature during springtime (Fig. 4), with higher biomasses at higher temperatures (>13 °C). Their relationships with salinity were also nearly linear but negatively so; this factor was also relevant in determining the abundances of ANF and APP (Table 6). Temperature and salinity gradients explained the offshore increase in picophytoplankton biomass but the increase in nano-phytoplankton biomass was related to even lower salinity values (~33), linking it to waters influenced by river inputs (i.e. higher stratification) within the coastal zone. Altogether, most of the best models for describing the response of microbial abundances to oceanographic and/or biological (Chl-a) variations explained less than 33% of the changes in abundance, except for the APP (Table 6). This implies that other sources of variation not considered here, perhaps oceanographic (e.g. light penetration, turbulence) or ecological (e.g. predation, viral infection) might also contribute to controlling the abundances of these planktonic components (e.g. Böttjer and Morales, 2007).

In summary, the fixed time series station (St. 18) appears to adequately represent the mean oceanographic conditions and the structure of the planktonic community in the upper layer of the coastal upwelling system off Concepción. The high dispersion of the data around the mean values, however, suggests that spatial (mesoscale and submesoscale) variability in the coastal area and the coastal transition zone should be taken into account in the interpretations of temporal changes at this fixed station as well as in the assessments of carbon flow in, and exportation processes from, this upwelling system. For most of the planktonic components analyzed, a significant part of the spatial variability (25–65%) was explained by changes in water column structure (temperature and salinity) of the upper layer; the biological responses were linear in some cases and nonlinear in others. Further research should disentangle the complexities associated with temporal versus spatial sources of variability in the plankton before we can fully use St. 18 as representative of the changes taking place in the coastal system off Concepción.

## 4.5. ACKNOWLEDGEMENTS

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## 4.6 REFERENCES

Alarcón, G., 2008. Variabilidad estacional de la comunidad picoplanctónica en la zona de surgencia altamente productiva. M.Sc. Oceanography thesis, Graduate School, University of Concepción, Chile. 192 pp.

Anabalón, V., Morales, C.E., Escribano, H.R., Varas, M.A., 2007. The contribution of nano- and micro-planktonic assemblages in the surface layer (0–30 m) under different hydrographic conditions in the upwelling area off Concepción, central Chile. Prog. Oceanogr. 75, 396–414.

Arguez, A., Waple, A.M., Sanchez-Lugo, A.M., 2007. Introduction. State of the climate in 2006. Bulletin of the American Meteorological Society 88 (6), S8–S132.

Avaria, S., Palma, S., Sievers, H., Silva, N., 1989. Revisión sobre aspectos oceanográficos físicos, químicos y planctológicos de la Bahía de Valparaíso y áreas adyacentes. Biología Pesquera (Chile) 18, 67–96.

Bakun, A., Nelson, C.S., 1991. The seasonal cycle of wind stress curl in subtropical boun- dary current regions. J. Phys. Oceanogr. 21, 1815– 1834.

Baltar, F., Arístegui, J., Montero, M.F., Espino, M., Gasol, J.M., Herndl, G.J., 2009. Meso- scale variability modulates seasonal changes in the trophic structure of nano- and picoplankton communities across the NW Africa–Canary Islands transition zone. Prog. Oceanogr. 83, 180–188.

Böttjer, D., Morales, C.E., 2007. Nanoplanktonic assemblages in the upwelling area off Concepción (36 S), central Chile: abundance, biomass, and grazing potential during the annual cycle. Prog. Oceanogr. 75, 415–434.

Carr, M.-E., Strub, P.T., Thomas, A., Blanco, J.L., 2002. Evolution of 1996–1999 La Niña and El Niño conditions off the western coast of South America: a remote sensing perspective. J. Geophys. Res. 107, C12, 3236. doi:10.1029/2001JC001183.

Chavez, F.P., Messié, M.A., 2009. Comparison of eastern boundary upwelling ecosystems. Prog. Oceanogr. 83 (1–4), 80–96.

Cloern, J.E., Dufford, R., 2005. Phytoplankton community ecology: principles applied in San Francisco Bay. Mar. Ecol. Progr. Ser. 285, 11–28.

Correa-Ramirez, M.A., Hormazabal, S., Yuras, G., 2007. Mesoscale eddies and high chlorophyll concentrations off central Chile (29–39 S). Geophysical Research Letters L12604. doi:10.1029/2007GL029541.

Correa-Ramírez, M., Hormazabal, S., Morales, C.E.,. 2012. Spatial patterns of the annual and interannual chlorophyll-a variability in the Peru–Chile Current System. (92), 8-17

Criales-Hernández, M.I., Schwamborn, R., Graco, M., Ayón, P., Hirche, H.-J., Wolff, M., 2008. Zooplankton vertical distribution and migration off central Peru in relation to the oxygen minimum layer. Helgoland Marine Research (Suppl. 1), S85–S100.

Cuevas, L.A., Daneri, G., Jacob, B., Montero, P., 2004. Microbial activity and organic carbon flow in the upwelling area off Concepción (36 S), central Chile. Deep-Sea Research II 51, 2427–2440.

Eissler, Y., Letelier, J., Cuevas, L.A., Morales, C.E., Escribano, R., 2010. The microbial community in the coastal upwelling system off Concepción, Chile, 36 S, 2002– 2003 period. Revista de Biología Marina y Oceanografía 45 (1), 1–18.

Escribano, R., Hidalgo, P., González, H.E., Giesecke, R., Riquelme-Bugueño, R., Manríquez, K., 2007. Seasonal and inter-annual variation of mesozooplankton in the coastal upwelling zone off central-southern Chile. Prog. Oceanogr. 75, 470–485.

Faúndez, P., Morales, C.E., Arcos, D., 2001. Variabilidad espacial y temporal en la hidrografía invernal del sistema de bahías frente a la VIII región (Chile centro- sur). Revista Chilena de Historia Natural 74, 817–831.

Gómez, F., 2008. Variabilidad ambiental y pequeños pelágicos de la zona norte y centro sur de Chile. M.S. Thesis, Fisheries. Universidad de Concepción, 85 pp.

González, H.E., Menschel, E., Aparicio, C., Barría, C., 2007. Spatial and temporal variability of microplankton and detritus, and their export to the shelf sediments in the upwelling area off Concepción, Chile (36 S), during 2002– 2005. Prog. Oceanogr. 75, 435–451.

Hass, L.W., 1982. Improved epifluorescence microscopy for observing planktonic microorganisms. Annales de l Institut Oceanographique Paris 58, 261–266.

Hormazabal, S., Shaffer, G., Letelier, J., Ulloa, O., 2001. Local and remote forcing of sea surface temperature in the coastal upwelling system off Chile. J. Geophys. Res. 106 (C8), 16657–16671.

Hormazabal, S., Shaffer, G., Pizarro, O., 2002. Tropical Pacific control of intraseasonal oscillations off Chile by way of oceanic and atmospheric pathways. Geophysical Research Letters 29 (6), 1081. doi:10.1029/2001GL013481.

Hormazabal, S., Shaffer, G., Leth, O., 2004. Coastal transition zone off Chile. Journal of Geophysical Research (109), C01021. doi:10.1029/2003JC001956.

Hutchings, L., Pitcher, G.C., Probyn, T.A., Bailey, G.W., 1995. The chemical and biological consequences of coastal upwelling. In: Summerhayes, C.P., Emeis, K.- C., Angel, M.V., Smith, R.L., Zeitzschel, B. (Eds.), Upwelling in the Ocean Modern Processes and Ancient Records. Dahlem Workshop Reports. Environmental Sciences Research Report 18. Wiley, pp. 67–72.

Lassiter, A.M., Wilkerson, F.P., Dugdale, R.C., Hogue, V.E., 2006. Phytoplankton assem- blages in the CoOP-WEST coastal upwelling area. Deep-Sea Research Part II 53, 3063–3077.

Levinson, D.H., Lawrimore, J.H., 2008. State of the Climate in 2007. Special Supplement Bulletin of the American Meteorological Society 89 (7), 181.

Marie, D., Partensky, F., Simon, N., Guillou, L., Vaulot, D., 2000. Flow cytometry analysis of marine picoplankton. In: Diamond, R.A., DeMaggio, S. (Eds.), Living Colors: Protocols in Flow Cytometry and Cell sorting. Springer-Verlag, Berlin, Heidelberg.

McCune, B., Mefford, M.J., 2004. Nonparametric Multiplicative Habitat Modeling Version 1.0. MjM Software, Gleneden Beach, OR.

Morales, C.E., González, H.E., Hormazabal, S.E., Yuras, G., Letelier, J., Castro, L.R., 2007. The distribution of chlorophyll-a and dominant planktonic components in the coastal transition zone off Concepción, central Chile, during different oceanographic conditions. Prog. Oceanogr. 75, 452–469.

Morales, C.E., Torreblanca, M.L., Hormazabal, S., Correa, M., Nuñez, S., Hidalgo, P., 2010. Mesoscale structure of copepod assemblages in the coastal transition zone and oceanic waters off central-southern Chile. Prog. Oceanogr. 84, 158–173.

Narváez, D.A., Poulin, E., Leiva, G., Hernández, E., Castilla, J.C., Navarrete, S.A., 2004. Seasonal and spatial variation of nearshore hydrographic conditions in central Chile. Continental Shelf Research 24, 279–292.

Ochoa, N., Taylor, M.H., Purca, S., Ramos, E., 2010. Intra- and interannual variability of nearshore phytoplankton biovolume and community changes in the northern Humboldt Current system. J. Plankton Res. 32, 843–855.

Planque, B., Bellier, E., Lazure, P., 2007. Modelling potential spawning habitat of sardine (Sardina pilchardus) and anchovy (Engraulis encrasicolus) in the Bay of Biscay. Fisheries Oceanography 16, 16–30.

Porter, K.G., Feig, Y.S., 1980. The use of DAPI for identifying and counting aquatic microflora. Limnol. Oceanogr. 25, 943–948.

Rutllant, J., Montecino, V., 2002. Multiscale upwelling forcing cycles and biological res- ponse off north-central Chile. Revista Chilena de Historia Natural 75, 217–231.

Sandwell, D.T., Smith, W.H.F., 1997. Marine gravity from Geosat and ERS 1 satellite altimetry. J. Geophys. Res. 102 (B5), 10039–10054.

Shaffer, G., Hormazabal, S., Pizarro, O., Salinas, S., 1999. Seasonal and interannual variability of currents and temperature off central Chile. J. Geophys. Res. 104 (C12), 29951–29961.

Sherr, E.B., Sherr, B.F., Wheeler, P.A., 2005. Distribution of coccoid cyanobacteria and

small eukaryotic phytoplankton in the upwelling ecosystem off the Oregon coast during 2001 and 2002. Deep-Sea Research II 52, 317–330.

Sobarzo, M., Djurfeldt, L., 2004. Coastal upwelling process on a continental shelf limited by submarine canyons, Concepción, central Chile. J. Geophys. Res. 109, C12012. doi:10.1029/2004JC002350.

Sobarzo, M., Bravo, L., Donoso, L., Garcés-Vargas, J., Schneider, W., 2007. Coastal upwelling and seasonal cycles that influence the water column over the continental shelf off central Chile. Prog. Oceanogr. 75, 363–382.

Strub, P., Mesías, J., Montecino, V., Ruttlant, J., 1998. Coastal ocean circulation off western South America. In: Robinson, A., Brink, K. (Eds.), The Global Coastal Ocean. The Sea, vol. 11. John Wiley and Sons, Inc., N.Y., pp. 273–313.

Ulloa, O., Escribano, R., Hormazabal, S., Quiñones, R.A., Ramos, M., González, R.R., 2001. Evolution and biological effects of the 1997–98 El Niño in northern Chile. Geophy- sical Research Letters 28 (8), 1591–1594.

Vargas, C.A., Martínez, R., Cuevas, L.A., Pavez, M., et al., 2007. The relative importance of microbial and classical food webs in a highly productive coastal upwelling area. Limnol. Oceanogr. 52, 1495–1510.

Wieters, E.A., Kaplan, D.M., Sotomayor, A., Navarrete, S.A., Largier, J., Nielsen, K.J., Veliz, F., 2003. Alongshore and temporal variability in chlorophyll-a concentrations in Chilean nearshore waters. Mar. Ecol. Progr. Ser. 249, 93–105.

Wolter, K., Timlin, M.S., 1998. Measuring the strength of ENSO events – how does 1997/98 rank? Weather 53, 315–324.

Zar, J.H., 1984. Biostatistical Analysis. Prentice-Hall International, Inc., New Jersey, 718 pp.

Zarauz, L., Irigoien, X., Fernandes, J.A., 2008. Modelling the influence of abiotic and bio- tic factors on plankton distribution in the Bay of Biscay, during three consecutive years (2004–2006). J. Plankton Res. 30, 857–872.

***The triumph of the man emerges***
***from the ashes of error***
*El triunfo del verdadero hombre*
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# CHAPTER 3

# Micro-phytoplankton community structure in the coastal upwelling zone off Concepción (central Chile): Annual and inter-annual fluctuations in a highly dynamic environment

Valeria Anabalón, C.E. Morales, H.E. González, E. Menschel,
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## ABSTRACT

An intensification of upwelling favorable winds in recent decades has been detected in some of the main eastern boundary current systems, especially at higher latitudes, but the response of coastal phytoplankton communities in the Humboldt Current System (HCS) remains unknown. At higher latitudes in the HCS (35–40°S), strong seasonality in wind-driven upwelling during spring-summer coincides with an annual increase in coastal chlorophyll-a and primary production, and a dominance of microphytoplankton. In order to understand the effects of potential upwelling intensification on the microphytoplankton community in this region, annual and interannual variability in its structure (total and taxa-specific abundance and biomass) and its association with oceanographic fluctuations were analyzed using in situ time series data (2002–2009) from a shelf station off Concepcion (36.5°S). At the annual scale, total mean abundance and biomass, attributed to a few dominant diatom taxa, were at least one order of magnitude greater during spring-summer than autumn-winter, in association with changes in upwelling and surface salinity and temperature, whereas macronutrient concentrations remained relatively high all the year. At the interannual scale, total abundance and biomass decreased during the upwelling season of the 2006–2009 period compared with the 2002–2006 period, notably due to lower abundances of *Skeletonema* and *Leptocylindrus*, but the relative dominance of a few taxa was maintained. The 2006–2009 period was characterized by higher upwelling intensity, colder and higher salinity waters, and changes in nutrient concentrations and ratios compared with the first period. The interannual changes in the microphytoplankton community were mostly associated with changes in surface salinity and temperature (changes in upwelling intensity) but also with changes in Si/N and N/P, which relate to other land-derived processes.

## 5.1. INTRODUCTION

Eastern boundary current systems (EBCSs) are subject to environmental forcing on a wide range of temporal and spatial scales and generate different degrees of ecological variability (Mackas et al., 2006; Chavez and Messié, 2009; Escribano and Morales, 2012). The impact of climatic and oceanographic changes on phytoplankton community structure is highly relevant since EBCSs sustain much of the ocean’s productivity. Intensification of winds has been predicted and observed in most EBCSs (Sydeman et al., 2014; Bakun et al.,

2015) but the impact on phytoplankton community structures and production remains uncertain (García-Reyes et al., 2015). In general terms, EBCSs share oceanographic and ecological characteristics. They usually are dominated by a few microplanktonic diatom taxa during upwelling events or seasons (Tilstone et al., 2000; Wilkerson et al., 2000; Lassiter et al., 2006), when a combination of lower temperature, higher mixing, and/or elevated nutrient concentrations in the photic layer are found.

Regional differences and seasonal to interannual variability of total phytoplankton biomass in the Humboldt Current System (HCS) in the eastern South Pacific EBCS (~5–40°S) has been described using satellite time series data of surface Chl-a (Yuras et al., 2005; Thomas et al., 2009, 2012; Correa-Ramirez et al., 2012). Results from these studies have shown there are regional differences in the oceanographic mechanisms involved in the generation of the annual Chl-a maxima in the HCS (Echevin et al., 2008; Correa-Ramirez et al., 2012). Also, these studies analyzed the effects of climate forcing, such as El Niño Southern Oscillation (ENSO), on the interannual variability of Chl-a (Thomas et al., 2009; Correa-Ramirez et al., 2012). On the other hand, in situ HCS phytoplankton time series of more than two years have been limited to a few coastal stations off Peru (Ochoa et al., 2010) and Chile (Avaria, 1971; González et al., 2007; Sanchez et al., 2012). All of them have mostly focused on the temporal variability of the microplankton fraction and used light microscopy for taxonomic identification and enumeration. While being consistent with satellite Chl-a based studies in terms of spatial and temporal patterns, they also contain a detailed characterization of taxonomic composition. For example, in situ time series data off Peru have shown that microphytoplankton abundance and taxanomic composition is dominated by large diatoms under La Niña conditions and by dinoflagellates under El Niño conditions (Ochoa et al., 2010).

The coastal upwelling zone off central Chile (~30–40°S) is distinct from others in the HCS (off Peru and northern Chile) in that seasonal wind-driven upwelling is coupled with the annual increase in satellite-derived Chl-a (Yuras et al., 2005; Correa- Ramirez et al., 2012; Morales et al., 2013). Increased solar radiation during the annual cycle is also coupled to this Chl-a increase (Corredor-Acosta et al., 2015). In this zone, nutrient enrichment of the surface layer has been attributed to wind-driven upwelling during spring-summer and river inputs from late autumn to early spring (Sanchez et al., 2012). Data from the few, short-term, in situ time series located in the coastal band of this region have shown a spring-summer increase in Chl-a, cell abundance and/or carbon-biomass of the microphytoplankton in the water column (Avaria, 1971; González et al., 2007; Sanchez et al., 2012). Interannual variability of phytoplankton in this region has only been analyzed in terms of satellite Chl-a time series and the impact of ENSO-related climate variability on Chl-a has been shown to be relatively weak in the coastal zone (Thomas et al., 2009; Correa-Ramirez et al., 2012; Corredor-Acosta et al., 2015).

In the coastal upwelling zone off central Chile, an in situ time series at the so-called St. 18 off Concepción (~36.5°S; Fig. 1a) has contributed to characterize annual to interannual variability in the southern HCS. There, the annual temperature and salinity cycles in the upper layer are associated with variations in net surface heat flux, river discharge, precipitation, and coastal upwelling (Sobarzo et al., 2007). Low dissolved oxygen (DO) values (<1 mL $^{-1}$) reach shallower waters during the upwelling season, exposing the euphotic zone to hypoxia (Escribano and Morales, 2012). Phytoplankton studies with St. 18 data have been based on short periods (<3 consecutive years) and have shown that most of the microphytoplankton abundance is found in surface waters (<20 m depth) and is dominated by a few diatom genera (Anabalón et al., 2007; González et al., 2007; Sanchez et al., 2012). Tintinnids and dinoflagellates also peak in summer but with abundances one order of magnitude lower than that of diatoms (González et al., 2007). In contrast, the seasonality of nanophytoplankton at St. 18 (2004–2006 time series) is weak but the highest mean abundance and biomass values are registered during the upwelling season (Anabalón et al., 2007; Böttjer and Morales, 2007). The year-round contribution of the pico-phytoplankton at St. 18 (2006–2008 time series), represented by the <3 lm fraction Chl-a, is small (mean of the series: 11% of total Chl-a) (Collado- Fabbri et al., 2011).

Recent analysis of a satellite Chl-a time series for the southern section of the HCS (35–38°S) indicated a significant trend of negative Chl-a anomalies during the upwelling season combined with positive wind (upwelling) anomalies in the coastal area for the period between 2002 and 2012 (Corredor-Acosta et al., 2015). Together with this, St. 18 time series data for the same period have shown a change in the oceanographic conditions between 2002–2006 and 2007–2012 (Schneider et al., in press) and, associated with this, changes in the meta-zooplankton community structure between these two periods (Medellín-Mora et al., 2016). The present study focused on the extent to which seasonal to interannual upwelling intensification, and associated water column variability, influence micro-phytoplankton community structure in the strongly seasonal coastal upwelling regime of the southern HCS, using ~7 year of in situ time series at St. 18.

## 5.2. METHODS

### 5.2.1. TIME SERIES DATA

The time series St. 18 is located ~18 nautical miles (~30 km) from the coast on the Itata Terrace off Concepcion (36°30'08''S; 73°07'97''W; 90m depth), an area of high Chl-a concentrations (Fig. 1a). Sampling was conducted monthly (the FONDAP-COPAS Center at the U. of Concepcion; www.copas.udec.cl) and includes oceanographic, biological, and biogeochemical variables. The study includes samplings carried out between August 2002 (beginning of the time series) and July 2009, with a total of 76 sampling cruises on board the L/C Kay-Kay (University of Concepcion). A large gap in the micro-phytoplankton sampling and data occurred between 2009 and 2010 after the 2010 tsunami off central Chile and therefore, data after July 2009 were not considered.

Each sampling at St. 18 included a continuous hydrographic profile obtained from a CTD (Sea Bird SBE-19 plus; SeaBird SBE- 25) equipped with dissolved oxygen (DO) and fluorescence sensors (WetStar). Temperature (°C) and salinity (no units) data were used to estimate water density (as sigma-t, kg $m^{-3}$) and, with that, stability or stratification intensity (expressed as potential energy anomaly, J $m^{-3}$; Bowden, 1983) was determined for the upper 30 m depth. Discrete water samples (Niskin 8 L bottles) for DO, nutrients ($PO_4$, $Si(OH)_4$, $NO_2$, $NO_3$, and $NH_4$), and size-fractionated Chl-a (micro, nano, and pico-plankton) were obtained from 6 depth levels in the upper 30 m (0, 5, 10, 15, 20, and 30 m depth). Nutrient concentrations (μM) were determined with an auto-analyzer (Alpkem flow solution IV; Strickland and Parsons, 1972), except for $NH_4$, which was analyzed by the fluorometric method (Turner Designs 10AU and Turner Design TD-700; Holmes et al., 1999). DO (mL

$L^{-1}$) was analyzed by the Winkler method (Carpenter, 1965) and Chl-a (mg $m^{-3}$) by the fluorometric method (Turner Designs 10AU and Turner Design TD-700; Holm- Hansen et al., 1965).

In addition, wind satellite time series data were analyzed in order to calculate an upwelling index (Bakun, 1973). Daily wind data (2002–2009) for the 3 pixels closest to the coast (from the coast to 75 km offshore) in the area including St. 18 were obtained from the CCMP L3.0 product (Cross-Calibrated, Multi-Platform Ocean Surface Wind Velocity; 25 x 25 km resolution; source: http://podaac.jpl.nasa.gov/). Wind data for 18:00 h GMT (14:00 local time) were selected for the calculations of the upwelling index since daily maximum values are usually attained around this time in the region of study (eg. Corredor-Acosta et al., 2015). Available data on climatological indices were used to explore remote effects of low-frequency signals on oceanographic variability. For this purpose, the Multivariate El Niño Southern Oscillation (MEI:http://www.esrl.noaa.gov/psd/data /correlation / mei.data), the Antarctic Oscillation (AAO: http://www.cpc.ncep.noaa.gov/ products/precip/CWlink / daily_ao_index/aao/monthly.aao.index.b79. current.ascii.table), and the Pacific Decadal Oscillation (PDO: http://jisao.washington.edu/pdo/PDO.latest) indexes were analyzed.

### 5.2.2. MICRO-PLANKTON COMMUNITY STRUCTURE

Micro-plankton samples were collected at a depth of 10 m using 30 L Niskin bottles and cells were gently concentrated through a 20 µm sieve to obtain a final volume of 100 mL. From 2004, samples were also collected at the surface. The samples were immediately preserved in buffered formalin (4%) and later on taxonomic composition and abundance was analyzed using sedimentation chambers and then an inverted microscope (Olympus CK2, 400 magnification), following the Utermöhl method (Utermöhl, 1958 cited in González et al., 2007). At least one hundred cells of the most common taxa in each sample were counted and half or all of the fields of view were examined depending on total cell concentration in the sedimentation chamber.

Taxonomic composition of micro-planktonic diatoms and autotrophic/mixotrophic dinoflagellates was analyzed using the descriptions in Tomas (1997), Anderson et al. (2002), Taylor et al. (1995), Rivera and Arcos (1975), and Rivera et al. (1982). The distinction of autotrophic/mixotrophic dinoflagellates was based on literature reports (e.g. Jacobson and Andersen, 1994; Stoecker et al., 1996; Jeong et al., 2010; Ochoa et al., 2010). A low percentage of specimens (~5% of total abundance) were not identified and the counts of resting spores were not included in our analyses. Since different analysts were involved at different times and only light microscopy was used for taxonomic identification, our analyses focused on genera. However, we rechecked some samples to identify the most common and easily identified species of the dominant genera. Phytoplankton species composition has been detailed in previous studies in the same region (Rivera, 1968; Romero and Hebbeln, 2003) and for St. 18 (Sanchez et al., 2012).

Phytoplankton carbon biomass was obtained from cell volume estimates for each taxon, including a total of 52 genera (38 diatoms and 15 dinoflagellates). Cell volume was derived from geometric models (Chrzanowski and Simek, 1990; Sun and Lui, 2003) using size measurements (length, width, diameter and height) of randomly selected cells (at least 20 of each taxon to obtain a median value. The carbon/biovolume conversion factors for diatoms were derived from Strathmann (1967), Edler (1979) and Menden-Deuer and Lessard

(2000) were used for thecate and athecate dinoflagellates. We compared the biomass estimates obtained with different factors and, in general, we found that those provided by Menden-Deuer and Lessard (2000) are intermediate between those obtained with other factors (Anabalón et al., 2014). In the case of mixotrophic dinoflagellates, 40% of the total cell biomass was allocated to the autotrophic fraction using the approach of Stoecker et al. (1996). Micro-phytoplankton carbon biomass (mC) and micro-phytoplankton Chl-a (mChl-a or >20 µm size fraction) data were used to derive mean mC/mChl-a ratios.

### 5.2.3. STATISTICAL ANALYSES

The annual cycles of environmental (hydrography and nutrients) and biological (Chl-a and mChl-a) variables in the upper layer (0–30 m) were investigated through harmonic analysis using a least-square fitting (Aslan et al., 1997) for oscillations from 3, 4, 6 and 12 months. The contribution of these harmonics to total variance was evaluated but here we only report the results for the annual period of environmental and biological variables. For this purpose, transformed data ($\log_{10} n + 1$) were detrended (removal of temporal mean and linear tendencies) but the temporal mean was added later to reproduce the harmonic annual cycles with magnitudes comparable to the original signals. A cubic spline interpolation function was applied to plot these data. The patterns displayed by the annual harmonic cycles were adjusted with those obtained from the monthly climatologies of the variables. In addition, the monthly climatologies of the total abundance and biomass of microphytoplanktonic diatoms and dinoflagellates were obtained (10 m depth). For each taxon, the central values (mean and medians, plus one standard deviation from the mean) and an index of relative importance

(IRI; the mean between the relative abundance/biomass and the relative frequency) were estimated. Of the total of sampling in the 2002–2009 period (76), only 63 were selected for the statistical analyses after removing outliers and one of the sampling dates when bi-monthly frequency was applied during part of the first two years of the time series.

To explore annual and interannual variations in the structure (composition, abundance and biomass) of the microplanktonic communities and the associated environmental variables, multivariate analyses were applied using PRIMER-E (version 6.1.13) with PERMANOVA (version 1.0.3) add-on software (Clarke and Gorley, 2006; Anderson et al., 2008). Micro-phytoplankton and environmental data were categorized according to season (calendar seasons: summer, autumn, winter, and spring) and year (phenological years: from July year N to June year N + 1). For the microphytoplankton matrices, only the 10 m depth samples were analyzed since the sampling at the surface level began ~2 y later. However, both data sets were highly correlated (Spearman, $p < 0.001$; $n = 43$; r = correlation coefficient) in terms of abundance ($r = 0.81$) and biomass ($r = 0.87$). Similarly, total Chl-a ($r = 0.93$) and mChl-a ($r = 0.88$) were highly correlated at both depths ($n = 72$).

The environmental matrix included 16 variables: upwelling index (UPI, represented by a 7-d mean value of the sampling date and the 6 d previous days), upwelling constancy (UPC, represented by the number of days with positive UPI values before the sampling date); stratification index (ST30), surface temperature (SST) and salinity (SSAL), vertical gradient (difference between the surface and 30 m depth) in temperature (Tgr) and salinity (Sgr), water density (10 m depth, sigma-t), integrated (0–30 m depth) nutrient concentrations ($NO_3$, $NO_2$, $NH_4$, $PO_4$, $Si(OH)_4$, and the mean ratios (values between 0 and 30 m depth) between pairs of nutrients ($Si(OH)_4/N$: Si/N; $Si(OH)_4/PO_4$: Si/P; and $N/PO_4$: N/P, with N representing all three inorganic nitrogen forms). Since some of these variables were strongly correlated (Spearman, $r > 0.60$), those included in the multivariate analyses were reduced to 11 (UPI, UPC, ST30, SST, SSAL, $PO_4$, $NO_2$, $NH_4$, $Si(OH)_4$, Si/N, and N/P). In addition, preliminary analyses using the values of temperature and salinity at 10 m depth instead of the surface, and water column instead of integrated nutrient data, provided similar results (data not shown). Prior to the analyses, the environmental data were $\log_{10} (n + 1)$ transformed, except for SST and SSAL, and then normalized. The biological data were transformed to square root for both abundance and biomass. Taxa included in the multivariate matrices were those representing 1% or more of the total abundance considering all the sampling dates. As resemblance measures, the Euclidean distance was used for the environmental data and the zero-adjusted Bray-Curtis coefficient for the biological data.

Non-metric multi-dimensional scaling (NMDS) was applied to the matrices to produce an unconstrained ordination (maximizing total data variation) of samples in the multivariate space. A permutational analysis of variance (PERMANOVA) was applied to the environmental and microphytoplankton matrices to assess the significance of the between-group variation (differences in the location of the NMDS groups) with respect to total data variation. The PERMANOVA procedure was based on type III (partial) sum of squares and unrestricted permutation of raw data. Since PERMANOVA is sensitive to differences in the dispersions among groups, a permutational analysis of multivariate dispersions (PERMDISP, based on deviation from centroids) tested the homogeneity of the within-group dispersion of the NMDS groups. In addition, a constrained ordination was obtained with a canonical analysis of principal coordinates (CAP; Anderson et al., 2008) in order to represent the ordination axes in the multivariate space that: a) maximized the between-group differences

(CDA: canonical discriminant analysis) and b) maximized the correlations between the biological ordination and the environmental variables (CCorA: canonical correlation analysis). PERMANOVA, PERMDISP, and CAP analyses were run with 9999 permutations. For the PERMANOVA, the two factors (season and year) were evaluated separately since a two-factor analysis produced similar results but the within-group differences (PERMDISP) were found to be significant.

## 5.3. RESULTS

Time series data during the 2002–2009 time series indicated intense upwelling favorable winds during spring and summer (September to March), weaker during autumn, and downwelling events or relaxation periods during winter (Fig. 1b). At St. 18, water column stratification in the upper layer (0–30 m depth) was less clear in seasonality (Fig. 1b) but in both variables interannual variability was evident when comparing the first four phenological years (2002–2006) and the last three (2006–2009), with stronger upwelling and lower stratification during the later period. The climatological indexes PDO and MEI were mostly positive (warm phase) during the first period and mostly negative (cold phase) during the last period, whereas the AAO index was mostly positive during the last two years (Fig. 1c). Strong seasonality in the St. 18 time series raw data was also detected in temperature, salinity, and density (Fig. 2a–c) in the upper layer whereas this pattern was less evident in the macronutrients $NO_3$, $PO_4$, and $Si(OH_4)$ (Figs. 2d–f). In all cases, however, interannual variability was detected, with warmer and fresher waters, and higher integrated $PO_4$ and Si

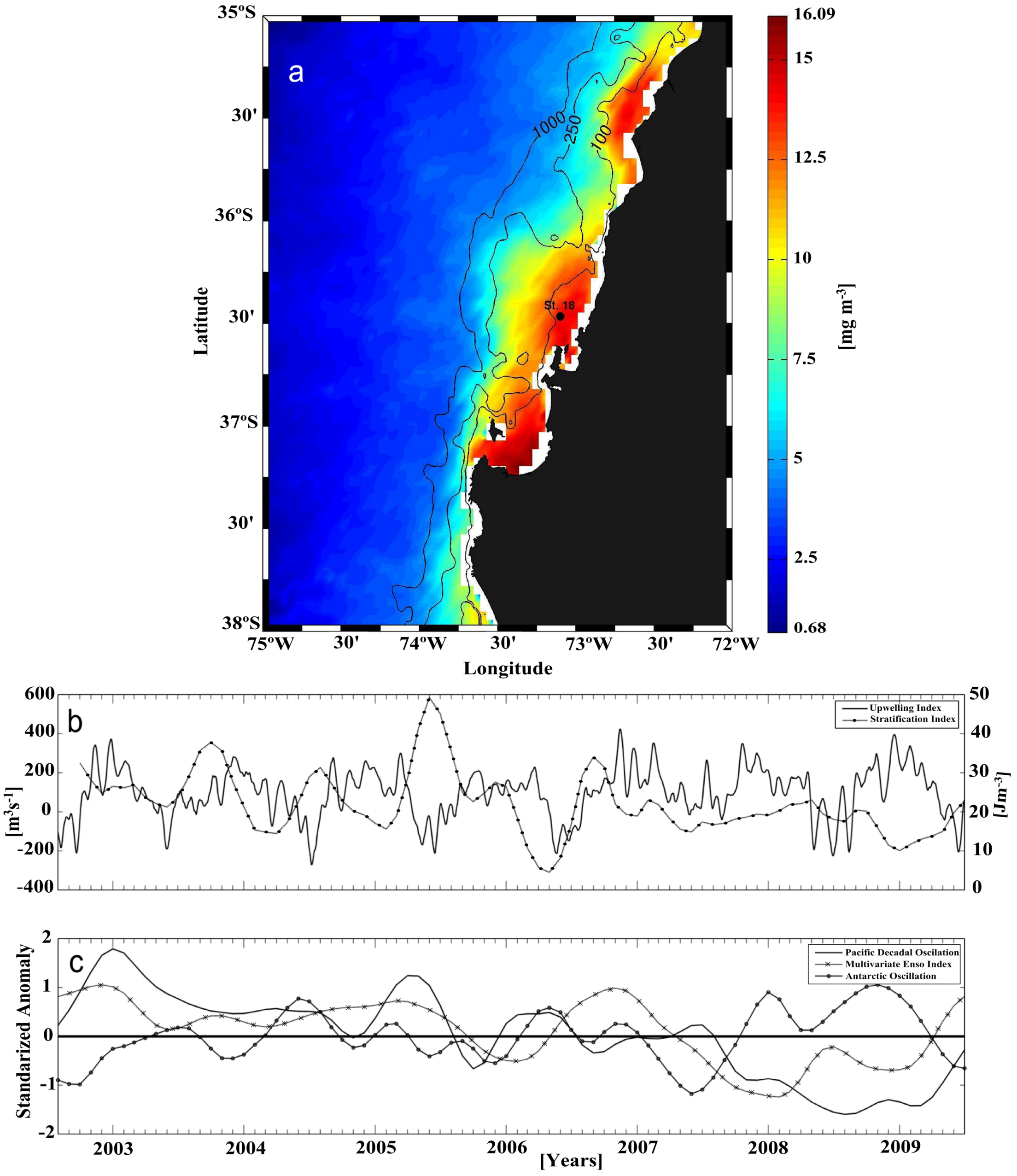

**Fig. 1**. Region of study off Concepción: (a) position of the time series St. 18 and bathymetry, overlaid over a satellite colour image on mean Chl-a concentration (composite from August 2002 to July 2009); (b) upwelling index ($m^3$ $s^{-1}$ along 100 m of coastline) for the area around St. 18 and stratification index (J $m^{-3}$) from in situ data at St. 18; and (c) climatic indexes (MEI, AAO, and PDO; 3-month running means) during the time series.

(OH$_4$) concentrations in the upper layer during the first period compared with the last one. Based on these preliminary observations, the following analyses were focused on the annual and interannual variability of the environmental and microphytoplankton community structure at St. 18, with emphasis on upwelling versus non-upwelling seasons and 2002–2006 versus 2006–2009 periods.

### 5.3.1. ANNUAL VARIABILITY IN ENVIRONMENTAL CONDITIONS AND MICRO-PHYTOPLANKTON STRUCTURE

The annual harmonic cycle of the oceanographic variables in the upper layer was characterized by a thermal stratification and warmer waters during the spring-summer upwelling period and a stronger stratification during winter (June to August), the latter associated with lower salinity (<34.0) and density waters (sigma-t < 26.0 kg m$^{-3}$) (Fig. 3a–c). The DO annual cycle indicated relatively homogenous conditions during the winter whereas waters with lower values (<3.5 mL L$^{-1}$) appeared during the upwelling season (Fig. 3d). In the upper layer, the annual cycle of nutrient concentration (NO$_3$, NO$_2$, PO$_4$, and Si(OH)$_4$) (Fig. 3e–h) indicated an homogenous distribution during the winter compared to the upwelling season, when lower values were found in the top layer (0–15 m depth) compared to the subsurface (15–30 m depth). In terms of total Chl-a and mChl-a concentration in the upper layer, their annual harmonic cycles displayed a similar seasonality (Fig. 4a and b), with higher values (>3 mg m$^{-3}$) in the top layer from spring to autumn (September to April). The monthly climatologies of biomass (10 m depth) for diatoms (Fig.

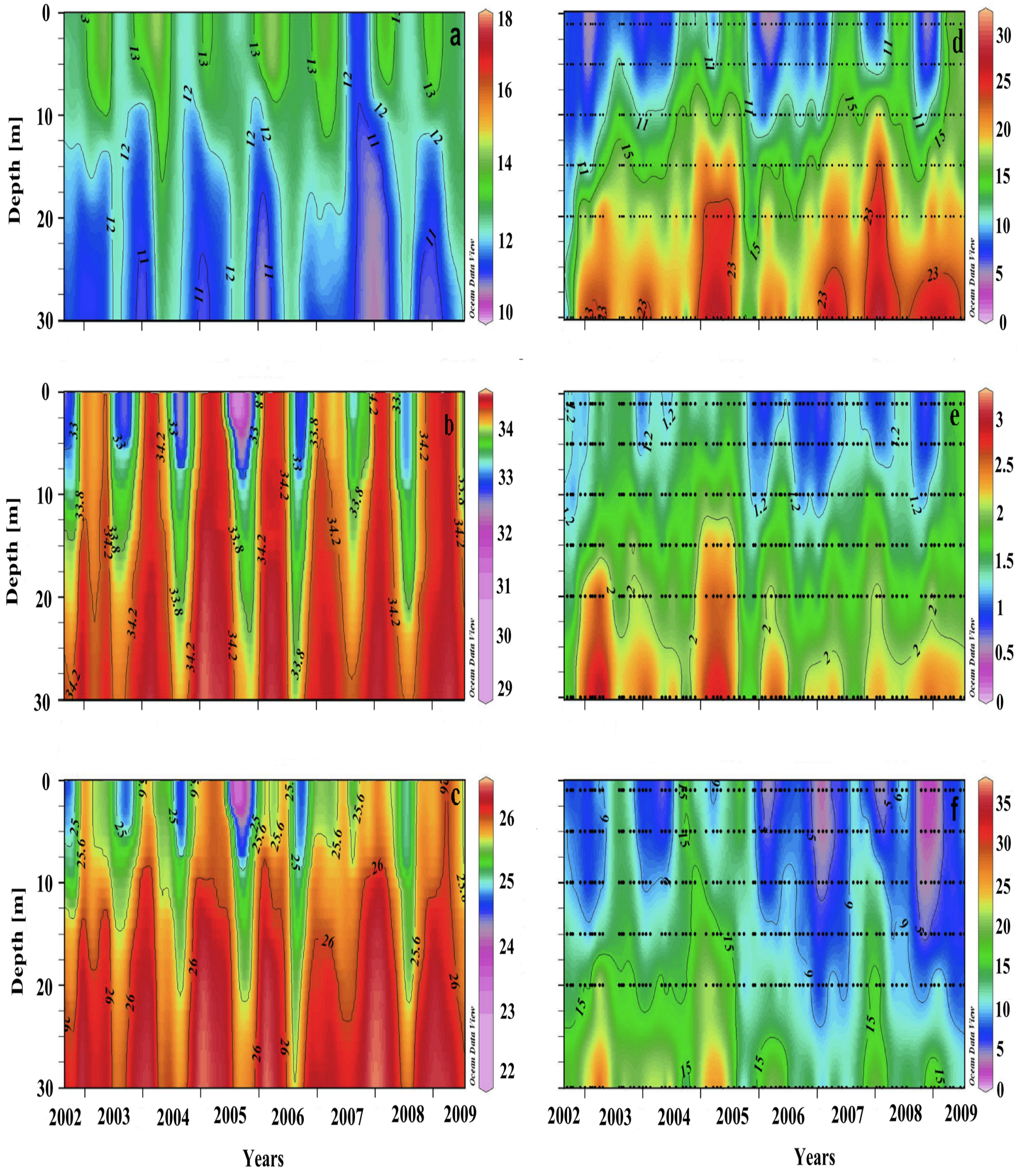

**Fig. 2.** Time series of environmental variables in the upper layer (0–30 m depth) at St. 18 (2002–2009): (a) temperature (C); (b) salinity; (c) density (sigma-t, kg m$^{-3}$); (d) $NO_3$ (µM); (e) $PO_4$ (µM); and (f) $Si(OH)_4$ (µM). Figure created using Ocean Data View [version number] (Schlitzer, R., Ocean Data View, http://www.awi-bremerhaven.de/GEO/ ODV, 2005).

4e) and autotrophic/mixotrophic dinoflagellates (Fig. 4f) displayed a similar annual pattern as the Chl-a and mChl-a.

Exploratory NMDS analyses of environmental and microphytoplankton matrices identified two large annual groups, upwelling and non-upwelling seasons, and a PERMANOVA based on these groups was highly significant ($p < 0.001$) for the microphytoplankton abundance and biomass data (pseudo-F = 9.5 and 10.5, respectively), as well as for the environmental data (pseudo-F = 14.5); within-group dispersion in all cases was not significant (PERMDISP $p > 0.1$). CAP-CDA analyses with the two NMDS annual groups were represented, for simplicity, in two dimensional graphs (4 levels or seasons). For the environmental matrix, the between group difference was highly significant ($p < 0.001$) and the first canonical axis clearly segregated the upwelling and non-upwelling groups (canonical correlation $\delta 1 = 0.87$); the total CAP correct classification of the samplings in each group was high (97%). The variables that contributed most to the segregation in the ordination along the first axis (Fig. 5b) were surface salinity ($r = -0.83$) and the upwelling index ($r = -0.55$). The environmental variables were characterized by higher upwelling (UPI and UPC), higher SST and Tgr values, and lower stratification (ST30 index and Sgr) during the upwelling compared with the non-upwelling season whereas the integrated nutrient concentrations in the upper layer were relatively high year-round and the differences in the central values were small (<30%) or very small (<5% in the case of $Si(OH_4)$) (Table 1).

For the microphytoplankton biomass data, a CAP-CDA analysis indicated that the between group annual differences were highly significant ($p < 0.001$), with the first canonical axis segregating taxa associated with upwelling and non-upwelling seasons ($\delta 1 = 0.87$); the total CAP correct classification of the samplings in each group was high (92%). The taxa that contributed most to the segregation in the ordination along the first axis (Fig. 5b) were *Corethron*, representative of non-upwelling (r = 0.58), whereas *Skeletonema* and some species of *Thalassiosira* (*T. anguste-lineata, T. aestivalis*) and *Chaetoceros* (*C. compressus* and *C. debilis*), together with *Eucampia, Pseudo-nitzschia*, and *Protoperidinium*, were representative of upwelling (r = -0.53 to -0.67).

Total diatom abundance and biomass values (10 m depth) were one to two orders of magnitude higher during upwelling compared to non-upwelling; the same pattern was observed for mChl-a (integrated and at 10 m depth) (Table 2). *Chaetoceros, Skeletonema, Thalassiosira*, and *Leptocylindrus* contributed most to total abundance and biomass during upwelling (combined IRI ~50), increasing from one to three orders of magnitude with respect to non-upwelling (Table 3). These taxa remained important in abundance during non-upwelling (combined IRI ~30%), together with *Corethron, Pseudo-nitzschia*, and *Asterionellopsis* (combined IRI ~31%). In terms of biomass, however, *Corethron* became the most important contributor during non-upwelling (IRI ~20%), as reflected in the CAP-CDA analysis (Fig. 5b).

The CAP-CCorA analysis combining the microphytoplankton biomass with the environmental variables (Fig. 5c and d) indicated that there were some strong and significant relationships between both sets ($p < 0.001$; $\delta 1 = 0.85$ and $\delta 2 = 0.69$). The seasonal shift in microphytoplankton structure was strongly associated (canonical eigenvector) with surface salinity (-0.67) and SST (-0.43) in the first axis (r = 0.85) and by the upwelling index (0.50), SST (-0.47), and the N/P ratio (-0.44) in the second axis (r = 0.69).

| Season | | UPI | UPC | ST30 | SST | Tgr | SSAL | Sgr | $PO_4$ | $NO_3$ | $NO_2$ | $NH_4$ | $SiOH_2$ | Si/N | N/P |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| UPW | Mean | 180 | 4.2 | 20 | 13.3 | 2.3 | 34.2 | 0.3 | 55.3 | 515.8 | 14.5 | 21.5 | 349.6 | 0.7 | 9.5 |
| | Std | 124 | 2.2 | 10 | 1.4 | 1.3 | 0.4 | 0.3 | 10.9 | 139.2 | 12.2 | 20.7 | 141.9 | 0.3 | 2.4 |
| | Median | 157 | 5.0 | 19 | 13.0 | 2.0 | 34.3 | 0.2 | 55.9 | 525.3 | 10.1 | 15.3 | 336.4 | 0.7 | 9.5 |
| NUPW | Mean | 16 | 2.0 | 27 | 12.3 | 0.8 | 32.9 | 1.3 | 43.4 | 441.6 | 14.1 | 15.3 | 338.3 | 0.8 | 10.7 |
| | Std | 113 | 1.6 | 16 | 0.6 | 0.6 | 1.0 | 0.9 | 9.3 | 144.7 | 5.8 | 12.7 | 93.6 | 0.3 | 1.8 |
| | Median | 28 | 2.0 | 25 | 12.4 | 0.6 | 33.0 | 1.2 | 43.3 | 412.7 | 13.5 | 12.0 | 355.2 | 0.8 | 10.5 |

**Table 1.** Environmental variables in the upper layer (0–30 m depth) at the St. 18-time series (2002–2009). Mean, one standard deviation from the mean (Std), and median values during upwelling (UPW) and non-upwelling (NUPW) seasons. UPI: upwelling index (m$^{3}$ s-$^{1}$ along 100 m coastline); UPC: number of successive days with upwelling favorable conditions before the sampling date (positive UPI values); ST30: stratification intensity (0–30 m depth; J m$^{-3}$ ); SST: sea surface temperature ( C); SSAL: surface salinity; Tgr (ºC) and Sgr: vertical gradients (0 and 30 m depth) in temperature and salinity; integrated nutrient concentrations (0–30 m depth; mmol m$^{-2}$); and mean (0–30 m depth) ratios (w/w) between nutrients (Si/N and N/P, with N representing the sum of the N-forms).

| Season | | in-Chl-a (mg $m^{-2}$) | in-mChl-a (mg $m^{-2}$) | Chl-a (mg $m^{-3}$) | mChl-a (mg $m^{-3}$) | Abundance ($10^3$ cells $m^{-3}$) | | Biomass (mg C $m^{-3}$) | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | dinoflagellates | diatoms | dinoflagellates | diatoms |
| UPW | Mean | 181 | 134 | 8.8 | 6.2 | 616 | 1565017 | 3.4 | 346 |
| | Std | 180 | 141 | 10.2 | 7.6 | 680 | 1419485 | 6.1 | 442 |
| | Median | 131 | 86 | 4.7 | 3.5 | 443 | 1166589 | 1.5 | 170 |
| NUPW | Mean | 32 | 15 | 1.5 | 0.7 | 26 | 51998 | 0.5 | 36 |
| | Std | 36 | 32 | 1.9 | 1.7 | 39 | 75101 | 1.0 | 77 |
| | Median | 23 | 5 | 1.0 | 0.2 | 7 | 17525 | 0.1 | 9 |

**Table 2:** Integrated (0–30 m depth) total Chl-a (in-Chl-a) and micro-phytoplankton Chl-a (in-mChl-a), and total Chl-a, mChl-a, and micro-phytoplankton abundance and biomass (10 m depth) of autotrophic/mixotrophic dinoflagellates (DINOF) and diatoms (DIATO) at the St. 18-time series (2002–2009). Mean, one standard deviation from the mean (Std), and median values during upwelling (UPW) and non-upwelling (NUPW) conditions.

### 5.3.2. INTER-ANNUAL VARIABILITY IN ENVIRONMENTAL CONDITIONS AND MICRO- PHYTOPLANKTON STRUCTURE

Exploratory NMDS analyses of the environmental matrix indi- cated a separation of two groups of phenological years, 2002–2006 and 2002–2009, and a PERMANOVA for these groups was highly significant ($p < 0.001$; pseudo-F = 8.0) whereas the within-group dispersion was not significant (PERMDISP, $p > 0.07$). In contrast, a PERMANOVA with the microphytoplankton abundance and biomass matrices displayed no significant differences between the two periods ($p > 0.2$, pseudo-F = 1.1 and 1.3, respectively) and for the within-group dispersion (PERMDISP, $p > 0.2$). Next, these analyses were applied to data separated into upwelling and non- upwelling samplings for the two periods of years. The results for the environmental matrix remained similar and the microphytoplankton matrices for the upwelling season formed the same NMDS groups detected in the environmental matrix, with significant differences between groups (PERMANOVA, $p < 0.05$; pseudo- F = 1.9 and 2.3, respectively) and no significant differences in the within group dispersion (PERMDISP, $p > 0.4$). For the non-upwelling season, the period differences remained not significant in the micro-phytoplankton matrices (PERMANOVA, $p > 0.2$; pseudo-F = 0.8 and 1.2, respectively; PERMDISP, $p > 0.1$).

CAP-CDA analyses with the two NMDS interannual groups for the environmental and biological matrices were represented, for simplicity, in two dimensional graphs (7 levels or years). For the environmental matrix, including the total and a seasonal separation of the data, the differences were highly significant ($p < 0.001$; $\delta 1 = 0.77–0.88$) and the total CAP correct classification was high (81–91%). The CAP-CDA ordination for data during the

| | Abundance ($10^3$ cells $m^{-3}$) | | | | | | | | Biomass (mg C $m^{-3}$) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Taxa | | | NUPW | | | UPW | | | NUPW | | | UPW | | |
| | Sigla | D (µm) | Mean AB | STDEV | IIR | Mean AB | STDEV | IIR | Mean BM | STDEV BM | IIR | Mean BM | STDEV BM | IIR |
| *Chaetoceros* | | | 6136 | 8879 | 11.3 | 657391 | 936647 | 25.2 | 0.9 | 1.2 | 7.1 | 49.5 | 101.2 | 13.1 |
| *Chaetoceros spp* | Cp | 22 | 2720 | 4859 | 3.7 | 153802 | 449221 | 6.7 | 0.3 | 0.5 | 0.9 | 17.3 | 55.1 | 4.1 |
| *Ch. compressus* | Cm | 10 | 201 | 553 | 0.4 | 158231 | 354798 | 5.8 | 0.0 | 0.0 | 0.6 | 3.4 | 6.4 | 2.7 |
| *Ch. radicans* | Cr | 8 | 1383 | 5683 | 1.4 | 101098 | 197327 | 4.7 | 0.0 | 0.0 | 0.0 | 4.5 | 11.5 | 1.3 |
| *Ch. debilis* | Cb | 16 | 422 | 1819 | 0.5 | 168247 | 305683 | 6.6 | 0.0 | 0.1 | 0.4 | 7.7 | 14.3 | 2.8 |
| *Ch. socialis* | Cs | 7 | 125 | 449 | 0.5 | 30600 | 74122 | 2.5 | 0.1 | 0.2 | 0.7 | 1.8 | 5.7 | 1.8 |
| *Ch. convolutus* | Cv | 20 | 489 | 1725 | 5.2 | 13672 | 56331 | 2.6 | 0.3 | 1.0 | 1.2 | 5.2 | 32.4 | 1.7 |
| *Ch. didymus* | Cd | 15 | 160 | 364 | 1.1 | 16302 | 34849 | 1.6 | 0.0 | 0.0 | 0.4 | 3.2 | 9.9 | 1.5 |
| *Ch. decipiens* | Ci | 22 | 24 | 88 | 0.4 | 3906 | 10118 | 1.2 | 0.0 | 0.1 | 0.4 | 1.3 | 5.7 | 1.4 |
| *Ch. curvisetus* | Cu | 15 | 161 | 606 | 0.6 | 5844 | 16764 | 1.0 | 0.1 | 0.4 | 3.3 | 2.5 | 12.1 | 1.6 |
| *Ch. teres* | Ct | 30 | 26 | 82 | 0.4 | 1142 | 2238 | 0.9 | 0.0 | 0.1 | 0.5 | 1.2 | 2.8 | 1.2 |
| *Ch. contrictus* | Cn | 17 | 424 | 1053 | 0.8 | 3884 | 16136 | 0.8 | 0.1 | 0.2 | 0.6 | 1.6 | 7.8 | 1.6 |
| *Leptocylindrus* | | | 805 | 1541 | 4.0 | 129672 | 595106 | 6.9 | 0.4 | 0.7 | 4.4 | 11.4 | 51.2 | 5.1 |
| *L. minimus* | Li | 2.4 | 76 | 250 | 0.3 | 2585 | 9393 | 0.5 | 0.0 | 0.0 | 0.8 | 0.1 | 0.2 | 1.3 |
| *L. mediterraneum* | Lm | 10 | 374 | 1142 | 2.3 | 420 | 1591 | 0.3 | 0.2 | 0.6 | 1.7 | 0.2 | 0.8 | 0.4 |
| *L. danicus* | Ld | 7 | 356 | 1140 | 1.6 | 126667 | 593274 | 5.8 | 0.2 | 0.4 | 1.2 | 11.1 | 50.5 | 3.6 |
| *Skeletonema* | Sk | 11 | 5795 | 12633 | 6.5 | 452511 | 995544 | 13.5 | 1.1 | 2.5 | 5.6 | 72.3 | 148.4 | 12.4 |
| *Thalassiosira* | | | 12796 | 30789 | 10.9 | 202741 | 426857 | 9.4 | 4.1 | 9.7 | 10.5 | 183.5 | 368.6 | 18.1 |
| *Th. minuscula* | Tu | 15 | 1279 | 3743 | 2.4 | 57010 | 278368 | 2.8 | 0.6 | 1.7 | 2.9 | 38.2 | 186.4 | 2.8 |
| *Th. angulata* | Td | 22 | 145 | 383 | 0.7 | 13698 | 61807 | 1.4 | 0.0 | 0.1 | 0.3 | 3.6 | 16.4 | 1.5 |
| *Th. anguste - lineata* | Ta | 35 | 162 | 528 | 0.9 | 86421 | 229654 | 4.9 | 0.2 | 0.6 | 1.7 | 107.7 | 287.3 | 9.4 |
| *Th. aestivalis* | Te | 30 | 468 | 2123 | 0.3 | 10268 | 29291 | 1.6 | 0.5 | 2.5 | 0.7 | 12.2 | 34.8 | 3.2 |
| *Th. minima* | Tm | 8 | 7001 | 21813 | 3.9 | 1980 | 11511 | 0.3 | 0.3 | 0.9 | 1.5 | 0.1 | 0.7 | 1.1 |
| *Thalassiosira spp* | Tp | 20 | 3741 | 11325 | 4.4 | 33196 | 167151 | 2.1 | 2.4 | 7.4 | 3.4 | 21.7 | 109.4 | 2.1 |
| *Pseudonitszchia* | Ps | 3.2 | 3359 | 7009 | 9.6 | 34926 | 80857 | 4.2 | 0.6 | 1.3 | 2.6 | 6.3 | 15.0 | 2.1 |
| *Asterionellopsis* | As | 8 | 12397 | 40174 | 5.8 | 16326 | 40083 | 2.1 | 1.0 | 3.1 | 3.1 | 1.2 | 2.9 | 1.8 |
| *Detonula* | De | 21 | 2980 | 7747 | 3.8 | 20959 | 73361 | 2.4 | 2.1 | 5.4 | 4.9 | 14.7 | 51.4 | 3.1 |
| *Cylindrotheca* | Cy | 3.3 | 932 | 1943 | 3.0 | 3634 | 12185 | 1.7 | 0.0 | 0.1 | 0.1 | 0.1 | 0.5 | 0.3 |
| *Thalassionema* | Tn | 5.3 | 391 | 988 | 2.6 | 39 | 138 | 0.7 | 0.3 | 0.8 | 4.7 | 0.0 | 0.1 | 2.9 |
| *Guinardia* | Gi | 20 | 474 | 1189 | 1.6 | 3579 | 20240 | 0.7 | 0.1 | 0.4 | 1.3 | 1.1 | 6.3 | 0.8 |
| *Cerataulina* | Ca | 22 | 200 | 601 | 1.5 | 16162 | 74375 | 2.8 | 0.2 | 0.7 | 2.0 | 7.9 | 28.3 | 3.6 |
| *Rhizosolenia* | Rh | 15 | 196 | 756 | 1.5 | 587 | 1416 | 1.6 | 0.2 | 0.5 | 2.2 | 0.9 | 2.3 | 1.9 |
| *Coscinodiscus* | Cc | 134 | 130 | 521 | 1.2 | 70 | 239 | 0.8 | 2.1 | 5.7 | 5.7 | 1.4 | 5.1 | 1.2 |
| *Odontella* | Od | 50 | 1041 | 3698 | 1.1 | 1583 | 4869 | 1.1 | 1.6 | 5.4 | 3.6 | 2.6 | 10.3 | 1.1 |
| *Pleurosigma* | Pl | 15 | 106 | 305 | 0.9 | 336 | 992 | 1.1 | 0.1 | 0.2 | 0.8 | 0.2 | 0.7 | 0.3 |
| *Lauderia* | La | 24 | 237 | 946 | 0.5 | 1838 | 7590 | 1.3 | 0.6 | 2.5 | 1.0 | 4.9 | 20.3 | 2.3 |
| *Eucampia* | Eu | 19 | 5 | 26 | 0.4 | 21914 | 40558 | 3.2 | 0.0 | 0.0 | 0.4 | 1.9 | 6.7 | 2.4 |
| *Corethron* | Co | 29 | 449 | 1066 | 15.5 | 101 | 443 | 1.8 | 2.2 | 5.1 | 20.3 | 0.5 | 2.2 | 3.0 |
| *Protoperidinium* | Pt | 45 | 11 | 21 | 2.2 | 367 | 470 | 3.1 | 0.1 | 0.4 | 2.8 | 1.6 | 2.0 | 4.4 |
| *Gyrodinium* | Gr | 40 | 1 | 3 | 0.7 | 44 | 100 | 2.4 | 0.0 | 0.0 | 0.7 | 0.2 | 0.5 | 2.6 |
| *Gymnodinium* | Gm | 35 | 1 | 3 | 0.7 | 41 | 91 | 2.3 | 0.0 | 0.0 | 0.7 | 0.2 | 0.5 | 2.5 |
| *Scrippsiella* | Sc | 25 | 6 | 23 | 0.6 | 75 | 208 | 1.2 | 0.0 | 0.0 | 0.6 | 0.1 | 0.3 | 1.3 |
| *Dinophysis* | Dn | 35 | 1 | 2 | 0.4 | 15 | 27 | 1.8 | 0.0 | 0.0 | 0.4 | 0.3 | 0.9 | 2.1 |
| *Diplopsalis* | Dp | 37 | 1 | 3 | 0.4 | 31 | 89 | 1.2 | 0.0 | 0.0 | 0.4 | 0.2 | 0.5 | 1.3 |

**Table 3.** Abundance and biomass of micro-phytoplankton taxa at the St. 18-time series (2002–2009). Mean, one standard deviation from the mean (Std), and index of relative importance (IRI, %) during upwelling (UPW) and non-upwelling (NUPW) seasons. ABB: abbreviations used in Figs. 5 and 6; D: mean cell diameter (µm) in St. 18 samples.

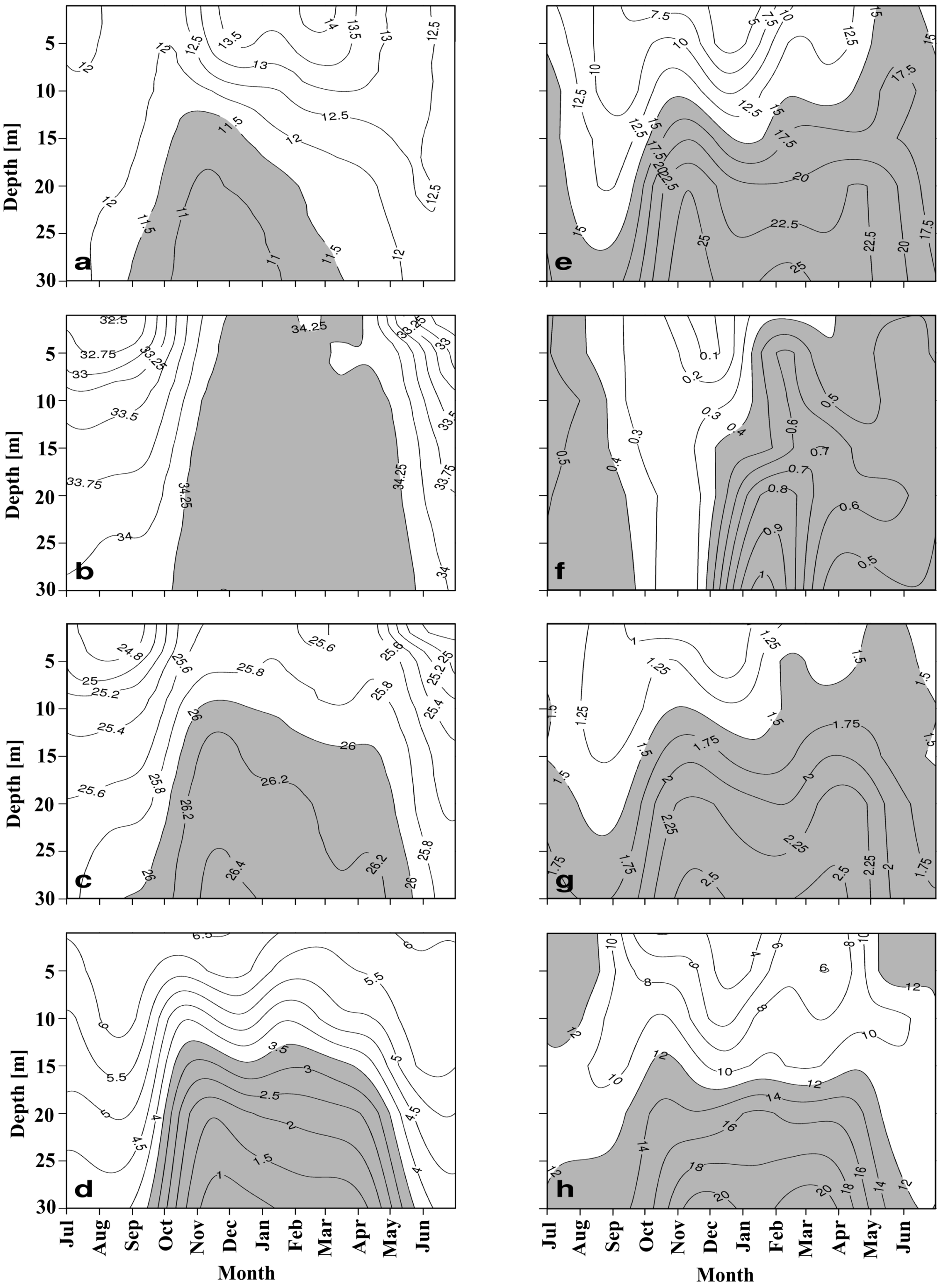

**Fig. 3.** Annual harmonic cycles of environmental variables in the upper layer at St. 18 (2002–2009): (a) temperature (C); (b) salinity; (c) density (sigma-t, kg $m^{-3}$); (d) DO (mL $L^{-1}$); (e) $NO_3$ (μM); (f) $NO_2$ (μM); (g) $PO_4$ (μM); and (h) $Si(OH)_4$ (μM).

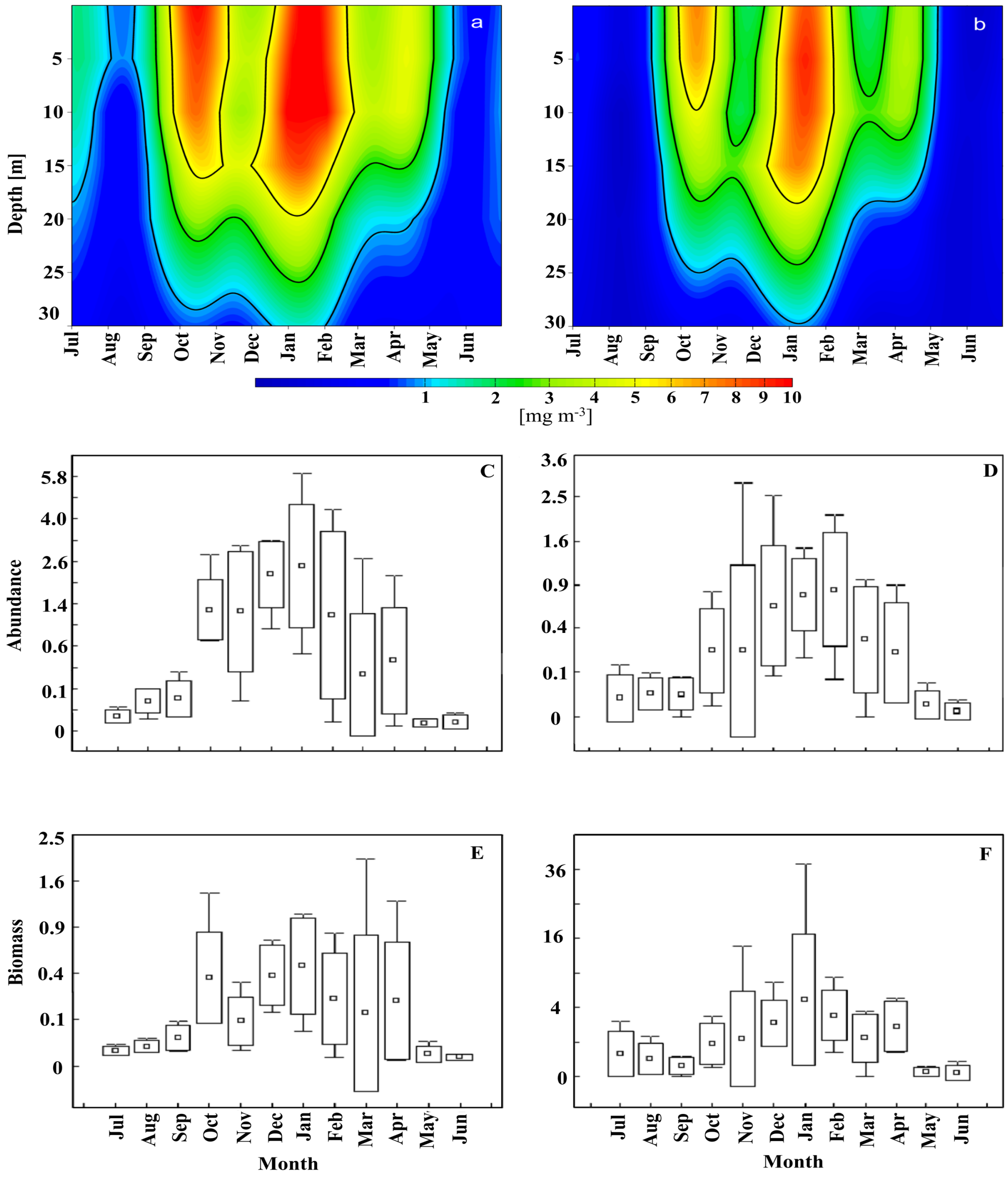

**Fig. 4.** Annual variability of phytoplankton in the upper layer (0–30 m depth) at St. 18 (2002–2009): harmonic cycles for total Chl-a (a) and mChl-a (b); monthly climatologies (10 m depth) of abundance in diatoms (c) and autotrophic/mixotrophic dinoflagellates (d); and monthly climatologies (10 m depth) of biomass in diatoms (f) and autotrophic/ mixotrophic dinoflagellates (e). In the box-plots, cell abundance or biomass include the median (squares), one standard deviation (rectangles), and the range (lines) estimates.

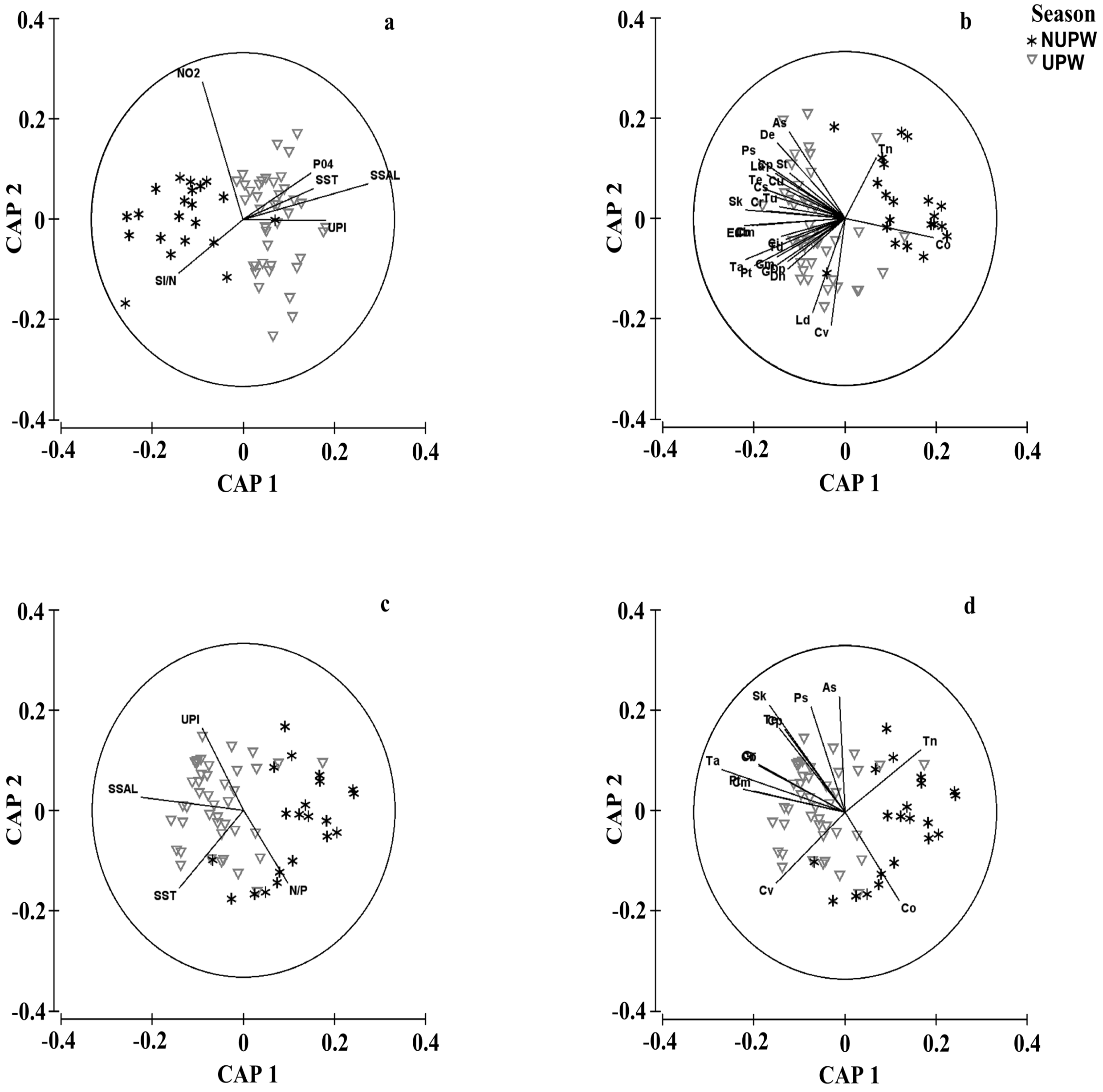

**Fig. 5.** CAP ordination plots for the factor season (4 levels) applied to the environmental and the micro-phytoplankton (biomass) matrices. Only two symbols were used in these diagrams to emphasize the differences between two groups of seasons, upwelling (UPW) and non-upwelling (NUPW). Upper panels: CAP-CDA on environmental variables (a) and micro-phytoplankton taxa (b). Lower panels: CAP-CCorA combining both matrices to explore their relationships; the environmental variables (c) and biomass of different taxa (d) are represented. In all the cases, the vector overlay of the rank correlations was restricted to those having lengths ≥ 0.4 for the biological data and ≥ 0.6 for the environmental data; these values are not reflected in the axis because the multiple vectors are distributed in a multispace (sphere) but they are provided by the CAP analysis (canonical eigenvectors in the space of X; Anderson et al., 2008). Abbreviations for the environmental variables are detailed in Table 1 and for the micro- phytoplankton in Table 3.

upwelling season (Fig. 6a) clearly separated the two periods of years along the first axes ($\delta 1 = 0.79$), mostly on the basis of nutrients, including Si/N ($r = -0.89$), $Si(OH)_4$ (-0.75), $PO_4$ (-0.63), and N/P (0.70). $Si(OH)_4$ and Si/N values during both seasons were higher (30–40% and 45–50%, respectively) in the first period than in the last one, while those of N/P were slightly lower (<30%) (Table 4). In addition, SST values were was slightly higher during both seasons of the first period, together with a higher salinity gradient and lower surface salinity during the non-upwelling season, when compared with the last period.

For the microphytoplankton biomass matrix, a CAP-CDA analysis indicated that both total and non-upwelling data associated with the two periods of years were not significantly different ($p > 0.1$). However, the upwelling data for these two periods was highly significant ($p < 0.001$; $\delta 1 = 0.93$) and total CAP correct classification was high (91%). A CAP-CDA ordination for the upwelling season of the two periods of years (Fig. 6b) clearly separated them along the first axis ($\delta 1 = 0.86$). Different species of *Chaetoceros* and *Thalassiosira* were represented mostly in one of the periods: (a) *Ch. decipiens*, *Ch. didymus*, *Ch. curvisetus*, *Th. anguste-lineata*, and *Th. minuscula* in the first period ($r = -0.40$ to $-0.49$), and (b) *Ch. socialis*, *Ch. debilis*, and *Thalassiosira* spp. ($r = 0.35$–$0.40$), together with other diatoms (*Corethron* and *Coscinodiscus*; $r = 0.30$–$0.36$) and dinoflagellates (*Diploneis* and *Scrippsiella*; $r = 0.52$), in the last period. Total micro-phytoplankton abundance and biomass (10m depth), as well as Chl-a and mChl-a (integrated and at 10 m depth), were represented by lower values during the upwelling season of the last period compared to the first, whereas the abundance and biomass of autotrophic/mixothrophic dinoflagellates was lower during the latter. The differences between the central values of each period was highest (3–5 times) for mChl-a, and the abundance and biomass of diatoms and dinoflagellates (see Table 5).

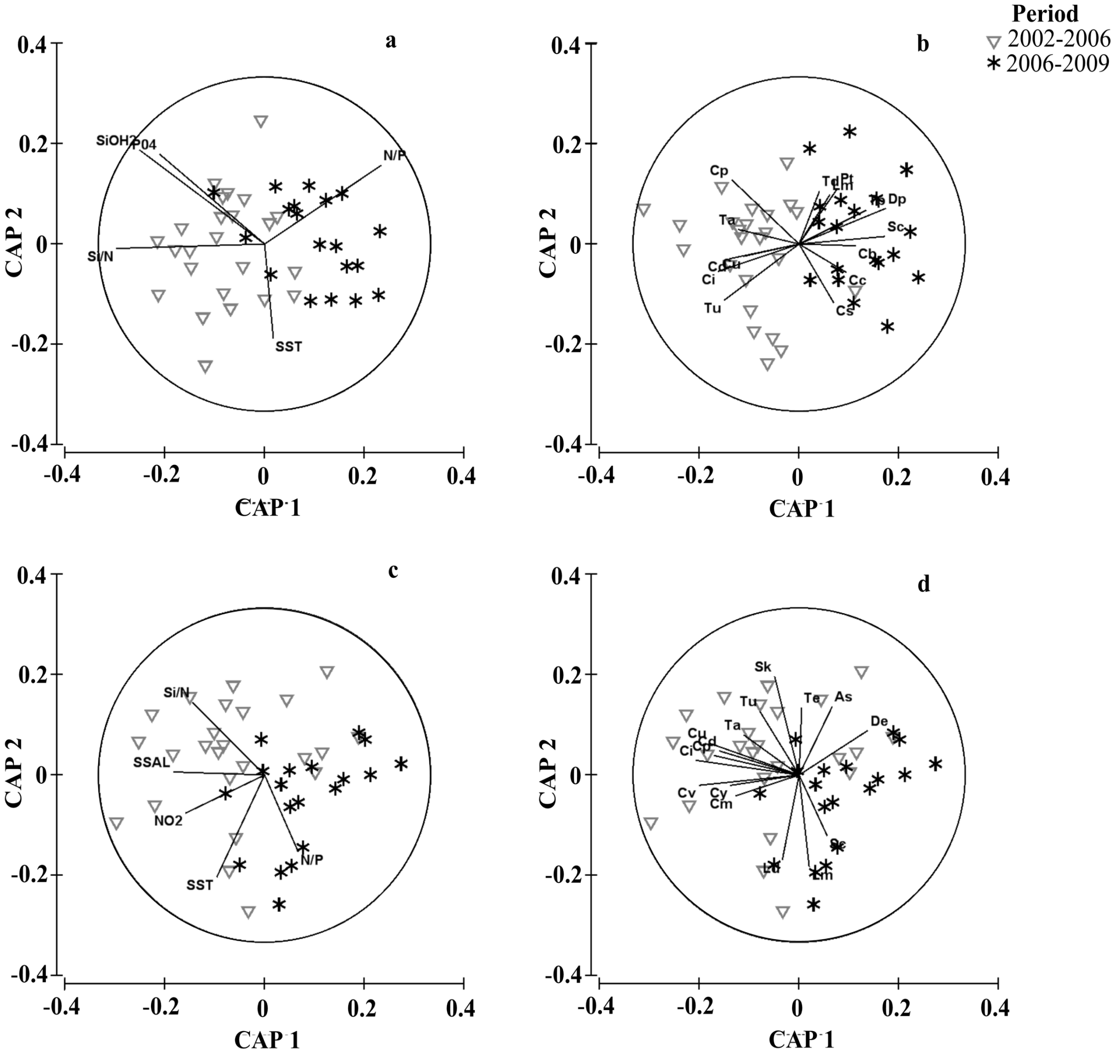

**Fig.6**. CAP ordination plots for the year factor (7 levels) applied to the environmental and the micro-phytoplankton (biomass) matrices. Only two symbols were used in these diagrams to emphasize the differences between two groups of phenological years, 2002–2006 and 2006–2009. Upper panels: CAP-CDA on environmental variables (a) and micro-phytoplankton taxa (b). Lower panels: CAP-CCorA combining both matrices to explore their relationships; the environmental variables (c) and biomass of different taxa (d) are represented. In all the cases, the vector overlay of the rank correlations was restricted to those having lengths ≥ 0.4 for the biological data and ≥ 0.6 for the environmental data (see explanation in Fig. 5). Abbreviations for the environmental variables are detailed in Table 4 and for the micro-phytoplankton in Table 3.

| Period | Season | | UPI | UPC | ST30 | SST | Tgrad | SSAL | Sgrad | $PO_4$ | $NO_3$ | $NO_2$ | $NH_4$ | $SiOH_2$ | Si/N | N/P |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2002-2006 | UPW | Mean | 158 | 4.0 | 20.1 | 13.4 | 2.4 | 34.2 | 0.2 | 59 | 494 | 17 | 24 | 414 | 0.8 | 8.2 |
| | | Std | 128 | 2.5 | 10.9 | 1.5 | 1.4 | 0.3 | 0.3 | 11 | 131 | 15 | 25 | 127 | 0.2 | 2.0 |
| | | median | 152 | 5.5 | 18.5 | 13.2 | 2.1 | 34.3 | 0.2 | 59 | 480 | 15 | 16 | 427 | 0.8 | 8.3 |
| | NUPW | Mean | -1 | 2.2 | 31.3 | 12.4 | 0.7 | 32.6 | 1.6 | 42 | 381 | 15 | 17 | 387 | 1.0 | 10.0 |
| | | Std | 57 | 1.5 | 15.9 | 0.4 | 0.5 | 1.0 | 0.9 | 11 | 128 | 6 | 14 | 69 | 0.3 | 1.8 |
| | | median | 9 | 2.0 | 34.9 | 12.4 | 0.5 | 32.8 | 1.4 | 44 | 334 | 14 | 12 | 410 | 0.9 | 10.2 |
| 2006-2009 | UPW | Mean | 204 | 4.5 | 18.8 | 13.1 | 2.1 | 34.2 | 0.3 | 51 | 543 | 11 | 19 | 275 | 0.5 | 11.1 |
| | | Std | 116 | 1.8 | 9.8 | 1.2 | 1.1 | 0.4 | 0.4 | 9 | 148 | 7 | 14 | 122 | 0.2 | 2.0 |
| | | median | 167 | 5.0 | 20.4 | 12.9 | 1.8 | 34.3 | 0.2 | 52 | 549 | 9 | 15 | 250 | 0.4 | 11.5 |
| | NUPW | Mean | 72 | 1.7 | 21.3 | 12.1 | 0.9 | 33.3 | 0.9 | 45 | 519 | 12 | 13 | 268 | 0.5 | 11.6 |
| | | Std | 158 | 1.7 | 13.8 | 0.8 | 0.6 | 0.8 | 0.8 | 7 | 132 | 5 | 11 | 80 | 0.2 | 1.3 |
| | | median | 66 | 2.0 | 16.7 | 12.1 | 0.8 | 33.4 | 0.8 | 43 | 501 | 13 | 12 | 276 | 0.5 | 11.2 |

**Table 4**. Environmental variables in the upper layer (0–30 m depth) at the St. 18 time series (2002–2009). Mean, one standard deviation from the mean (std), and median values for two periods of years under upwelling (upw) and non-upwelling (nupw) seasons. UPI: upwelling index (m3 s1 along 100 m coastline); UPC: number of successive days with upwelling favorable conditions before the sampling date (positive UPI values); ST30: stratification intensity (0–30 m depth; J $m^{-3}$); SST: sea surface temperature ( C); SSAL: surface salinity; Tgrad (ºC) and Sgrad: vertical gradients (0 and 30 m depth) in temperature and salinity; integrated nutrient concentrations (0–30 m depth; mmol $m^{-2}$); and mean (0–30 m depth) ratios (w/w) between nutrients.

| Period | Season | | in-Chl-a (mg m$^{-2}$) | in-mChl-a (mg m$^{-2}$) | Chl-a (mg m$^{-3}$) | mChl-a (mg m$^{-3}$) | Ratio mC/mChl-a | AB (10$^{3}$ cells m$^{-3}$) | | BM (mg C m$^{-3}$) | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | DINOF | DIAT | DINOF | DIAT |
| 2002-2006 | UPW | Mean | 202 | 165 | 10.2 | 8.3 | 61 | 378 | 1875620 | 1.4 | 463 |
| | | Std | 170 | 155 | 9.8 | 8.7 | 17 | 493 | 1940801 | 1.5 | 486 |
| | | Median | 158 | 116 | 8.7 | 7.0 | 57 | 163 | 1000432 | 1.0 | 366 |
| | NUPW | Mean | 24 | 8.7 | 1.0 | 0.4 | 60 | 15 | 57303 | 0.4 | 21 |
| | | Std | 90 | 7.2 | 0.6 | 0.4 | 16 | 25 | 89366 | 0.8 | 27 |
| | | Median | 22 | 6.4 | 0.9 | 0.2 | 52 | 6 | 14680 | 0.1 | 9 |
| 2006-2009 | UPW | Mean | 158 | 101 | 7.3 | 3.8 | 55 | 918 | 1067959 | 5.6 | 217 |
| | | Std | 193 | 118 | 10.7 | 5.3 | 13 | 920 | 1231772 | 8.2 | 357 |
| | | Median | 91 | 75 | 4.2 | 1.9 | 54 | 542 | 753476 | 3.1 | 87 |
| | NUPW | Mean | 42 | 23 | 2.1 | 1.2 | 50 | 95 | 194951 | 0.6 | 56 |
| | | Std | 54 | 49 | 2.9 | 2.6 | 8 | 183 | 431751 | 1.3 | 115 |
| | | Median | 24 | 4.0 | 1.1 | 0.1 | 49 | 11 | 11780 | 0.1 | 9 |

**Table 5.** Integrated (0–30 m depth) total Chl-a (in-Chl-a) and micro-phytoplankton Chl-a (in-mChl-a), and total Chl-a, mChl-a, mC/mChl-a ratios (w/w), and micro-phytoplankton abundance and biomass (10 m depth) of autotrophic/mixotrophic dinoflagellates (DINOF) and diatoms (DIAT) at the St. 18-time series (2002–2009). Mean, one standard deviation from the mean (Std), and median values during two periods of years separated into upwelling (UPW) and non-upwelling (NUPW) seasons.

The mean abundance of taxa that contributed most to the total decreased during the upwelling season of the last period (Table 6), slightly (<30%) in the case of *Chaetoceros* and *Thalassiosira* but moderately (~60–80%) in *Skeletonema* and *Leptocylindrus*. A similar pattern was observed for mean biomass except for a large decrease (~60%) in *Chaetoceros*, implying a change to smaller size species or sizes during the last period. The diatom genera remained a dominant component in abundance and biomass of the microphytoplankton during the upwelling season of both periods of years (combined IRI ~52–58% and 52–43%, respectively).

The species with the highest mean abundance during the upwelling season of the 2002–2006 period were *C. compressus*, *C. debilis*, *L. danicus*, and *T. anguste-lineata*; in terms of biomass, the latter was dominant (Table 6). During the upwelling season of the first period, *C. compressus* and *C. debilis* remained numerically dominant, together with *C. radicans*, whereas *T. anguste-lineata* was dominant in biomass; the IRI values reflected these patterns (Table 6). Some species decreased one to two orders of magnitude in mean abundance during the last period (*C. convolutus*, *C. didymus*, *C. decipiens*, *C. curvisetus*, *C. teres*, and *T. aestivalis*), whereas others did so during the first period (*T. decipiens* and *T. minima*); a similar pattern was detected for the biomass (Table 6).

The results of CAP-CCorA analysis based on the upwelling season of the two periods of years (2002–2006 and 2006–2009) indicated significant relationships between the microphytoplankton biomass and the environmental matrices ($p < 0.05$; $\delta 1 = 0.86$ and $\delta 2 = 0.75$; Fig. 6a and b). A shift in microphytoplankton structure between the two periods (Fig. 6c and d) was mostly associated (canonical eigenvectors) with surface salinity (-0.55), $NO_2$ (-0.48), and the Si/N ratio (-0.44) in the first axis (r = 0.86), and SST (-0.61), Si/N (0.44) and N/P (-0.46) in the second axis (r = 0.75).

## 5.4. DISCUSSION

Recent changes in climatic and oceanographic conditions in the southern HCS have had an impact on the community structure of the microphytoplankton (this study) and the meso-zooplankton (Medellín-Mora et al., 2016) in the coastal upwelling zone, based on the analysis of St. 18 time series data and the fact that this sampling station has been previously shown to adequately represent the spatial variability of the plankton in shelf waters in this region (Escribano et al., 2007; Morales and Anabalón, 2012). In the following sections, we explore the potential forcing factors behind the observed annual and interannual changes in microphytoplankton community structure to understand the effects of sustained wind intensification on microphytoplankton communities of this coastal system.

### 5.4.1. FACTORS INVOLVED IN THE ANNUAL VARIABILITY IN MICRO-PHYTOPLANKTON COMMUNITY STRUCTURE

Results of the present study show that the seasonal variation of the microphytoplankton in the southern HCS was strongly associated with changes in surface salinity and wind-driven upwelling. SST and N/P ratio were also involved but the magnitude of their seasonal change in terms of central values was relatively low. Wind-driven upwelling has been usually identified as an indirect factor of phytoplankton annual variability in EBCs since it contributes to the transport of subsurface nutrient-rich waters to the surface layer (Mackas et al., 2006; Chavez and Messié, 2009). However, St. 18 time series data on integrated nutrient concentrations in the upper layer showed a weak seasonality (mean percentage of the annual harmonic variance <30%) and the mean values remained relatively high throughout the annual cycle (this study; Montero et al., 2007), except for sporadic exhaustion events (González et al., 2007). These results suggest that the input of nutrients to the upper layer in shelf waters of this region is attributable to seasonal wind-driven upwelling and to other processes occurring during the non-upwelling season. Riverine nutrient input to coastal waters in this region (Itata and Bio-Bio Rivers) is a relevant source (Iriarte et al., 2012; Leniz et al., 2012; Yévenes et al., 2015). So, if macro-nutrient supply to the upper layer in the coastal zone is relatively constant during the year, what are the factors shaping the annual micro-phytoplankton cycle?

It has been previously proposed that water column mixing and turbulence in the upper layer induced by seasonal upwelling directly contributes to a substantial seasonal increase in the diatom-dominated microphytoplankton community (González et al., 2007), as oppose to a condition of higher water column stratification associated with the seasonal increases in river discharge and precipitation (late autumn to early spring). Nevertheless, annual fluctuations in stratification in the upper layer have been shown to be minimal (Sobarzo et al., 2007). Part of this may be explained by the strong mixing events produced by downwelling winds during the winter together with a narrowing and deepening of the Itata plume in the coastal zone adjacent to St. 18 (Saldías et al., 2012). Also, river plumes in the southern HCS are shallower (~20 m depth in winter) than those in high latitudes of the

| | Abundance ($10^3$ cells m$^{-3}$) | | | | | | Biomass (mg C m$^{-3}$) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 2002-2006 | | | 2006-2009 | | | 2002-2006 | | | 2006-2009 | | |
| | Mean AB | STDEV AB | IIR | Mean AB | STDEV AB | IIR | Mean BM | STDEV BM | IIR | Mean BM | STDEV BM | IIR |
| *Chaetoceros* | 747489 | 1099787 | 25.4 | 543582 | 690683 | 24.9 | 68 | 130 | 14.5 | 26 | 34 | 11 |
| *Chaetoceros spp* | 249569 | 583946 | 8.7 | 31381 | 71587 | 4.3 | 28 | 72 | 5.7 | 3.3 | 7.5 | 2.5 |
| *Ch. compressus* | 171146 | 389155 | 6.1 | 134546 | 300340 | 5.4 | 3.3 | 7.1 | 3.2 | 2.3 | 5.3 | 2.0 |
| *Ch. radicans* | 73247 | 120517 | 4.0 | 136278 | 264491 | 5.7 | 3.2 | 8.1 | 0.8 | 5.4 | 14 | 1.8 |
| *Ch. debilis* | 149571 | 333769 | 4.0 | 191838 | 273189 | 9.8 | 6.2 | 14.3 | 2.1 | 9.7 | 15 | 3.7 |
| *Ch. socialis* | 35036 | 90957 | 2.9 | 24997 | 46785 | 2.0 | 2.2 | 7.4 | 2.1 | 1.4 | 1.8 | 1.5 |
| *Ch. convolutus* | 24324 | 74340 | 2.8 | 216 | 352 | 2.4 | 9.2 | 43.3 | 1.9 | 0.1 | 0.2 | 1.4 |
| *Ch. didymus* | 24916 | 42874 | 2.1 | 5422 | 16156 | 1.0 | 5.3 | 12.9 | 2.0 | 0.5 | 1.2 | 0.9 |
| *Ch. decipiens* | 6674 | 12923 | 1.6 | 409 | 1536 | 0.8 | 2.0 | 7.5 | 1.3 | 0.4 | 1.6 | 1.5 |
| *Ch. curvisetus* | 10157 | 21648 | 1.4 | 396 | 887 | 0.5 | 3.3 | 15.4 | 1.6 | 1.4 | 5.9 | 1.5 |
| *Ch. teres* | 1636 | 2797 | 1.0 | 517 | 979 | 0.7 | 1.8 | 3.6 | 1.1 | 0.4 | 0.8 | 1.3 |
| *Ch. contrictus* | 1213 | 2513 | 0.7 | 7260 | 24040 | 0.9 | 0.2 | 0.6 | 1.3 | 3.4 | 11.6 | 2.0 |
| *Leptocylindrus* | 184049 | 781254 | 4.9 | 60984 | 193725 | 9.4 | 16 | 67 | 4.1 | 5.6 | 20.2 | 6.3 |
| *L. minimus* | 1026 | 4338 | 3.7 | 4553 | 13209 | 0.6 | 0.03 | 0.1 | 1.2 | 0.1 | 0.3 | 1.4 |
| *L. mediterraneum* | 440 | 1271 | 0.1 | 400 | 1876 | 0.4 | 0.2 | 1.0 | 0.4 | 0.2 | 0.7 | 0.5 |
| *L. danicus* | 182657 | 779713 | 0.5 | 55944 | 187046 | 8.4 | 16 | 66 | 2.7 | 5.3 | 20 | 4.8 |
| *Skeletonema* | 714106 | 1271927 | 16.9 | 122074 | 197228 | 9.3 | 113 | 188 | 14.3 | 21 | 32 | 10 |
| *Thalassiosira* | 224326 | 448165 | 10.0 | 175787 | 408802 | 8.6 | 221 | 412 | 19.3 | 137 | 310 | 16 |
| *Th. minuscula* | 92149 | 370686 | 4.1 | 12623 | 38779 | 1.2 | 62 | 248 | 3.4 | 8.5 | 26 | 2.0 |
| *Th. angulata* | 1482 | 3378 | 1.0 | 29129 | 91917 | 2.0 | 0.4 | 0.9 | 1.5 | 7.7 | 24 | 1.4 |
| *Th. anguste - lineata* | 111139 | 263647 | 5.3 | 55198 | 180002 | 4.3 | 138 | 330 | 10.9 | 69 | 225 | 7.7 |
| *Th. aestivalis* | 15005 | 38187 | 1.9 | 4284 | 8417 | 1.2 | 18 | 45 | 3.7 | 5.1 | 10.0 | 2.5 |
| *Th. minima* | 443 | 1431 | 0.3 | 3591 | 16455 | 0.3 | 0.02 | 0.1 | 0.8 | 0.2 | 1.0 | 1.2 |
| *Thalassiosira spp* | 3791 | 11311 | 1.3 | 47933 | 206671 | 3.1 | 2.4 | 7.4 | 0.7 | 46 | 164 | 3.8 |
| *Pseudonitszchia* | 33114 | 60308 | 4.0 | 37215 | 102946 | 4.4 | 0.0 | 0.1 | 2.9 | 0.0 | 0.1 | 2.8 |
| *Asterionellopsis* | 18105 | 48611 | 2.0 | 14079 | 26832 | 2.2 | 1.2 | 3.4 | 1.9 | 1.1 | 2.1 | 1.8 |
| *Detonula* | 16728 | 49733 | 2.9 | 26304 | 96660 | 1.7 | 12 | 35 | 3.9 | 18 | 68 | 2.3 |
| *Cylindrotheca* | 4114 | 15356 | 1.7 | 3029 | 6666 | 1.7 | 0.03 | 0.2 | 1.4 | 0.0 | 0.0 | 1.5 |
| *Thalassionema* | 38 | 142 | 0.6 | 40 | 135 | 0.7 | 0.00 | 0.0 | 0.7 | 0.0 | 0.1 | 0.8 |
| *Guinardia* | 273 | 988 | 0.2 | 7755 | 30358 | 1.3 | 0.1 | 0.3 | 0.2 | 2.4 | 9.5 | 1.5 |
| *Cerataulina* | 9856 | 39979 | 2.0 | 24128 | 103657 | 3.8 | 7.4 | 21.8 | 2.8 | 8.7 | 35 | 4.4 |
| *Rhizosolenia* | 889 | 1837 | 1.9 | 205 | 308 | 1.2 | 1.4 | 3.0 | 2.3 | 0.3 | 0.5 | 1.5 |
| *Coscinodiscus* | 89 | 314 | 0.6 | 46 | 78 | 1.0 | 1.1 | 3.9 | 0.4 | 1.7 | 6.4 | 1.9 |
| *Odontella* | 1114 | 3617 | 1.0 | 2176 | 6160 | 1.2 | 0.6 | 0.9 | 1.4 | 1.7 | 6.1 | 1.1 |
| *Pleurosigma* | 63 | 191 | 1.0 | 680 | 1422 | 1.2 | 0.01 | 0.0 | 1.8 | 0.3 | 0.9 | 2.5 |
| *Lauderia* | 2762 | 10060 | 1.3 | 671 | 1588 | 1.3 | 7.4 | 26.9 | 2.5 | 1.8 | 4.2 | 2.0 |
| *Eucampia* | 26577 | 45075 | 3.5 | 16025 | 34299 | 2.8 | 2.8 | 8.9 | 2.6 | 0.7 | 1.4 | 2.1 |
| *Corethron* | 158 | 591 | 1.8 | 28 | 41 | 2.0 | 0.8 | 2.9 | 2.9 | 0.1 | 0.2 | 2.9 |
| *Protoperidinium* | 254 | 297 | 3.1 | 510 | 603 | 3.0 | 0.8 | 0.8 | 3.5 | 2.6 | 2.5 | 5.5 |
| *Gyrodinium* | 14 | 17 | 2.3 | 82 | 142 | 2.6 | 0.1 | 0.1 | 2.4 | 0.4 | 0.7 | 3.0 |
| *Gymnodinium* | 14 | 18 | 2.1 | 75 | 130 | 2.6 | 0.1 | 0.1 | 2.2 | 0.3 | 0.6 | 3.0 |
| *Scrippsiella* | 5 | 17 | 0.4 | 164 | 292 | 2.2 | 0.01 | 0.02 | 0.5 | 0.2 | 0.4 | 2.4 |
| *Dinophysis* | 15 | 31 | 1.9 | 15 | 20 | 1.8 | 0.4 | 2.1 | 2.1 | 0.4 | 0.9 | 1.9 |
| *Diplopsalis* | 1 | 4 | 0.3 | 70 | 125 | 2.4 | 0.01 | 0.03 | 0.3 | 0.4 | 0.7 | 2.5 |

**Table 6:** Abundance and biomass of micro-phytoplankton taxa at St. 18 (2002–2009). Mean, one standard deviation from the mean (Std), and index of relative importance (IRI, %) for the two periods of years during the upwelling season (spring-summer samplings).

California Current System, notably that of the Columbia River (Oregon), so that less wind forcing is necessary for their dispersal (Sobarzo et al., 2007). Altogether, a weak annual signal in stratification and macro-nutrients suggests that there are appropriate conditions for year-round dominance of microplanktonic diatoms in shelf waters and they do not explain the large annual changes in their abundance and biomass.

Seasonal changes in salinity in the upper layer may directly affect micro-phytoplankton community structure in this upwelling region if the tolerance levels to reduced salinity in the dominant diatom genera are low. However, the composition and biomass of the dominant diatom taxa at St. 18 with those at a station near the Itata River mouth were found to be similar during different seasons (Iriarte et al., 2012). In summary, it appears that other factors not included in this study, such as seasonal changes in water column light intensity, micro-nutrient availability (eg. iron), and/or in grazing pressure, may directly influence the observed strong annual variability in micro-phytoplankton community structure, whereas salinity and wind-driven upwelling are indirectly involved.

### 5.4.2. MECHANISMS BEHIND INTER-ANNUAL VARIABILITY IN MICRO-PHYTOPLANKTON COMMUNITY STRUCTURE

An intensification of wind-driven upwelling in the southern HCS region has been observed from 2002 to 2012 (Corredor-Acosta et al., 2015) and this condition has been related to an intensification of the Southeast Pacific Subtropical Anticyclone together with its shift towards the southwest (Ancapichún and Garcés-Vargas, 2015; Schneider et al., in press). At St. 18, a decrease in water column stratification and a cooling of the entire water column, together with an increase in the upper layer salinity onwards from 2007 has been observed (Schneider et al., in press). During the same period, a negative trend in meso-zooplankton biomass has been reported (Escribano et al., 2012), together with a significant change in its taxonomic and size composition from 2007 on (Medellín-Mora et al., 2016). Our findings confirm that there were significant environmental changes during the 2002–2009 time series, notably in terms of surface salinity, SST, and macronutrient ratios (Si/N and N/P), which were associated with changes in the micro-phytoplankton community structure at St. 18 during the productive season.

In the upper layer, lower salinity waters in the 2002–2006 period compared with the 2006–2009 period in the southern HCS can be related to pronounced reductions in precipitation and river discharge between 2007 and 2012, when 3 La Niña events occurred (Yévenes et al., 2015; Schneider et al., in press). Also, a decrease in silicate and a slight to moderate increase in nitrate during the last period were detected, resulting in a large reduction (up to 100%) of the mean Si/N ratios and an moderate increase of the mean N/P ratios (this study). An increase in nitrate levels during the period of study could be partly associated with an increase (from 2004 on) in the mean annual discharge of nitrogen in the local rivers through antrophogenic activity (Yévenes et al., 2015), which, in turn, would produce changes in the Si/N and N/P ratios of coastal waters. Changes in Si/N ratio associated with increasing nitrate loading from land to coastal waters, without large changes in Si, influence diatom growth dynamics and eventually can lead to Si-limitation (Gilpin et al., 2004). Thus, it is likely that the observed changes in both total and taxa-specific diatom biomass observed in the present study were stimulated by recent changes of the Si/N ratios in the coastal zone. At the same time, the dominance of different diatoms species in coastal waters may affect the ambient Si/ N ratios through differences in their uptake rates. For example, *Chaetoceros* and *Thalassiosira* species were found to have cellular Si/N ratio changing with the ambient Si/N ratio but their Si/N uptake ratios during the growth phase were found to be different, being almost constant at ~0.5 during exponential growth in the first case and an increase in it with higher ambient ratios in the latter (Kudo, 2003).

In our study, a change in the Si/N ratio between the two periods of years appears to have had a greater impact on some but not all the dominant diatom genera at St. 18. *Skeletonema* and *Leptocylindrus* exhibited the largest reduction in abundance (~82 and ~66% in terms of the central values, respectively) during the last period (2006–2009) whereas the impact on *Chaetoceros* and *Thalassiosira* was low. This decrease may be partly explained by differences in the physiological response of the dominant taxa to changes in Si-availability. For example, the cosmopolitan species *Skeletonema costatum* appears to be more sensitive to silicate deficit than other dominant taxa, such as *Chaetoceros* spp., but with severe silicate limitation they all can rapidly decrease in abundance (Harrison and Davis, 1979; Yamamoto and Tsuchiya, 1995; Nelson and Dortch, 1996). Climate-induced changes in total phytoplankton abundance but with different response patterns at the species level has also been observed in the NE Atlantic upwelling region (Bode et al., 2015), suggesting that quantifications of total community variations takes no account of the different species/genera responses.

In summary, the inter-annual changes in the microphytoplankton community in the southern HCS were mostly associated with changes in surface salinity and temperature (related to changes in upwelling intensity) but also with changes in Si/N and N/P, which relate to other land-derived processes. Under a scenario of a sustained increase in upwelling intensity in the coastal upwelling zone in this region, an increase in offshore transport of plankton and/or in water-column turbulence would negatively affect microphytoplankton biomass and total primary production on shelf areas of EBCSs (Lachkar and Gruber, 2012). However, reduction in river discharges and precipitation under colder conditions would decrease nutrient inputs to the coastal zone and, thus, negatively affect total microphytoplankton abundance and biomass in shelf waters. Nevertheless, the diatom genera *Chaetoceros*-*Skeletonema*-*Thalassiosira* are highly persistent components in the highly dynamic system of the southern HCS (Romero and Hebbeln, 2003; this study), other EBCs (Bode et al., 2015; Abrantes et al., 2016), and coastal zones (Carstensen et al., 2015), which implies that they have a rapid adaptability to changing environmental conditions.

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## 5.6. REFERENCES

Abrantes, F., Cermeño, P., Lopes, C., Romero, O., Matos, L., Van Iperen, J., Rufino, M., Magalhães, V., 2016. Diatoms Si uptake capacity drives carbon export in coastal upwelling systems. Biogeosciences 13, 4099–4109.

Anabalón, V., Morales, C.E., Escribano, H.R., Varas, M.A., 2007. The contribution of nano- and micro-planktonic assemblages in the surface layer (0–30 m) under different hydrographic conditions in the upwelling area off Concepción, central Chile. Prog. Oceanogr. 75, 396–414.

Anabalón, V., Arístegui, J., Morales, C.E., Andrade, I., Benavides, M., Correa-Ramirez, M.A., Espino, M., Ettahiri, O., Hormazabal, S., Makaoui, A., Montero, M.F., Orbi, A., 2014. The structure of planktonic communities under variable coastal upwelling conditions off Cape Ghir (31°N) in the Canary Current System (NW Africa). Prog. Oceanogr. 120, 320–339.

Ancapichún, S., Garcés-Vargas, J., 2015. Variability of the Southeast Pacific Subtropical Anticyclone and its impact on sea surface temperature off north- central Chile. Ciencias Marinas 41 (1), 1–20.

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth, UK.

Anderson, O.R., Nigrini, N., Boltovskoy, D., Takahashi, K., Swanberg, N., 2002. Class Polycystinea. In: Lee, J. (Ed.), An Illustrated Guide to the Protozoa, 2nd Protozoologists, Lawrence, Kansas, pp. 371–656.

Aslan, Z., Okçu, D., Kartal, S., 1997. Harmonic analysis of precipitation, pressure and temperature over Turkey II. Nuovo Cimento 20, 595–605.

Avaria, S., 1971. Variaciones mensuales del Fitoplancton de la bahía de Valparaíso, entre julio de 1963 y julio de 1966. Revista de Biología Marina (Valparaíso) 14 (3), 15–43.

Bakun, A., 1973. Coastal upwelling indices, west coast of North America, 1946–71. National Oceanic and Atmospheric Administration. Technical Report 671, 103 pp.

Bakun, B., Black, B.A., Bograd, S.J., García-Reyes, M., Miller, A.J., Rykaczewski, R.R.,Sydeman, W.J., 2015. Anticipated effects of climate change on coastal upwelling ecosystems. Curr. Climate Change Report 1, 85–93.

Bode, A., Estévez, M.G., Varela, M., Vilar, J.A., 2015. Annual trend patterns of phytoplankton species abundance belie homogeneous taxonomical group responses to climate in the NE Atlantic upwelling. Mar. Environ. Res. 110, 81– 92.

Böttjer, D., Morales, C.E., 2007. Nanoplanktonic assemblages in the upwelling area off Concepción (36°S), central Chile: abundance, biomass, and grazing potential during the annual cycle. Prog. Oceanogr. 75, 415–434.

Bowden, K.F., 1983. Physical oceanography of coastal waters. In: Ellis Horwood Series on Marine Science. John Wiley and Sons, New York, p. 302.

Carpenter, J.H., 1965. The Chesapeake Bay Institute technique for the Winkler dissolved oxygen method. Limnol. Oceanogr. 10, 141–143.

Carstensen, J., Kleis, R., Cloern, W., 2015. Phytoplankton blooms in estuarine and coastal waters: seasonal patterns and key species. Estuar. Coast. Shelf Sci. 162, 98–109.

Chrzanowski, T.H., Simek, K., 1990. Prey-size selection by freshwater flagellated Protozoa. Limnol. Oceanogr. 35 (7), 1429–1436.

Chavez, F.P., Messié, M., 2009. A comparison of eastern boundary upwelling systems. Prog. Oceanogr. 83, 80–96.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth, UK.

Collado-Fabbri, S., Vaulot, D., Ulloa, O., 2011. Structure and seasonal dynamics of the eukaryotic picophytoplankton community in a wind-driven coastal upwelling ecosystem. Limnol. Oceanogr. 56, 2334–2346.

Correa-Ramirez, M.A., Hormazabal, S., Morales, C.E., 2012. Spatial patterns of annual and interannual surface chlorophyll-a variability in the Peru-Chile Current System. Prog. Oceanogr. 92, 8–17.

Corredor-Acosta, J.A., Morales, C.E., Hormazabal, S., Andrade, I., Correa-Ramirez, M. A., 2015. Phytoplankton phenology in the coastal upwelling region off central- southern Chile (35°S–38°S): time-space variability, coupling to environmental factors, and sources of uncertainty in the estimates. J. Geophys., Oceans. http://dx.doi.org/10.1002 /2014JC010330.

Echevin, V., Aumont, O., Ledesma, J., Flores, G., 2008. The seasonal cycle of surface chlorophyll in the Peru upwelling system: a modelling study. Prog. Oceanogr. 79, 167–176.

Edler, L. (Ed.), 1979. Recommendations on methods for marine biological studies in the Baltic Sea. Phytoplankton and chlorophyll. The Baltic Marine Biologists Publications, vol. 5. University of Lund, Sweeden, pp. 1–38.

Escribano, R., Hidalgo, P., González, H.E., Giesecke, R., Riquelme-Bugueño, R., Manríquez, K., 2007. Seasonal and inter-annual variation of mesozooplankton in the coastal upwelling zone off central-southern Chile. Prog. Oceanogr. 75, 470–485.

Escribano, R., Morales, C.E., 2012. Spatial and temporal scales of variability in the coastal upwelling and coastal transition zones off central-southern Chile (35– 40S). Prog. Oceanogr. 92–95, 1–7.

Escribano, R., Hidalgo, P., Fuentes, M., Donoso, K., 2012. Zooplankton time series in the coastal zone off Chile: variation in upwelling and responses of the copepod community. Prog. Oceanogr. 97–100, 174–186.

García-Reyes, M., Sydeman, W.J., Schoeman, D.S., Rykaczewski, R.R., Black, B.A., Smit, A.J., Bograd, S.J., 2015. Under pressure: climate change, upwelling, and ecosystem boundary upwelling ecosystems. Front. Mar. Sci. 2, 109. http://dx. doi.org/10.3389 /fmars.2015.00109.

Gilpin, L.C., Davidson, K., Roberts, E., 2004. The influence of changes in nitrogen: silicon ratios on diatom growth dynamics. J. Sea Res. 51, 21–35.

González, H.E., Menschel, E., Aparicio, C., Barría, C., 2007. Spatial and temporal variability of microplankton and detritus, and their export to the shelf sediments in the upwelling area off Concepción, Chile (~36°S), during 2002– 2005. Prog. Oceanogr. 75, 435–451.

Harrison, P.J., Davis, C.O., 1979. The use of outdoor phyto-plankton continuous cultures to analyze factors influencing species selection. J. Exp. Mar. Biol. Ecol. 14, 19–23.

Holm-Hansen, O., Lorenzen, C.J., Holmes, R.W., Strickland, J.D.H., 1965. Fluorometric determination of chlorophyll. J. Conseil Int. pour l'Exploration de la Mer 30, 3– 15.

Holmes, R.M., Aminot, A., Kérouel, R., Hooker, B.A., Peterson, B.J., 1999. A simple and precise method for measuring ammonium in marine and freshwater ecosystems. Can. J. Fish. Aquat. Sci. 56 (10), 1801–1808.

Iriarte, J.L., Vargas, C.A., Tapia, F.J., Bermúdez, R., Urrutia, R.E., 2012. Primary production and plankton carbon biomass in a river-influenced upwelling area off Concepción, Chile. Prog. Oceanogr. 92–95, 97–109.

Jacobson, D.M., Andersen, R.A., 1994. The discovery of mixotrophy in photosynthetic species of Dinophysis (Dinophyceae): light and electron microscopical observations of food vacuoles in Dinophysis acuminata, D. norvegica and two heterotrophic dinophysoid dinoflagellates. Phycologia 33, 97–110.

Jeong, H.J., Yoo, Y.D., Kang, N.S., Rho, J.R., Seong, K.A., Park, J.W., Nam, G.S., Yih, W.H., 2010. Ecology of Gymnodinium aureolum. I. Feeding in western Korean water. Aquat. Microb. Ecol. 59, 239–255.

Kudo, I., 2003. Change in the uptake and cellular Si:N ratio in diatoms responding to the ambient Si:N ratio and growth phase. Mar. Biol. 143, 39–46.

Lachkar, Z., Gruber, N., 2012. A comparative study of biological production in eastern boundary upwelling systems using an artificial neural network. Biogeosciences 9, 293–308.

Lassiter, A.M., Wilkerson, F.P., Dugdale, R.C., Hogue, V.E., 2006. Phytoplankton assemblages in the CoOP-WEST coastal upwelling area. Deep-Sea Res. Part II 53, 3063–3077.

Leniz, B., Vargas, C., Ahumada, R., 2012. Characterization and comparison of microphytoplankton biomass in the lower reaches of the Biobío River and the adjacent coastal area off Central Chile during autumn-winter conditions. Latin Am. J. Aquat. Res. 40, 847–857.

Mackas, D., Strub, P.T., Thomas, A.C., Montecino, V., 2006. Eastern ocean boundaries pan-regional view. In: Robinson, A.R., Brink, K.H. (Eds.), The Sea. Harvard Press Ltd, Boston, pp. 21–60 (Chapter 2).

Medellín-Mora, J., Escribano, R., Schneider, W., 2016. Community response of zooplankton to oceanographic changes (2002–2012) in the central/southern upwelling system of Chile. Prog. Oceanogr. 142, 17–29.

Menden-Deuer, S., Lessard, E.J., 2000. Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. Limnol. Oceanogr. 45, 569–579.

Montero, P., Daneri, G., Cuevas, L.A., González, H.E., Jacob, B., Lizárraga, L., Menschel, E., 2007. Productivity cycles in the coastal upwelling area off Concepción: the importance of diatoms and bacterioplankton in the organic carbon flux. Prog. Oceanogr. 75, 518–530.

Morales, C.E., Anabalón, V., 2012. Phytoplankton biomass and microbial abundances during the spring upwelling season in the coastal area off Concepción, central-southern Chile: variability around a time series station. Prog. Oceanogr. 92, 81– 91.

Morales, C.E., Hormazabal, S., Andrade, I., Correa-Ramirez, M.A., 2013. Time-space variability of chlorophyll-a and associated physical variables within the region off Central-Southern Chile. Remote Sens. 5, 5550–5571.

Nelson, D.M., Dortch, Q., 1996. Silicic acid depletion and silicon limitation in the plume of the Mississipi River: evidence from kinetic studies in spring and summer. Mar. Ecol. Prog. Ser. 136, 163–178.

Ochoa, N., Taylor, M.H., Purca, S., Ramos, E., 2010. Intra- and interannual variability of nearshore phytoplankton biovolume and community changes in the northern Humboldt Current system. J. Plankton Res. 32, 843–855.

Rivera, P., 1968. Sinopsis de las diatomeas de la Bahía de Concepción, Chile. Gayana Botánica 18, 1–112.

Rivera, P., Arcos, D., 1975. Diatomeas más comunes en la desembocadura del Río Bío-Bío. Boletín de la Sociedad de Biología de Concepción 49, 223–230.

Rivera, P., Parra, O., González, M., Dellarossa, V., Orellana, M., 1982. Manual Taxonómico Del Fitoplancton De Aguas Continentales. IV. Bacillariophyceae. Editorial Universidad de Concepción, p. 97.

Romero, O., Hebbeln, D., 2003. Biogenic silica and diatom thanatocoenosis in surface sediments below the Peru-Chile Current: controlling mechanisms and relationship with productivity of surface waters. Mar. Micropaleontol. 48, 71– 90.

Saldías, G.S., Sobarzo, M., Largier, J., Moffat, C., Letelier, R., 2012. Seasonal variability of turbid river plumes off central Chile based on high-resolution MODIS imagery. Remote Sens. Environ. 123, 220–233.

Sanchez, G.E., Lange, C.B., González, H.E., Vargas, G., Muñoz, P., Cisternas, C., Pantoja, S., 2012. Siliceous microorganisms in the upwelling center off Concepción, Chile (36°S): preservation in surface sediments and downcore fluctuations during the past ~150 years. Prog. Oceanogr. 92–95, 50–65.

Schneider, W., Donoso, D., Garcés-Vargas, J., Escribano, R., 2016. Water-column cooling and sea surface salinity increase in the upwelling region off central Chile driven by a pole-ward displacement of the South Pacific High. Progr. Oceanogr. (in press).

Sobarzo, M., Bravo, L., Donoso, D., Garcés-Vargas, J., Schneider, W., 2007. Coastal upwelling and seasonal cycles that influence the water column over the continental shelf off central Chile. Prog. Oceanogr. 75, 363–383.

Stoecker, D.K., Gustafson, D.E., Verity, P.G., 1996. Micro- and mesoprotozooplankton at 140°W in the equatorial Pacific: heterotrophs and mixotrophs. Aquat. Microbiol. Ecol. 10, 273–282.

Strathmann, R.R., 1967. Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. Limnol. Oceanogr. 12, 411–418.

Strickland, J.D., Parsons, T.R., 1972. A practical handbook of seawater analysis. Bulletin of the Fisheries Research Board, Canada 167, 310 pp.

Sun, J., Lui, D., 2003. Geometric models for calculating cell biovolume and surface area for phytoplankton. J. Plankton Res. 25, 1331–1346.

Sydeman, W.J., García-Reyes, M., Schoeman, D.S., Rykaczewski, R.R., Thompson, S.A., Black, B.A., Bograd, S.J., 2014. Climate change and wind intensification in coastal upwelling ecosystems. Science 345, 77–80.

Taylor, F.J.R., Fukuyo, Y., Larsen, J. 1995. Taxonomy of harmful dinoflagellates. In: Hallegraeff, G.M., Anderson, D.M. and Cembella, A.D. (Eds.), Manual on Harmful Marine Microalgae, IOC Manuals and Guides No. 33. UNESCO (France), 283–317.

Thomas, A.C., Brickley, P., Weatherbee, R., 2009. Inter-annual variability in chlorophyll concentrations in the Humboldt and California Current Systems. Prog. Oceanogr. 83, 386–392.

Thomas, A.C., Ted Strub, P., Weatherbee, R.A., James, C., 2012. Satellite views of Pacific chlorophyll variability: comparisons to physical variability, local versus nonlocal influences and links to climate indices. Deep Sea Res. Part II 77–80, 99– 116.

Tilstone, G.H., Míguez, B.M., Figueiras, F.G., Fermin, E.G., 2000. Diatom dynamics in a coastal ecosystem affected by upwelling: coupling between species succession, circulation and biogeochemical processes. Mar. Ecol. Prog. Ser. 205, 23–41.

Tomas, C.R., 1997. Identifying Marine Phytoplankton. Academic Press, New York, p. 858.

Wilkerson, F.P., Dugdale, R.C., Kudela, R.M., Chavez, F.P., 2000. Biomass and productivity in Monterey Bay, California: contribution of the large phytoplankton. Deep-Sea Res. Part II 47, 1003–1022.

Yamamoto, T., Tsuchiya, H., 1995. Physiological response of Si-limited Skeletonema costatum to silicate supply with salinity decrease. Bull. Plankton Soc. Japan 42, 1–17.

Yévenes, M., Figueroa, R., Parra, O., Farias, L., 2015. Inter-annual variability of dissolved inorganic nitrogen in the Biobío River, Central Chile: an analysis base on a decadal database along with 1-D reactive transport modeling. Hydrol. Earth Syst. Sci. – Discussion 12, 705–738.

Yuras, G., Ulloa, O., Hormazabal, S., 2005. On the annual cycle of coastal and open ocean satellite chlorophyll off Chile (18–40°S). Geophys. Res. Lett. 32, L23604. http://dx.doi.org/10.1029/2005GL023946.

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*Mira profundamente dentro de la naturaleza*
*y entonces comprenderás todo mejor*
***Einstein***

# CHAPTER 4

## 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)

Carmen E. Morales, **Valeria Anabalón,** Joaquim P. Bento, Samuel Hormazabal,
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# CHAPTER

# 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.

## 6.1. 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 and 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 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 and 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 physical-biological 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 (~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 and McTaggart, 2010; Thomsen et al., 2016). Off Punta Lavapié (~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., 2001).

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 (~36– 37°S).

## 6. 2. METHODS

### 6.2.1 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°S and 72-76°W (Fig. 1a) were obtained from the Climate Forecasting System (CFSv2) [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 bulk algorithm COARE-v3.0 (COARE) [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 PM) observations of SST were obtained from the Multiscale 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].

### 6.2.2. 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.uibcsic.es/users emason/py-eddytracker) [Mason et al., 2014], based on previously described procedures for the detection of closed contours of sea level anomaly [Penven et al., 2005; Chelton et al., 2011; Kurian et al., 2011].

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 1cm 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 to 150 cm), radius (0.35-4.46°), and number of local extremes (limited to 1). In order to detect the birth-time of the specific eddy analyzed in this study, we skipped the shape test, which is usually performed to filter out highly irregular closed contours.

### 6.2.3. 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 (Fig. 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.bbemoldaenke.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 months (plankton) after the cruise. Nutrient samples were stored at -20°C in 60-mL aseptic, high-density polyethylene flasks, and the analyses (Autoanalyzer) were done within 2-3 months after the survey, following standard protocols [Atlas et al., 1971]. Chl-a samples were filtered (GF/F filters) for both total and size fractions (<20 and <3 µm); 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 micro-planktonic organisms. For pico-plankton (<3 µm), 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 Ion-Argon Laser) following standard protocols [Marie et al., 2000]. Autotrophic picoplankton (*Prochlorococcus*, *Synechococcus*, and pico-eukaryotes) 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 µm, latex beads ($10^{5}$ mL beads mL $^{-1}$) was added as an internal standard (Polyscience Inc).

Nanoplankton samples were collected (50 mL centrifuge tubes) and immediately fixed 9 with a buffer of paraformaldehyde (1% final conc.), after which they were stored in cold (5°C) and darkness until further processing in the lab. Samples were stained with a mixture of DAPI (4,6-diamidino-2-phenylindole) and Proflavine (3–6 diaminoacridine hemi-sulfate) at a final concentration of 5 µg mL$^{-1}$ [Verity and Sieracki, 1993]. After this, samples were vacuum-filtered onto black polycarbonate membrane filters (0.6 µm 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; 1000x; UV, blue, and green filters). Counting included at least 100 cells of the most dominant groups in each sample (e.g. nano-flagellates, nano-dinoflagellates, nano-diatoms, and nano-ciliates).

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 [González et al., 2007;

Anabalón et al., 2016]. 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, 1969; Rivera, 1985; Rivera and Valdebenito, 1979].

Nano and micro-phytoplankton 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 and Bratbak, 1987], diatoms [Strathmann, 1967], and thecate-athecate dinoflagellates [Edler, 1979; Menden-Deuer and 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 pico-plankton C-biomass were 171 fg C cell-1 for *Synechococcus* [Grob et al., 2007] and 2.0 pg Ccell$^{-1}$ for pico-eukaryotes [Zubkov et al., 2000].

## 6.3. RESULTS AND DISCUSSION

### 6. 3.1. WIND-FORCING AND SATELLITE SST SHORT-TERM VARIABILITY (JANUARY-FEBRUARY 2014)

Mean daily alongshore WS during the time series (Fig. 1b), calculated for a fixed-point close to the middle of the northern transect (Fig. 1a), indicated the occurrence of two relatively strong coastal upwelling events (>0.2 N $m^{-2}$ for >5 d) during the first half of January (2-15) and another during the third week in February (19-23). A non-upwelling or wind relaxation event (<0.1 N $m^{-2}$), 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 (Fig.1c), calculated for three fixed points (Fig. 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 (Fig. 2) reflected the occurrence of a strong upwelling event (>0.3 N $m^{-2}$) 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

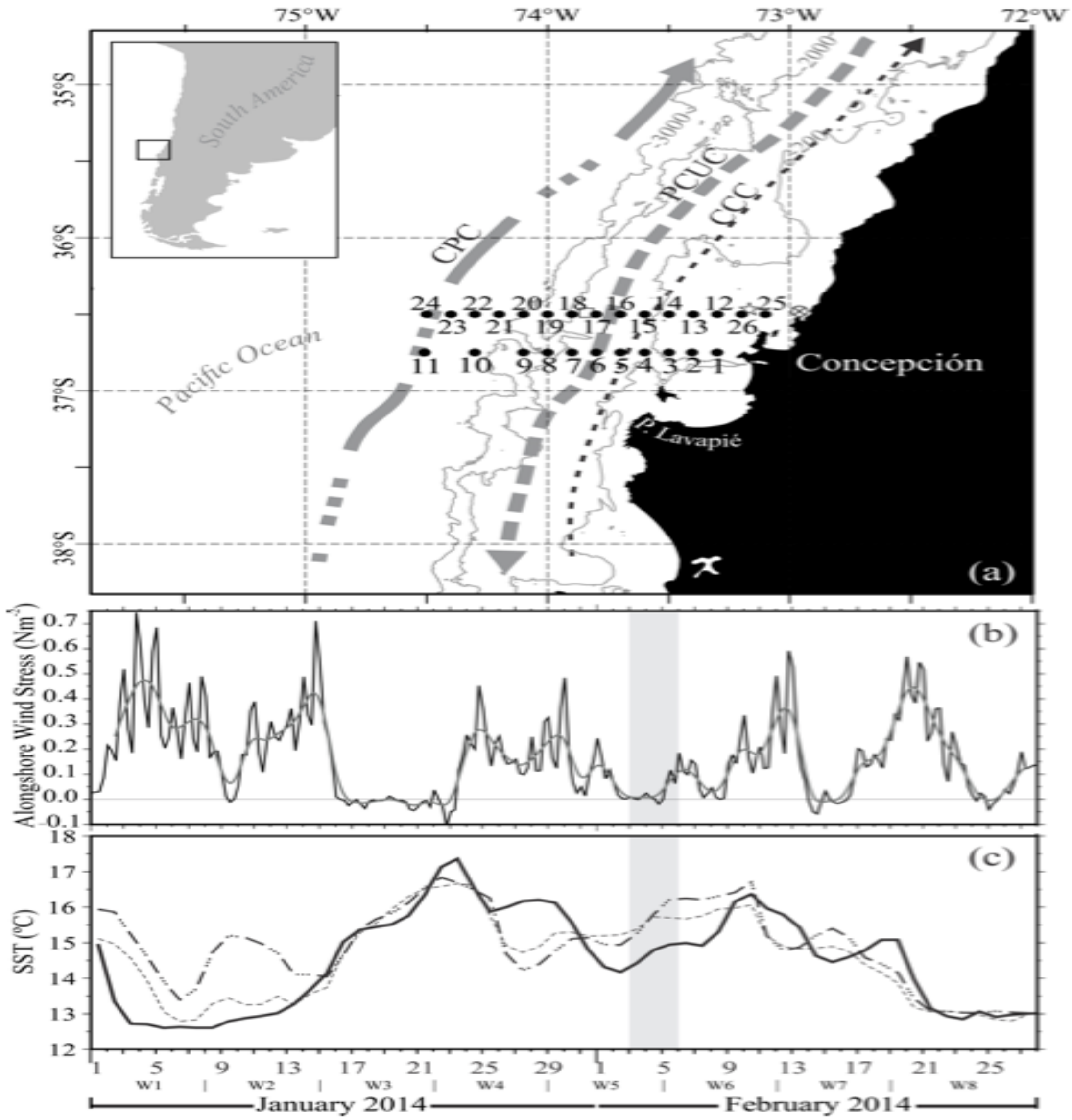

**Figure 1**. Region of study off central-southern Chile (a), for which satellite time series (January-February, 2014) were analyzed and within which the PHYTO-FRONT survey (black dots: sampling stations) was undertaken (3-6 February, 2014), and fixed-point time series data of daily WS (b) and SST (c). 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 b) represent a single position (blank square between St. 17 and 18 in a) for WS values (black line: 6-hourly data; grey line, data filtered with a low-pass Godin-type filer). Data in c) 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 b) and c), the grey bar denotes the survey time; W1 to W8 (bottom axis) represent the weeks covered by the satellite time series and used in the calculation of weekly means of WS and WSC (Fig. 2).

section (36-38°S), whereas mean conditions during W3, W5, and W8 represented wind relaxation events. The mean weekly WSC spatial distribution (Fig. 2) indicated strongly negative values (cyclonic; Ekman pumping) along the coast 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 and Muñoz, 2005].

The spatio-temporal distribution of daily MUR-SST in the region of study (Fig. 3, only for the initial dates of each week in Fig. 1) was highly variable during January-February 2014. 12 Colder waters (13.5-16°C) were found near the coast most of the time, except on Jan. 22 when the most prolonged wind relaxation event (7 d) in the time series took place. Cold waters occasionally extended further offshore (8 and 15 Jan), 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 non-upwelling activity (16-23 Jan.). It displayed a fairly irregular spatial pattern and it migrated further offshore (>100 km from the coast) during strong coastal upwelling (8 and 15 Jan.). Previous results in the same region have shown the satellite SST distribution changing from <14°C near the coast to

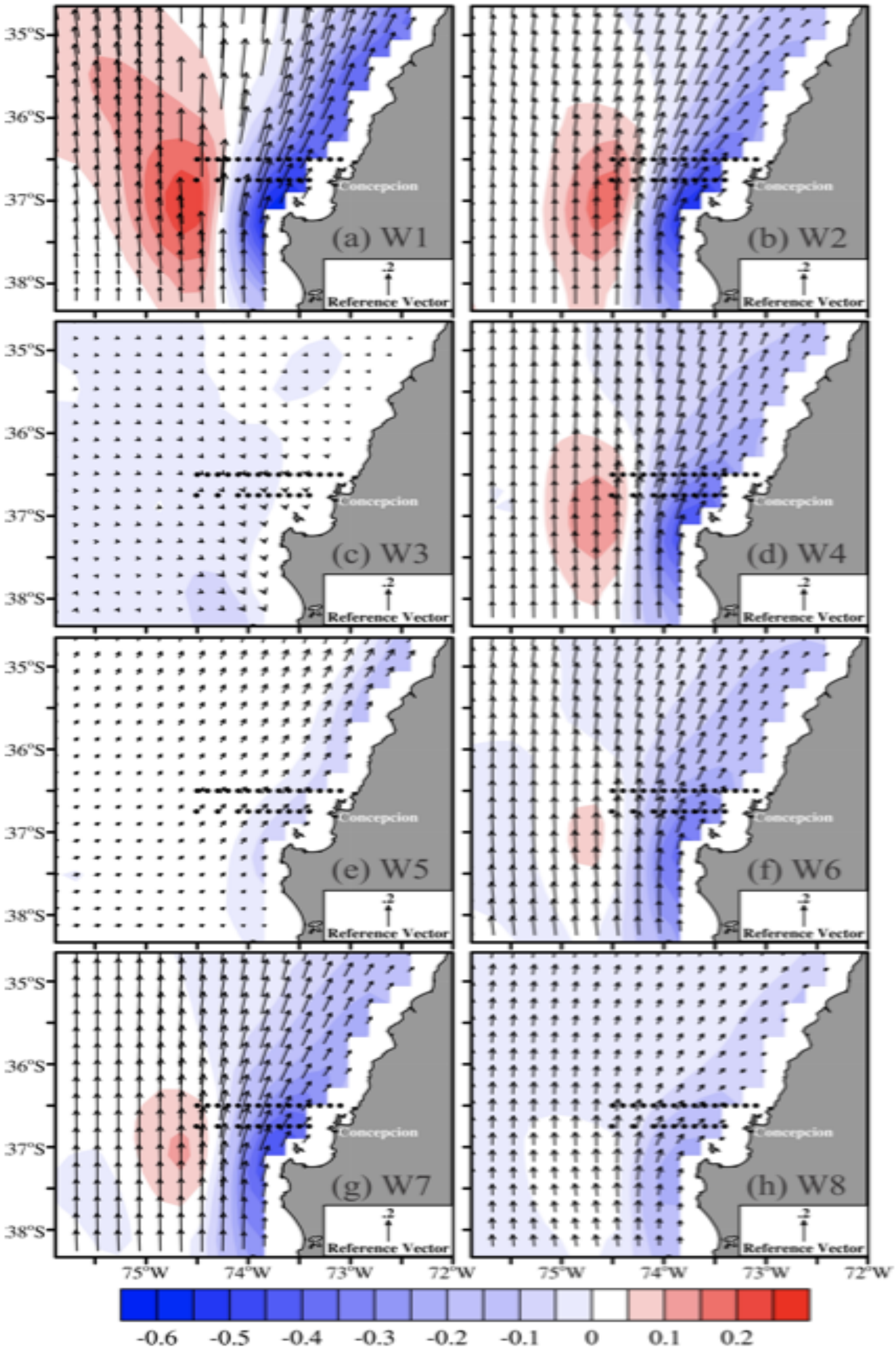

**Figure 2.** Weekly means (W1 to W8) of wind stress direction and magnitude (arrows; N m$^{-2}$) and wind stress curl magnitude (colour bar; $10^{-7}$N m$^{-3}$) data series (January-February, 2014) for the region of study. The images on weeks W5 and W6 cover the survey period (see Fig.1c).

>17°C in offshore zones in summer, separated by a frontal zone located, on average, at ~50-80 km from the coast [Letelier et al., 2009]. SST synoptic variability in the EBCS region of 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 intra-seasonal SST variability could also be influenced by remote forcing [Hormazabal et al., 2001; Renault et al., 2009; Dewitte et al., 2011; Gubanova et al., 2013].

### 6. 3.2. Eddy activity in the PHYTO-FRONT survey area

Satellite altimetry data (Fig. 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 13 generated in summer [Letelier et al., 2009; Morales et al., 2012; Hormazabal et al., 2013]. The detected eddy was relatively weak (EKE < 0.10 $m^{2} s^{-2}$) 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 $m^{2} s^{-2}$) to strong during the second half (~0.40 - 0.60$m^{2}s^{-2}$). At the end of January, the influence of the detected eddy on SSTsubmesoscale variability was clear, generating transport and mixing of cold coastal waters and offshore warmer CTZ waters.

During the short-term survey (3-6 Feb. 2014), satellite altimetry and MUR-SST data indicated that the two sampling transects were distributed in a transitional area including coastal, frontal, and eddy zones (Fig. 3, panels to the right). Also, a progressive intrusion of warm waters towards the coast took place from Feb. 2 to Feb. 6, consistent with the fact that the survey was carried out during a wind relaxation event preceded by moderate upwelling (Fig. 2d-e). 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 Feb.), but were closer to the eddy center in the northern transect (5-6 Feb.). At this time, the eddy center was located ~200 km from the coast, had an approximate diameter of ~160-180 km, and was moving at ~1.9 km $d^{-1}$. 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 towards the coast, whereas in the northern section, the offshore advection of coastal waters by the eddy contributed to extend FRN-1 further 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 14 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 and 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 ~1 month, and that it contributed to localized exchanges of

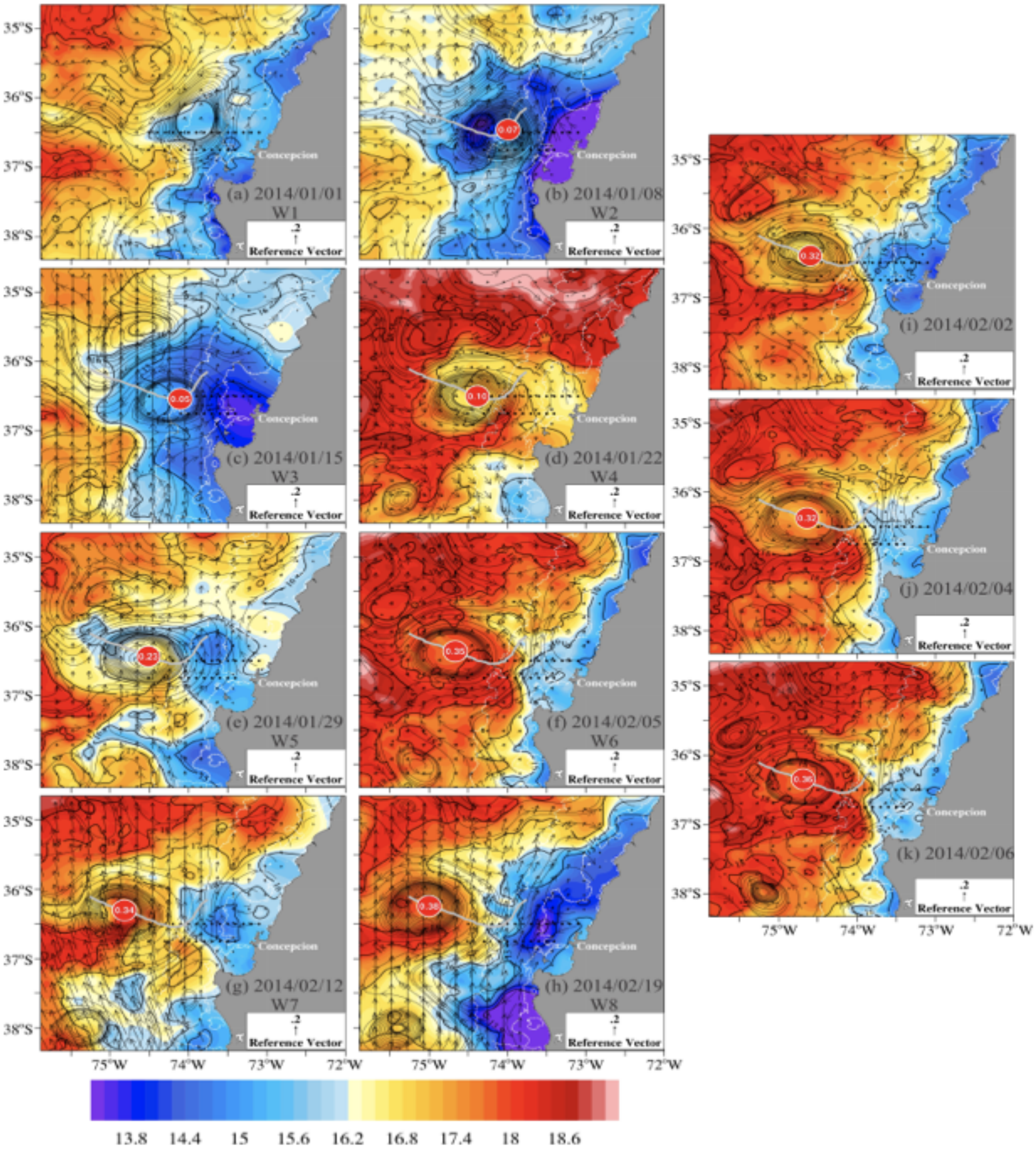

**Figure 3.** Daily satellite MUR-SST (color and thick lines) and altimetry (thin lines) data series (January-February, 2014) for the region of study. Selected images are shown for the first date in each week (W1 to W8; left and central panels: a-h) and for the dates just previous to the cruise, during it, and at its end (right panels: 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, $m^2 s^{-2}$).

water properties between coastal and CTZ waters.

### 6.3.3. 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 (Fig. 4). Temperature, salinity, and DO displayed a characteristic trend of shallower isolines towards 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 [Letelier et al., 2009; Hormazabal et al., 2013], with values characteristic of the Equatorial Subsurface waters (ESSW) [Strub et al., 1998; Silva et al., 2009; Llanillo et al., 2012]. On both transects, FR-1 was distinguishable by a SST gradient (0.12 and 0.22°C km$^{-1}$ in the northern and southern transects, respectively) but also by a surface salinity gradient (0.02 and -0.06 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 ~70 - 100 km from the coast during the survey (Sts. 6 to 7, and 16 to 18, respectively). The thermal gradient was distributed in the upper ~50 m depth whereas the salinity gradient reached ~75 m depth. In the same region, thermal fronts with similar gradients (~0.1-0.25°C km$^{-1}$) 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 (Fig. 4a-b) displayed strong vertical oscillations (amplitude of ~100 m in the northern section and ~50 m in the southern section), together with the presence of isolated subsurface (150-250 m depth) high salinity cores

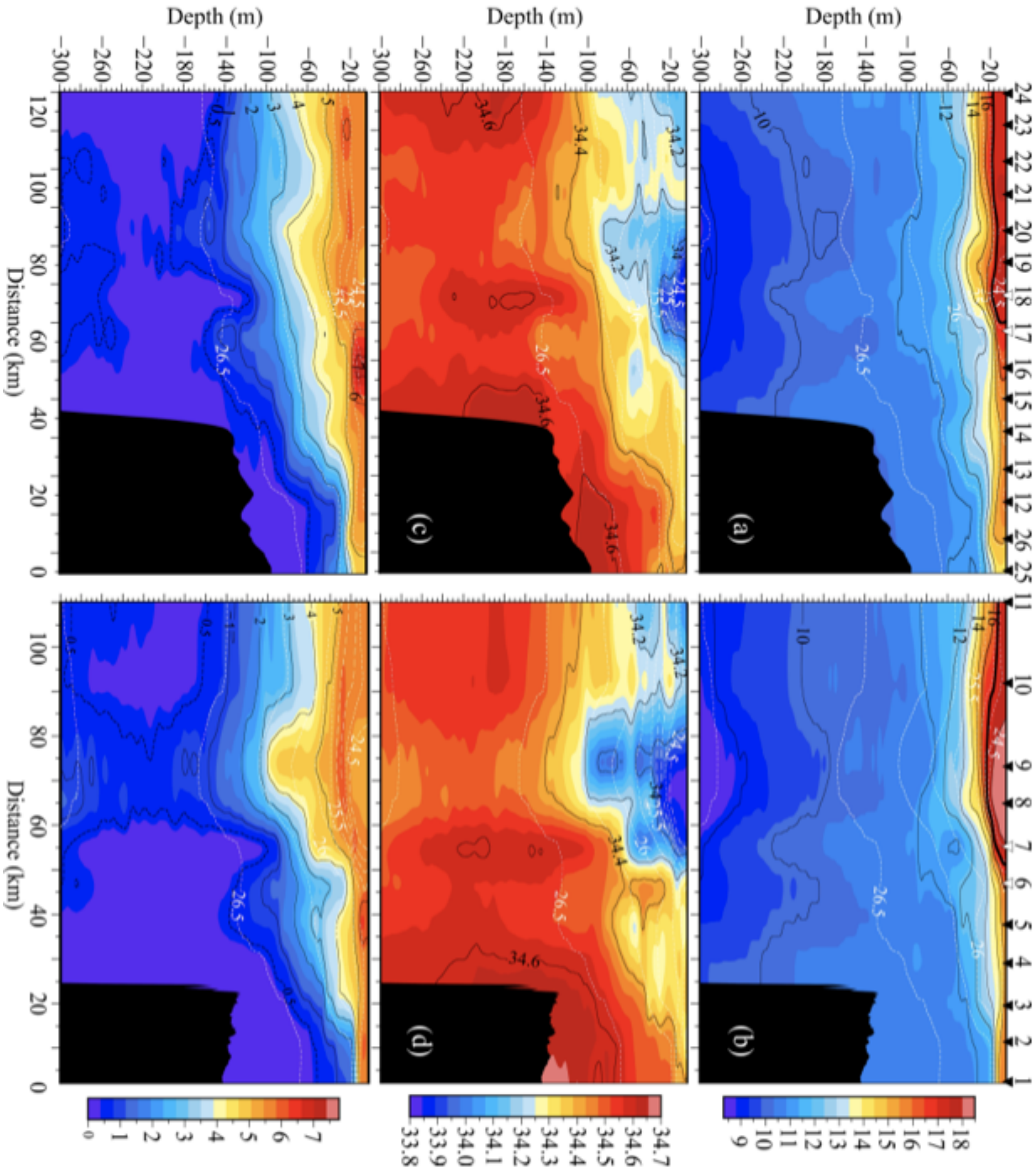

**Figure 4.** Spatial distribution of oceanographic variables (0-300 m depth) during the PHYTO-FRONT survey. Temperature (°C; a-b), salinity (c-d), and DO (mL $L^{-1}$; e-f) in the northern (left panels) and southern (right panels) transects. Isopycnals are also included in all the graphs (white dashed lines). The 17°C isotherm (a-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).

(>34.55) and steep up-lifting of the 34.2 isohaline (Fig. 4c-d); submesoscale changes in subsurface DO were also observed (Fig. 4e-f). 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 [Letelier et al., 2009; Hormazabal et al., 2013], 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 (Fig. 4), probably explained by the fact that the most offshore sampling stations were nearer to the eddy-center in the first case and towards its border or periphery in the second case (Fig. 3f).

Additional isolated, subsurface, higher salinity - low DO cores (Fig. 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 this area, 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 these waters from offshore and along the southern border of ITE-1 and/or to the advection from the south of SAAW along the coast  Off Concepción, these processes have been linked to the presence of a meandering coastal jet, associated with the frontal zone (inshore border) and eddies (offshore border), which is subjected to a strong offshore deflection north of P. Lavapié [Letelier et al., 2009], thereby generating instabilities in the water column.

### 6.3.4. 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 (Fig. 5a-b) and silicate or silicic acid (Fig. 5 c-d) concentrations in the subsurface layer, a characteristic of the ESSW [Llanillo et al., 2012], reached a shallower depth (~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 (Fig. 5a-d).

The ratios between nitrogen (nitrate + nitrite) and silicate (N: Si) were clearly distinct in coastal waters and most of the CTZ (Fig. 5e-f), 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 [Silva et al., 2009; Llanillo et al., 2012]. 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) towards the north, based also on SST (Fig. 3e- f) and salinity distributions (Fig.4c-d).

High N/Si ratios (>2:1) have been previously detected in the upwelling waters of the equatorial Pacific [Raimbault et al., 1999; Leynaert et al., 2001] 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]. In contrast, values close to 1:1 have been described for the coastal upwelling zone off central Chile [Goméz et al., 2007], though interannual variation at a shelf station off Concepción (St. 18; Fig. 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 the region [Anabalón et al., 2016].

High N/Si ratios can arise from differences in the relative rates at which silica and organic matter are recycled in the upper layer of a given region. In this context, the concept of a “silica pump” has been applied to describe a condition of Si-limitation in the coastal upwelling system off Peru and in the equatorial upwelling in the Pacific Ocean, and which sets the extent of the new production capacity in these systems. Such condition 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 [Dugdale et al., 1995; Dugdale and Wilkerson, 1998; Raimbault et al., 1999; Brzezinski et al., 2003].

The silica pump is also known to occur in 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 towards lower latitudes by the Antarctic Intermediate Water (AAIW) and the Subantarctic Mode Water (SAMW), the latter providing nutrients to the thermocline or lower latitudes in the southern hemisphere [Sarmiento et al.,

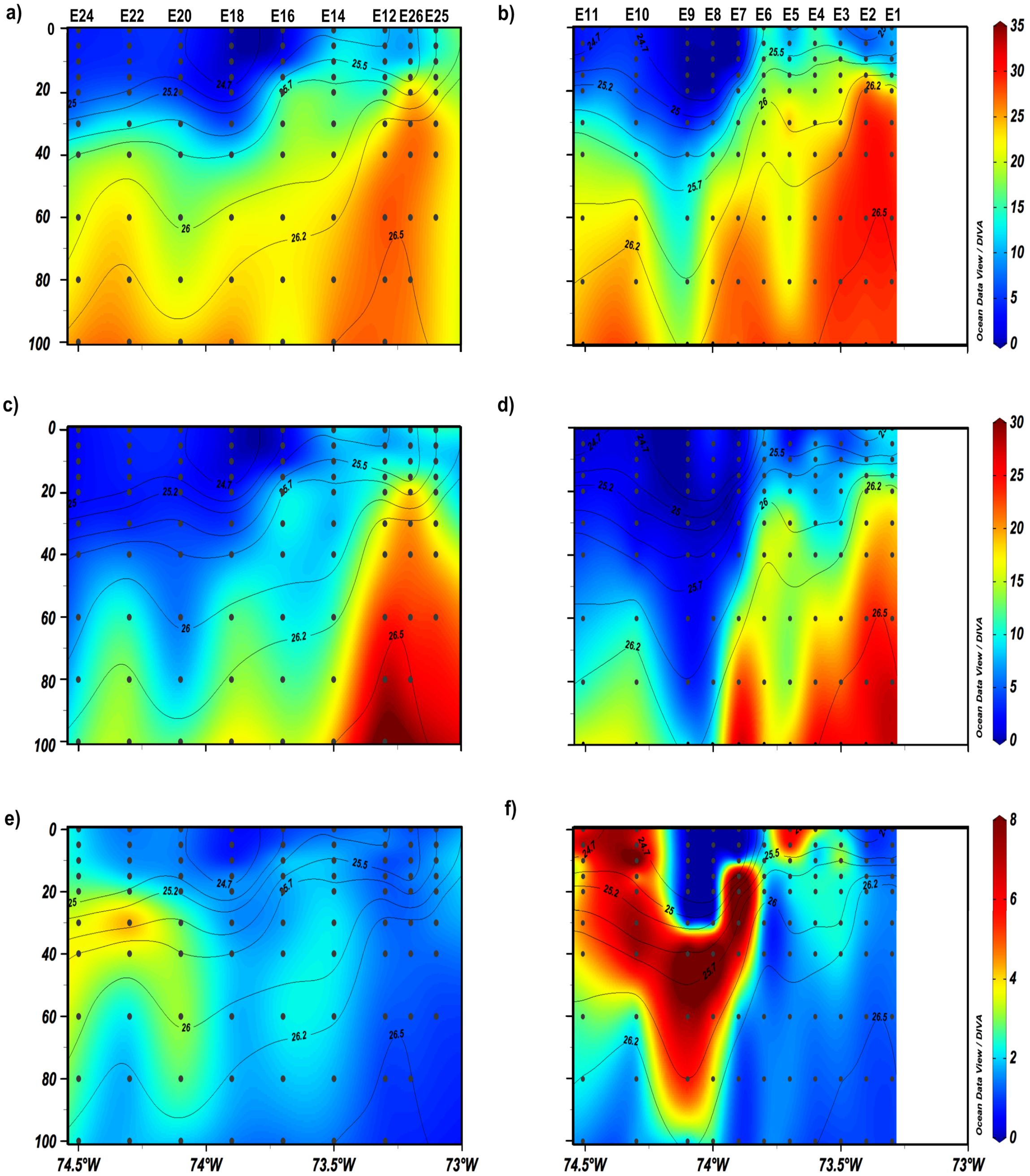

**Figure 5.** Spatial distribution of macro-nutrient concentrations (µM) in the upper 100 m layer during the PHYTO-FRONT survey. Profiles of a) nitrate + nitrite (N), b) silicate, and c) N/Si proportion in the northern (left panels) and southern (right panels) transects. The black lines correspond to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

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 [Gilpin et al., 2004; Davidson et al., 2012]. 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 and 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 [Gilpin et al., 2004; Davidson et al., 2012]. For the region of study, however, knowledge on phytoplankton nutrient requirements and nutrient uptake rates under different nutrient levels is scarce.

### 6.3.5. Phytoplankton community structure in the coastal zone and CTZ

Satellite surface Chl-a during the January-February 2014 time series (Fig. 6) was highest (>3 mg $m^{-3}$) in the coastal band, mostly to the north of 37°S, and patches of mostly moderate Chl-a concentration (1-2 mg $m^{-3}$) 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; Morales et al., 2007; Letelier et al., 2009]. In particular, the borders of the identified ITE-1 displayed higher Chl-a concentration during most part of the time series (~1.5 months; Fig. 6a-g). 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 towards the coast of very low Chl-a values (Fig. 6f); this intrusion persisted for >1 month (W4 to W8; Fig. 6d-h) 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 towards ITE-1 during W6 to W8 (Fig. 6 f-h).

During the survey, FluoroProbe-derived in vivo fluorescence profiles (0-60 m depth; Fig.7a-b) indicated that the highest Chl-a values (>5 mg m$^{-3}$) were concentrated in the surface layer at the eastern (onshore) side of FR-1 (Sts. 5 and 16) and in the subsurface layer (20-40m depth) between FR-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$^{-3}$). A similar pattern was exhibited by extracted Chl-a samples obtained from discrete fluorometric measurements in the upper 100m layer; Fig. 7c-d). The magnitudes of the in vivo 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 (Fig. 6f) and in situ Chl-a data (Fig. 7a-d) presented a similar distribution, especially in the area of high values at FRN-1.

Phytoplankton size structure during the survey (Fig. 7e-f) 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 micro-planktonic Chl-a fraction was highly variable along both transects but was maximum (~40-70%) at FR-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

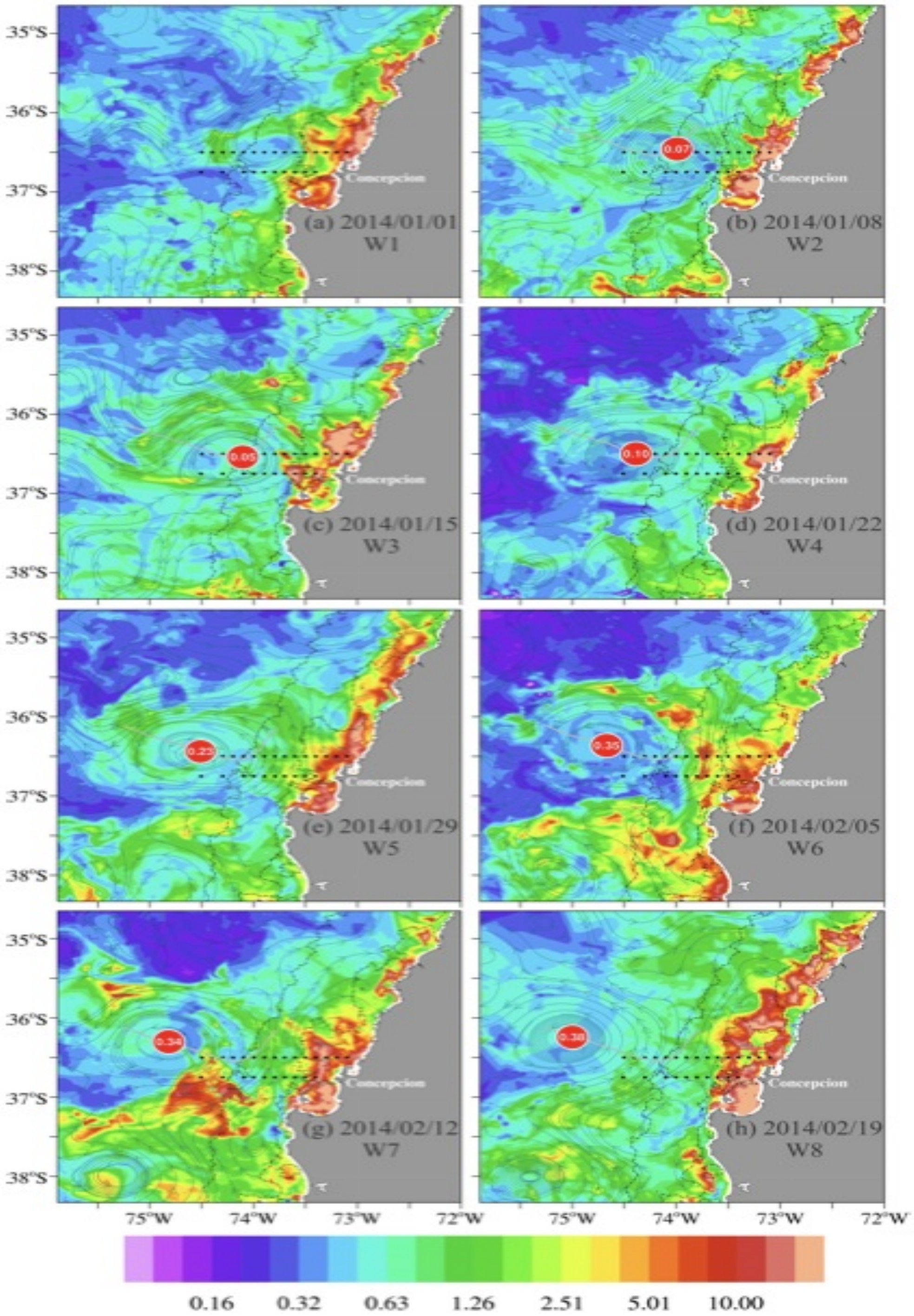

**Figure 6.** MODIS daily satellite Chl-a (mg $m^{-3}$; colour scale; 1 km resolution) and altimetry (lines) data in the region of study during selected dates (as in Fig. 3 for SST) in the January-February 2014 period. Red dot: central position of ITE-1; gray lines: ITE-1 trajectory.

pattern for this upwelling zone [Anabalón et al., 2016]. The pico-planktonic 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 micro-planktonic fraction.

In terms of phytoplankton C-biomass by size fraction (Fig. 8), a very similar pattern of distribution compared to that of Chl-a fractions (Fig. 7e-f) was found, with primary maxima (>40 mg C $m^{-3}$ ) for both the micro- and nanoplankton in the surface layer at FR-1 and secondary maxima (>20 mg C $m^{-3}$) in the subsurface layer (20-40 m depth) of the CTZ. In the coastal zone, secondary maxima in C-biomass were contributed by the nano-plankton (Fig. 8c-d) and the picoplankton (Fig. 8e-f). 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 micro-planktonic 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 that study took place during upwelling favorable conditions.

Localized patches of higher microplankton biomass in the inshore (Sts. 1 and 25; Fig. 8a-b) were contributed by dinoflagellates (~10 mg C $m^{-3}$) 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 surface waters of the FRN-1 area (Sts. 5 and 16: 25-70 mg C $m^{-3}$ ) and subsurface waters of the ITE-1 area (Sts. 10-11 and 20-24; 10-15 mg C $m^{-3}$ ). In the rest of the area or layers the microdinoflagellates were dominant (southern transect) or presented similar contributions as the micro-diatoms (northern transect). These results reveal the importance of dinoflagellates in CTZ waters of this region and their relative

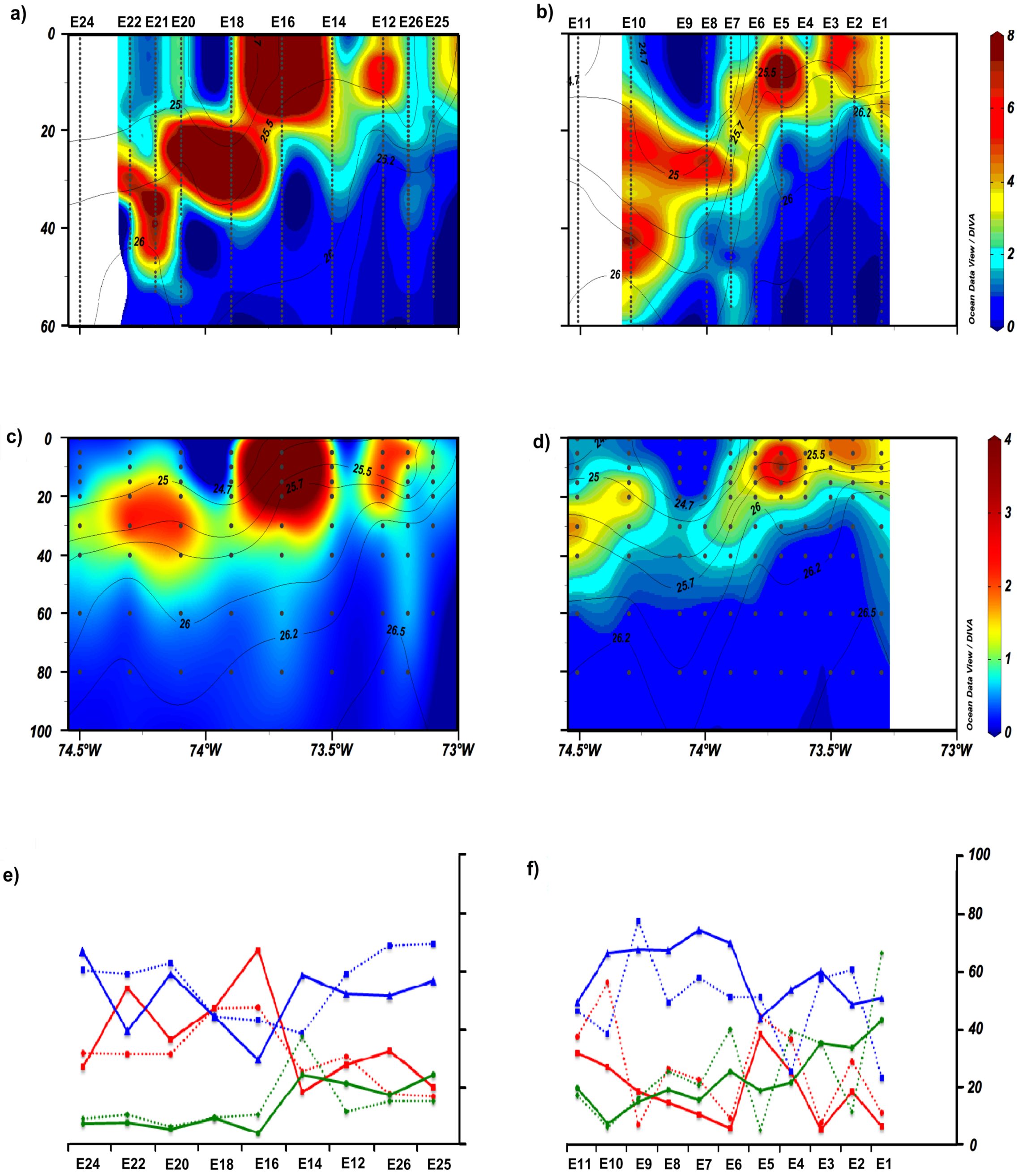

**Figure 7.** Chl-a concentration (mg m$^{-3}$) in the upper layer during the PHYTO-FRONT survey. Profiles of total Chl-a (in vivo fluorescence) obtained from the (a and b) FluoroProbe and from (c and d) extracted samples, together with the contribution of different Chl-a size fractions to (e and f) 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.

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 nano-phytoplankton was largely dominated by nanoflagellates in both transects (70-100%), as previously reported for the region of study [Böttjer and Morales, 2007; Morales and Anabalón, 2012]. In the pico-phytoplankton, *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 pico-eukaryotes 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 FRN-1 but pico-eukaryotes dominated in the ITE-1 area (Sts 20-24).

Phytoplankton dominance by micro-diatoms in coastal waters during the upwelling season in the region off Concepción has been found in monthly time-series studies [Gonzalez et al., 2007; Anabalón et al., 2016], however, nano-phytoplankton maxima also appear during the upwelling period in the coastal zone [Böttjer and Morales, 2007]. The lack of both microplankton Chl-a and micro-diatom dominance in coastal waters probably is the result of the wind relaxation event that characterized the PHYTO-FRONT survey (Fig. 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 to 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, macro-nutrient levels in surface waters of the coastal zone during the PHYTO-FRONT survey (Fig. 5a-d) were not depleted, as it was the case in the

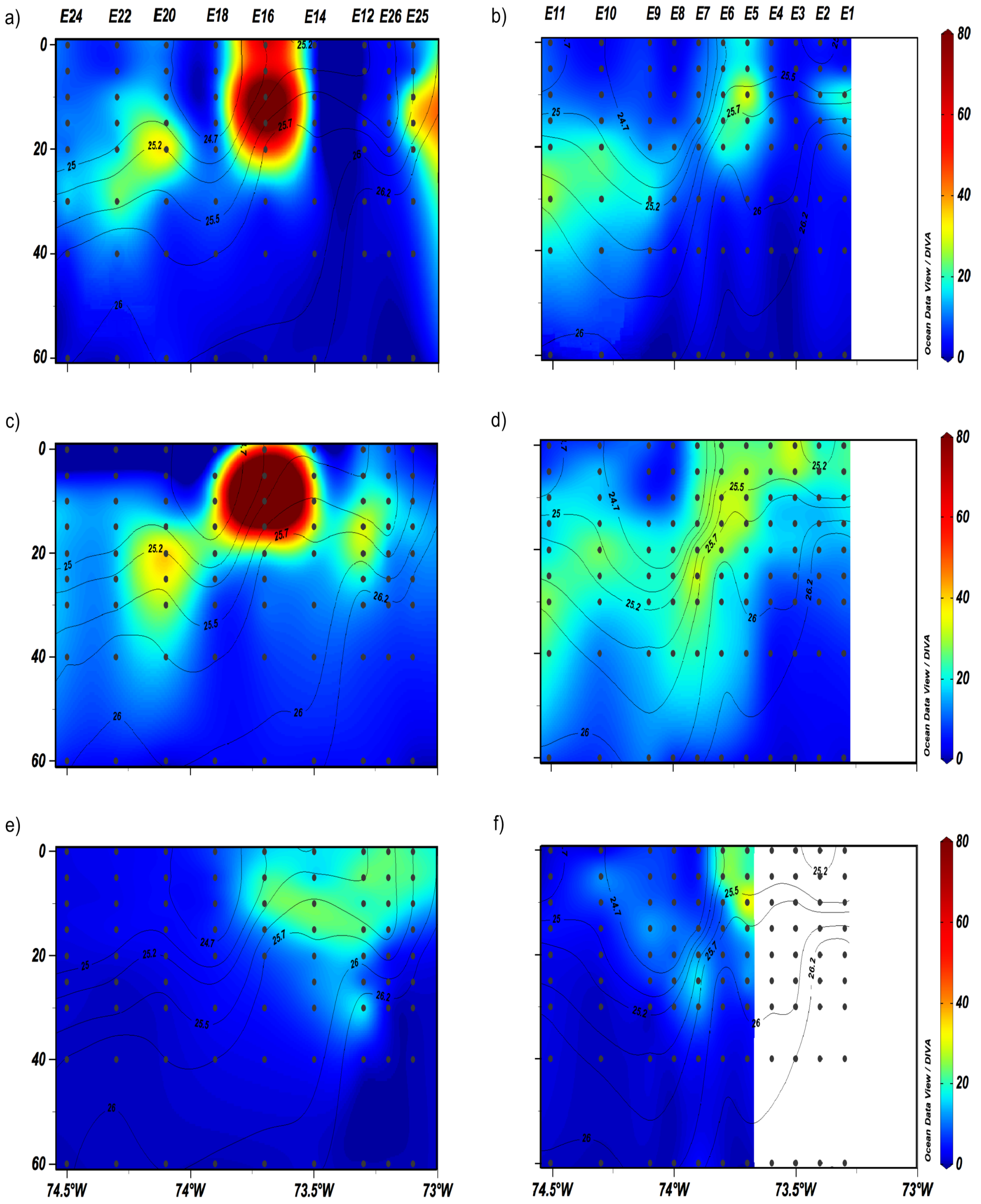

**Figure 8.** Phytoplankton C-biomass (mg C m$^{-3}$) in each size fraction in the upper layer (0-60m depth) during the PHYTO-FRONT survey. Profiles for the micro-phytoplankton (a-b), nano-phytoplankton (c-d), and the pico-phytoplankton biomass (e-f) in the northern (left panels) and southern (right panels) transects. The black lines correspond to isopycnals.

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; Nagai et al., 2012; Morales et al., 2012; Krause et al., 2015]. In the case of ITEs, their surface layer act as surface cyclonic eddies, pumping waters upwards at its center; therefore, both type of eddies can stimulate increases in biological production in this and other EBCS [Morales et al., 2012; Chenillat et al., 2015]. 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” [Lathuilière et al., 2010; Gruber et al., 2011], 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”.

### 6. 3.6. CROSS-SHORE DISTRIBUTION OF DIATOM TAXA

The distribution of different micro-planktonic diatom species along the cross-shore transects, as well as of total micro-dinoflagellates, was evaluated in terms of abundance (Fig.9). Diatom abundances were around one order of magnitude higher (>1,000 * $10^6$ cells m$^{-2}$) in the FRN-1 (Sts. 6 and 16) and ITE-1 zones than in the coastal zone, where their contributions were similar to those of autotrophic/mixotrophic dinoflagellates (Fig. 9a and 9b). Among the numerically dominant diatom species (>100 x 10$^{6}$ cells m$^{-2}$ at any station), the centric and chain-forming *Skeletonema* sp., *Chaetoceros debilis*, and *Thalassiosira anguste-lineata* (Fig. 9c-d) are usually found in the coastal waters of the region of study [González et al., 2007; Sánchez et al., 2012; Anabalón et al., 2016]. 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* (Fig. 9e and 9f).

*Pseudo-nitszchia* 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 et al., 2007], but they are not usually dominant in the coastal upwelling waters off Concepción [Sánchez et al., 2012; Anabalón et al., 2016]. 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* (Fig. 9g and 9h) and *Haslea* sp. (Fig. 9i and 9j) were concentrated in the ITE-1 zone, whereas *Fragilariopsis doliolus* was distributed in both the FRN-1 and ITE-1 zones (Fig. 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

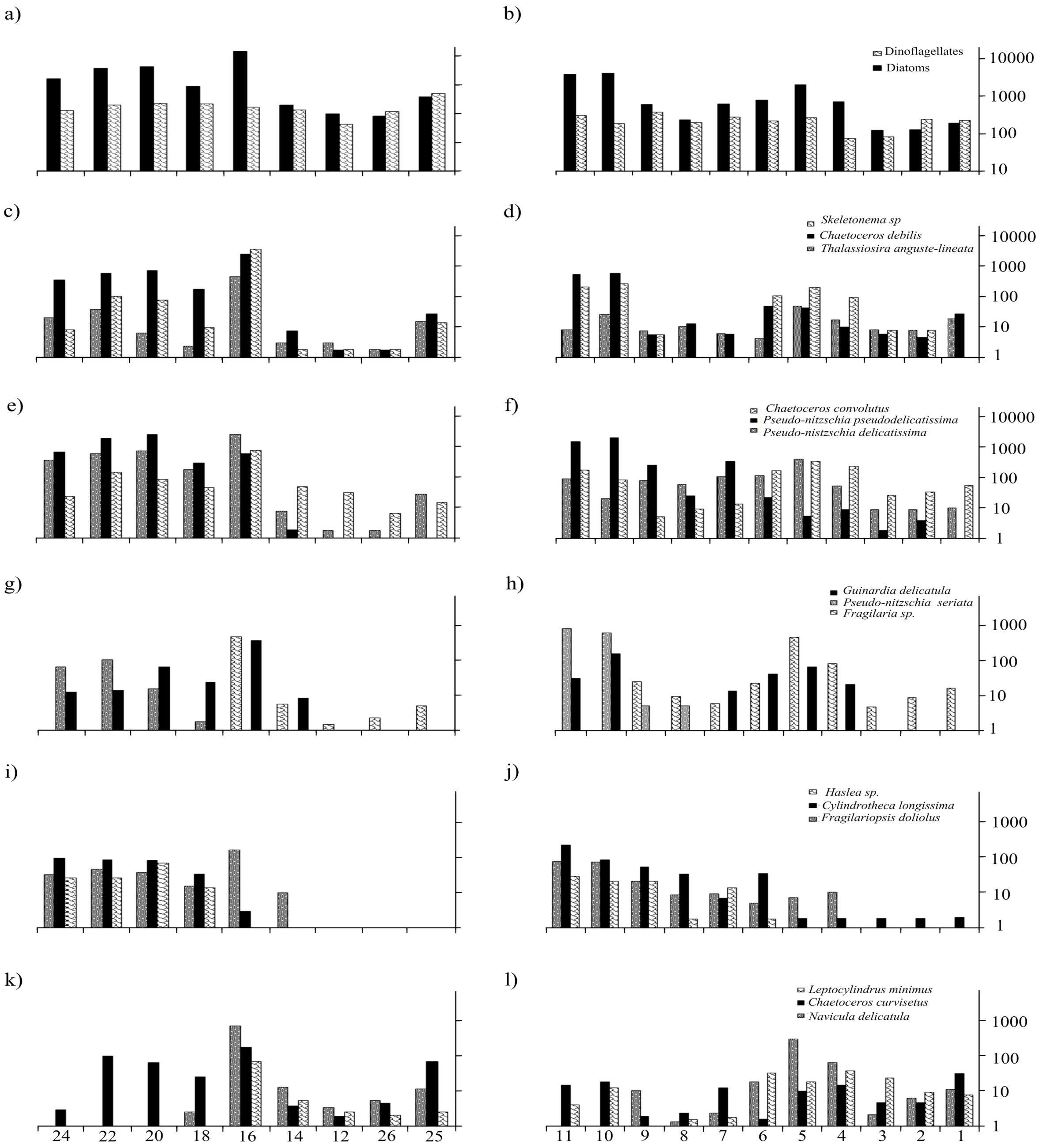

**Figure 9.** Cross-shelf distribution of integrated microphytoplankton abundance (cells*$10^6$ $m^{-2}$) in the upper 60 m layer during the PHYTO-FRONT survey: (left) northern and (right) southern transects. (a and b) Total diatom and autotrophic/mixotrophic dinoflagellate; (c and d*) Skeletonema sp., 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. curvisetus*, and *Navicula directa*. Note a log-10 scale and scales differences between plots.

in the upwelling system off Concepción [Sánchez et al., 2012]. *Guinardia delicatula* (Fig. 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 non-dominant 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 FR-1 (Fig. 9k and 9l).

The highest 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 (Fig. 2). In other EBCSs, coastal formations of *Pseudo-nitzschia* blooms have been found to be associated with events of wind relaxation or weak upwelling [Kudela et al., 2004; Diaz et al., 2014; 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-favourable winds on time scales of a few days [Trainer et al., 2002, 2012; Adams et al., 2006; Fawcett et al., 2007]. 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 towards 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 favoured by wind relaxation events, especially the long ones (~1 week) such as that observed in January 2014, and front-eddy activity facilitating the cross-shore exchange of diatom taxa from coastal and CTZ waters.

## 6.4. 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 this mixing is a result of the interactions between the 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, contributing to sustain both coastal and oceanic phytoplankton in the eddy center.

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## 6.6 REFERENCES

Adams, N. G., A. MacFadyen, B. M. Hickey, and V. L. Trainer (2006), The nearshore advection of a toxigenic Pseudo-nitzschia bloom and subsequent domoic acid contamination of intertidal bivalves, African J. Marine Science, 28(2), 271-276, doi: 10.2989/18142320609504161.

Aguirre, C., O. Pizarro, P. T. Strub, R. D. Garreaud, and J. Barth (2012), Seasonal dynamics of the near-surface alongshore flow off central Chile, J. Geophys. Res., 117, C01006, doi:http://dx.doi.org/10.1029/2011JC007379.

Aguirre, C., Garreaud, R. D., and J. A. Rutllant (2014), Surface ocean response to synoptic-scale variability in wind stress and heat fluxes off south-central Chile, Dynamics of Atmospheres and Oceans, 65, 64-85.

Akima, H. (1970), A new method of interpolation and smooth curve fitting based on local procedures, Journal of the ACM 17(4), 589-602, http://doi.acm.org/10.1145/321607.321609.

Alvera-Azcárate, A., A. Barth, J. M. Beckers, and R. H. Weisberg (2007), Multivariate reconstruction of missing data in sea surface temperature, chlorophyll, and wind satellite fields, J. Geophys. Res., 112 (C5), doi:10.1029/2007JC004243.

Anabalón, V., C. E. Morales, H. R. Escribano, and M. A. Varas (2007), The contribution of nano- and micro-planktonic assemblages in the surface layer (0–30 m) under different hydrographic conditions in the upwelling area off Concepción, central Chile, Prog. Oceanogr., 75, 396-414.

Anabalón, V., J. Arístegui, J., C. E. Morales, I. Andrade, M. Benavides, M. A. Correa-Ramirez, M. Espino, O. Ettahiri, S. Hormazabal, A. Makaoui, M. F. A. Montero, and A. Orbi (2014), The structure of planktonic communities under variable coastal upwelling conditions off Cape Ghir (31°N) in the Canary Current System (NW Africa), Prog. Oceanogr., 120, 320-339.

Anabalón, V., C. E. Morales, H. E. González, E. Menschel, W. Schneider, S. Hormazabal, L.Valencia, and R. Escribano (2016), Micro-phytoplankton community structure in the coastal upwelling zone off Concepción (central Chile): annual and inter-annual fluctuations in a highly dynamic environment, Prog. Oceanogr., 149, 174-188.

Atkinson, L. P., A. Valle-Levinson, D. Figueroa, R. De Pol-Holz, V. A. Gallardo,

W. Schneider, J. L. Blanco, and M. Schmidt (2002), Oceanographic observations in Chilean coastal waters between Valdivia and Concepción. J. Geophys. Res., 107 (C7), doi:10.1029/2001JC000991.

Atlas, E., S. Hager, L. Gordon, and P. Park (1971), A practical manual for use of the Technicon Autoanalyszer in sea water nutrient analyses, Oregon State University, Department of Oceanography, Technical Report, 215 pp.

Barth, J. A., S. D. Pierce, and T. J. Cowles (2005), Mesoscale structure and its seasonal evolution in the northern California Current System, Deep-Sea Res. II, 52, 5-28.

Batten, M. L. (1997), Wind-forced modeling studies of currents, meanders, and eddies in the California Current system, J. Geophys. Res., 102(C1), 985-1010.

Børsheim, K. Y. and G. Bratbak (1987), Cell volume to cell carbon conversion factor for a bacterivorous Monas sp. enriched from seawater. Mar. Ecol. Progr. Ser., 36, 171-175.

Böttjer, D. and C. E. Morales (2007), Nanoplanktonic assemblages in the upwelling area off Concepción (36°S), central Chile: abundance, biomass, and grazing potential during the annual cycle, Prog. Oceanogr., 75, 415-434.

Brannigan, L. 2016. Intense submesoscale upwelling in anticyclonic eddies, Geophys. Res. Lett., 43, 3360-3369.

Brink, K. H. and T. J. Cowles (1991), The Coastal Transition Zone program. J. Geophys. Res., 96, 14,637-14,647.

Brzezinski, M. A., J. L. Jones, K. D. Bidle, and F. Azam (2003), The balance between silica production and silica dissolution in the sea: Insights from Monterey Bay, California, applied to the global data set, Limnol. Oceanogr., 48(5), 1846-1854.

Callbeck, C. M., G. Lavik, L. Stramma, M. M. M. Kuypers, and L. A. Bristow (2017), Enhanced nitrogen loss by eddy-induced vertical transport in the offshore Peruvian Oxygen Minimum Zone, PLoS ONE 12(1): e0170059.doi:10.1371/ journal. pone.0170059.

Capet, X., F. Colas, P. Penven, P., Marchesiello, P., and J. McWilliams (2008), Eddies in eastern-boundary subtropical upwelling systemseddy-resolving ocean modeling. In: Hecht, M., Hasumi, H. (Eds.), Ocean modeling in an eddying regime. Washington, DC: American Geophysical Union. https://doi.org/10.1029/177GM10.

Capet, A., E. Mason, V. Rossi, C. Troupin, Y. Faugere, P. Isabelle, and A. Pascual (2014), Implications of refined altimetry on estimates of mesoscale activity and eddy-driven offshore transport in the eastern boundary upwelling systems, Geophys. Res. Lett., 41(21), 7602-7610, doi: 10.1002/2014GL061770.

Castelao, R. M., T. P. Mavor, J. A. Barth, and L. C. Breaker (2006), Sea surface temperature fronts in the California Current System from geostationary satellite observations, J. Geophys. Res., 111, C09026, doi:10.1029/2006JC003541

Chaigneau, A., M. Le Texier, G. Eldin, C. Grados, and O. Pizarro (2011), Vertical structure of mesoscale eddies in the eastern South Pacific Ocean: A composite analysis from altimetry and Argo profiling floats. J. Geophys. Res., 116, C11025. doi:10.1029/2011JC007134.

Chavez, F. P. and M. Messié (2009), A comparison of eastern boundary upwelling systems. Prog. Oceanogr., 83, 80-96.

Chelton, D. B., M. G. Schlax, and R. M. Samelson (2011), Global observations of nonlinear mesoscale eddies. Prog. Oceanogr., 91, 167-216. doi:10.1016/ j.pocean.2011.01.002.

Chenillat, F., P. J. S. Franks, P. Rivière, X. Capet, N. Grima, and B. Blanke (2015), Mesoscale activity in the Southern California Current System. Biological dynamics of a coastal eddy, J. Geophys. Res. Oceans, http://dx.doi.org/10.1002/2015JC010826.

Colas, F., J. C. Mcwilliams, X. Capet, J. Kurian (2012). Heat balance and eddies in the Peru-Chile current system. Clim. Dyn., 39(1-2), 509-529, doi: 10.1007/s00382-011-11706.

Collado-Fabbri, S., D. Vaulot, and O. Ulloa (2011), Structure and seasonal dynamics of the eukaryotic picophytoplankton community in a wind-driven coastal upwelling ecosystem, Limnol. and Oceanogr., 56, 2334-2346.

Combes, V., S. Hormazabal, and E. di Lorenzo (2015), Eddies and mesoscale processes, Eastern boundary currents, Decadal ocean variability, intrathermocline eddies, ocean modeling, Peru Chile undercurrent, ENSO, J. Geophys. Res. Oceans, http://dx.doi.org/10.1002/2014JC010265.

Correa-Ramirez, M., S. Hormazabal, and G. Yuras (2007), Mesoscale eddies and high chlorophyll concentrations off central Chile (29-39°S), Geophys. Res. Lett. 34 (L12604), doi:10.1029/2007GL029541.

Correa-Ramirez, M. A., S. Hormazabal, and C.E. Morales (2012), Spatial patterns of annual and inter-annual surface chlorophyll-a variability in the Peru–Chile Current System. Prog. Oceanogr., 92, 8-17. doi: 10.1016/j.pocean.2011.07.008.

Daneri. G., L. Lizárraga, P. Montero, H. E. González, and F. Tapia (2012), Wind forcing and short-term variability of phytoplankton and heterotrophic bacterioplankton in the coastal zone of the Concepción upwelling system, Prog. Oceanogr., 92-95, 92-96.

D'Asaro, E., C. Lee, L. Rainville, R. Harcourt, and L. Thomas (2011), Enhanced turbulence and energy dissipation at ocean fronts, Science, 15, 318-322, doi: 10.1126/ science.1201515.

Davidson, K., R. J. Gowen, P. Tett, E. Bresnan, P. J. Harrison, A. McKinney, S. Milligan, D.K. Mills, J. Silke, and A.-M. Crooks (2012), Harmful algal blooms: how strong is the evidence that nutrient ratios and forms influence their occurrence?. Estuar. Coast. and Shelf Science 115, 399-413, doi: 10.1016/j.ecss.2012.09.019.

Desboilles, F., B. Blanke, A. Bentamy, and N. Grima (2014), Origin of finescale wind stress curl structures in the Benguela and Canary upwelling systems, J. Geophys. Res. Oceans, 119, 7931-7948, doi:10.1002/2014JC010015.

Dewitte, B., S. Illig, L. Renault, K. Goubanova, K. Takahashi, D. Gushchina, K. Mosquera, and S. Purca (2011), Modes of covariability between sea surface temperature and wind stress intraseasonal anomalies along the coast of Peru from satellite observations (2000–2008), J.Geophys. Res., 116, C04028, doi:10.1029/2010JC006495.

Díaz, P.A., M. Ruiz-Villarreal, L. Velo-Suárez, I. Ramilo, P. Gentien, M. Lunven, L. Fernand, R. Raine, and B. Reguera (2014), Tidal and wind-event variability and the distribution of two groups of Pseudo-nitzschia species in an upwelling-influenced Ría, Deep-Sea Res. II, 101,163-179.

Duacs/AVISO (2014), A new version of SSALTO/Duacs products available in April 2014.Version 1.1, CNES. [Available at http://www.aviso.altimetry.fr/fileadmin/ documents/data/ duacs/Duacs2014.pdf.].

Dugdale, R. C., F. P. Wilkerson, and H. J. Minas (1995), The role of a silicate pump in driving new production, Deep Sea. Res. I, 42, 697-719.

Dugdale, R. C. and F. P. Wilkerson (1998), Silicate regulation of new production in the equatorial Pacific upwelling, Nature, 391, 270-273.

Edler, L. (1979). Recommendations on methods for marine biological studies in the Baltic

Sea. Phytoplankton and chlorophyll, The Baltic Marine Biologists Publications (University of Lund, Sweeden) 5, 1-38.

Everett, J. D., H. Macdonald, M. E. Baird, J. Humphries, M. Roughan, and I. M. Suthers (2015), Cyclonic entrainment of preconditioned shelf waters into a frontal eddy, J. Geophys. Res. Oceans, 120, 677-691, doi:10.1002/2014JC010301.

Fawcett, A. L., G. C. Pitcher, S. Bernard, A. D. Cembella, and R. M. Kudela (2007), Contrasting wind patterns and toxigenic phytoplankton in the southern Benguela upwelling system. Mar. Ecol. Prog. Ser., 348, 19-31.

Fuenzalida, R., W. Schneider, J. Garcés-Vargas, and L. Bravo (2008), Satellite altimetry data reveal jet-like dynamics of the Humboldt Current. J. Geophys. Res., 113, doi:10.1029/2007JC004684.

Garreaud, R. and R. Muñoz (2005), The low-level jet off the subtropical west coast of South America: structure and variability. Mon. Weather Rev., 133, 2246-2261.

Gilpin, L.C., K. Davidson, and E. C. Roberts (2004), The influence of changes in nitrogen:silicon ratios on diatom growth dynamics. J. Sea Res. 51, 21-35.

Gómez, F., H. Claustre, P. Raimbault, and S. Souissi (2007), Two High-Nutrient Low-Chlorophyll phytoplankton assemblages: the tropical central Pacific and the offshore Perú- Chile Current, Biogeosciences, 4, 1101-1113.

González, H.E., E. Menschel, C. Aparicio, and C. Barría (2007), Spatial and temporal variability of microplankton and detritus, and their export to the shelf sediments in the upwelling area off Concepción, Chile (~36°S), during 2002–2005, Prog. Oceanogr., 75, 435-451.

Goubanova, K., S. Illig, E. Machu, V. Garcon, and B. Dewitte (2013), SST subseasonal variability in the central Benguela upwelling system as inferred from satellite observations (1999-2009). J. Geophys. Res. Oceans, 118 (9), 4092-4110. DOI: 10.1002/jgrc.20287

Grob, C., O. Ulloa, H. Claustre, Y. Huot, G. Alarcon, and D. Marie. (2007) Contribution of picoplankton to the total particulate organic carbon concentration in the eastern South Pacific, Biogeosciences, 4, 837-852.

Gruber N., Z. Lachkar, H. Frenzel, P. Marchesiello, M. Münnich, J. C. McWilliams, T. Nagai, and G.-K. Plattner (2011), Eddy-induced reduction of biological production in eastern boundary upwelling systems. Nature Geosciences, 4, 787-792.

Harrison, C. S. and D. A. Siegel (2014), The tattered curtain hypothesis revised: Coastal jets limit cross-shelf larval transport. Limnol and Oceanogr. Fluids and Environments, 4, 50-66, doi: 10.1215/21573689-2689820.

Harrison, P. J. and C. O. Davis (1979), The use of outdoor phytoplankton continuous cultures to analyze factors influencing species succession, J. Exp. Mar. Biol. and Ecol. 41, 9-23.

Hasle, G. R. (1978), Some specific preparations: diatoms. In: Phytoplankton manual, Sournia, A (Ed.). 136-142. United Nations Educational, Scientific and Cultural Organization (UNESCO).

Hernández-Carrasco, I., V. Rossi, E. Hernández-García, V. Garçon, and C. López (2014), The reduction of plankton biomass induced by mesoscale stirring: a modeling study in the Benguela upwelling. Deep-Sea Res. I, 83, 65-80.

Hormazabal, S., G. Shaffer, J. Letelier, and O. Ulloa (2001), Local and remote forcing of sea surface temperature in the coastal upwelling system off Chile, J. Geophys. Res. Oceans, 106, 16657-16671.

Hormazabal S., G. Shaffer, and O. Leth (2004), Coastal transition Zone off Chile, J. Geophys. Res. Oceans, 109, C01021, doi:10.1029/2003JC001956.

Hormazabal, S., V. Combes, C. E. Morales, M. A. Correa-Ramirez, E. Di Lorenzo, and S. Nuñez (2013), Intrathermocline eddies in the coastal transition zone off central Chile (31–41°S), J. Geophys. Res. Oceans, 118, 4811-4821, doi:10.1002/jgrc.20337.

Hösen, E., J. Möller, K. Jochumsen, and D. Quadfasel (2016), Scales and properties of cold filaments in the Benguela upwelling system off Lüderitz, J. Geophys. Res. Oceans, 121, 1896-1913, doi:10.1002/2015JC011411.

Hyun, J. H., D. Kim, C. W. Shin, J. H. Noh, E. J. Yang, J. S. Mok, S. H. Kim, H. C. Kim, and S. Yoo (2009), Enhanced phytoplankton and bacterioplankton production coupled to coastal upwelling and an anticyclonic eddy in the Ulleung Basin. East Sea. Aquat. Microb. Ecol. 54(1), 45-54.

Johnson, G. C. and K. E. McTaggart (2010), Equatorial Pacific 13°C water eddies in the eastern subtropical South Pacific Ocean, J. Phys. Oceanogr., 40(1), 226-236, doi:10.1175/2009JPO4287.1.

Johnston, T., D. L. Rudnick, and E. Pallàs-Sanz (2011), Elevated mixing at a front, J. Geophys. Res. Oceans, 116, C11033, doi:10.1029/2011JC007192

Kaneko, H., I. Yasuda, K. Komatsu, and S. Itoh (2013), Observations of vertical turbulent nitrate flux across the Kuroshio. Geophys. Res. Lett., 40, 3123-3127, doi:10.1002/grl.50613.

Kara, A. B., H. E. Hurlburt, and A. J. Wallcraft (2005), Stability-dependent exchange coefficients for air–sea fluxes, J. Atmos. Oceanic Technol., 22(7), 1080-1094, doi:

http://dx.doi.org/10.1175/JTECH1747.1

Kim D., E. J. Yang, K. H. Kim, Shin, C-W., Park, J., Yoo, S., and J. H. Hyun (2011), Impact of an anticyclonic eddy on the summer nutrient and chlorophyll a distributions in the Ulleung Basin, East Sea (Japan Sea), ICES J. Mar. Sci. 69(1), 23-29.

Klein, P. and G. Lapeyre (2009), The oceanic vertical pump induced by mesoscale and submesoscale turbulence, Annu. Rev. Mar. Sci., 1, 351-375.

Kochanski, A., D. Koracin, and C. E. Dorman (2006), Comparison of wind-stress algorithms and their influence on wind-stress curl using buoy measurements over the shelf off Bodega Bay, California, Deep-Sea Res. II, 53, 2865-2886, doi:https://doi.org /10.1016/j.dsr2. 2006.07.008

Krause, J. W., M. A. Brzezinski, R. Goericke, M. R. Landry, M. D. Ohman, M. R. Stukel, and A. G. Taylor (2015), Variability in diatom contributions to biomass, organic matter production and export across a frontal gradient in the California Current Ecosystem, J. Geophys. Res. Oceans, 120, 1032-1047, doi:10.1002/2014JC010472.

Kudela, R., W. Cochlan, and A. Roberts (2004), Spatial and temporal patterns of Pseudo-nitzschia spp. in central California related regional oceanography. In: K. A. Steidinger, J. H. Landsberg, C. R. Tomas, and G. A. Vargo (Eds.), Harmful Algae 2002. Florida and Wildlife Conservation Commission, Florida Institute of Oceanography, and Intergovernmental Oceanographic Commission of UNESCO, pp. 347-349.

Kurian, J., F. Colas, X. Capet, J. C. McWilliams, and D. B. Chelton (2011), Eddy properties in the California Current System, J. Geophys. Res. Oceans, 116, C08027. doi:10.1029/2010JC006895.

Lathuilière, C., V. Echevin, M. Lévy, and G. Madec (2010), On the role of the mesoscale circulation on an idealized coastal upwelling ecosystem, J. Geophys. Res., 115, C09018, doi:10.1029/2009JC005827.

Letelier, J., O. Pizarro, and S. Nuñez (2009), Seasonal variability of coastal upwelling and the upwelling front off central Chile, J. Geophys. Res., 114, C12009, http://dx.doi.org/10.1029/2008JC005171.

Lévy, M., P. Franks, A. P. Martin, and P. Rivière (2012), Bringing physics to life at the submesoscale, Geophys. Res. Lett., 39, L14 602. doi:10.1029/2012GL052756.

Leynaert, A., P. Treguer, C. Lancelot, and M. Rodier (2001), Silicon limitation of biogenic silica production in the equatorial Pacific, Deep-Sea Res. I, 48, 639-660.

Llanillo, P. J., J. L Pelegrí, C. M. Duarte, M. Emelianov, M. Gasser, J. Gourrion, and A. Rodríguez-Santana (2012). Meridional and zonal changes in water properties along the continental slope off central and northern Chile, Ciencias Marinas, 38(1B), 307-332.

Louw, D. C., G. J. Doucette, and E. Voges (2016), Annual patterns, distribution and long-term trends of Pseudo-nitzschia species in the northern Benguela upwelling system, J. Plankton Res., 39(1), 35-47. doi:10.1093/plankt/fbw079.

Mahadevan, A. (2016), The impact of submesoscale physics on primary productivity of plankton, Annu. Rev. Mar. Sci., 8, 17.1-17.24, 10.1146/annurev-marine-010814-015912.

Marie, D., F. Partensky, N. Simon, L. Guillou, and D. Vaulot (2000), Flow cytometry analysis of marine picoplankton. In: Diamond R.A. and DeMaggio S. (Eds.), Living Colors: Protocols in Flow Cytometry and Cell sorting, p. 421-454. Springer-Verlag Berlin Heidelberg.

Mason, E., A. Pascual, and J. C. McWilliams (2014), A new sea surface height-based code for oceanic mesoscale eddy tracking, J. Atmos. Oceanic Technol., 31(5), 1181-1188, doi: http://dx.doi.org/10.1175/JTECH-D-14-00019.1

McGillicuddy, D. J. Jr. (2016), Mechanisms of physical-biological-biogeochemical interaction at the oceanic mesoscale, Annu. Rev. Mar. Sci., 8, 125-159, doi: 10.1146/ annurev-marine-010814-015606.

Menden-Deuer, S. and D. J. Lessard (2000) Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton, Limnol. and Oceanogr., 45, 569-579.

Menschel, E., H. E. González, and R. Giesecke (2016), Coastal-oceanic distribution gradient of coccolithophores and their role in the carbonate flux of the upwelling system off Concepción, Chile (36°S), J. Plankton Res., 38(4): 798-817.

Mesias, J., R. Matano, and P. T. Strub (2001), A numerical study of the upwelling circulation off central Chile, J. Geophys. Res., 106, 19611-19623, http://dx.doi.org/ 10.1029/ 2000JC000649.

Messié and F. Chavez (2015), Seasonal regulation of primary production in eastern boundary upwelling systems, Prog. Oceanogr., 134,1–18

Morales, C. E., H. E. González, S. E. Hormazabal, G. Yuras, J. Letelier, and L. R. Castro (2007), The distribution of chlorophyll-a and dominant planktonic components in the coastal transition zone off Concepción, central Chile, during different oceanographic conditions, Prog. Oceanogr., 75, 452-469.

Morales, C. E. and V. Anabalón (2012), Phytoplankton biomass and microbial abundances during the spring upwelling season in the coastal area off Concepción, central-southern Chile: Variability around a time series station, Prog. Oceanogr., 92, 81-91.

Morales, C. E., S. Hormazabal, M. A. Correa-Ramirez, O. Pizarro, N. Silva, C. Fernandez, C., V. Anabalón, and M. L. Torreblanca (2012), Mesoscale variability and nutrient–phytoplankton distributions off central-southern Chile during the upwelling season: the influence of mesoscale eddies. Prog. Oceanogr., 104, 17-29.

Nagai, T., N. Gruber, H. Frenzel, Z. Lachkar, J. C. McWilliams, and G.-K. Plattner (2015), Dominant role of eddies and filaments in the offshore transport of carbon and nutrients in the California Current System, J. Geophys. Res. Oceans, 120, 5318-5341, doi:10.1002/2015JC010889.

Pelegrí, J.L., J. Arístegui, L. Cana, M. González-Dávila, A. Hernández-Guerra, S. Hernández-León, A. Marrero-Díaz, M. F. Montero, P. Sangrà, P., and M. Santana-Casiano (2005), Coupling between the open ocean and the coastal upwelling region off northwest Africa: water recirculation and offshore pumping of organic matter, J. Mar. Sys. 54, 3-37.

Penven, P., V. Echevin, J. Pasapera, F. Colas, and J. Tam (2005), Average circulation, seasonal cycle, and mesoscale dynamics of the Peru Current System: a modeling approach, J. Geophys. Res., 110, 1-21. doi:10.1029/2005JC002945.

Pietri, A., P. Testor, V. Echevin, A. Chaigneau, L. Mortier, G. Eldin, and C. Grados (2013), Finescale vertical structure of the upwelling system off Southern Peru as observed from glider data, J. Phys. Oceanogr., 43(3), 631-646, doi:10.1175/JPO-D-12-035.1.

Pietri, A., V. Echevin, P. Testor, A. Chaigneau, L. Mortier, C. Grados, and A. Albert (2014), Impact of a coastal trapped wave on the near-coastal circulation of the Peru upwelling system from glider data, J. Geophys. Res. Oceans, 119, 2109-2120, doi:10.1002/ 2013JC009270.

Raimbault, P., G. Slawyk, B. Boudjellal, C. Coatanoan, P. Conan, B. Coste, N. Garcia, T. Moutin, and M. Pujo-Pay (1999), Carbon and nitrogen uptake and export in the equatorial Pacific at 150°W: Evidence of an efficient regenerated production cycle, J. Geophys. Res. Oceans, 104, 3341-3356.

Renault, L., B. Dewitte, M. Falvey, R. Garreaud, V. Echevin, and F. Bonjean (2009), Impact of atmospheric coastal jets on SST off central Chile from satellite observations (2000–2007), J. Geophys. Res., 114, C08006, doi:10.1029/2008JC005083.

Rivera, P. R. (1968), Sinopsis de las diatomeas de la Bahía de Concepción, Chile, Gayana, Botánica, 18, 1-112.

Rivera, P. R. (1985), Las especies del Género Nitzschia Hassall, Sección Pseudonitzschia (Bacillariophyceae), en las aguas marinas chilenas, Gayana Botánica 42(3-4), 9-40.

Rivera, P. R. and H. Valdebenito (1979), Diatomeas recolectadas en las desembocaduras de los Ríos Chivilingo, Laraquete y Carampangue, Chile, Gayana Botánica 35, 1-99.

Rossi, V., C. López, J., Sudre, E. Hernández-García, and V. Garcon (2008), Comparative study of mixing and biological activity of the Benguela and Canary upwelling systems, Geophys. Res. Lett., 35, L11602.

Saha, S., S. Moorthi, X. Wu, J. Wang, S. Nadiga, P. Tripp, D. Behringer, Y. Hou, H. Chuang, M. Iredell, M. Ek, J. Meng, R. Yang, M. P. Mendez, H. van den Dool, Q. Zhang, W. Wang, M. Chen, and E. Becker (2011), NCEP Climate Forecast System Version 2 (CFSv2) 6-hourly Products. Research Data Archive at the National Center for Atmospheric Research, Computational and Information Systems Laboratory, https://doi.org/10.5065/D61C1TXF. Accessed 30-nov-2016.

Sánchez, G. E, C. B. Lange, H. E. González, G. Vargas, P. Muñoz, C. Cisternas, C., and S.

Pantoja (2012), Siliceous microorganisms in the upwelling center off Concepción, Chile (36°S): Preservation in surface sediments and downcore fluctuations during the past ~150 years, Prog. Oceanogr., 92-95, 50-65.

Sarmiento, J., N. Gruber, M. Brzezinski, and J. Dunne (2004), High latitude controls of thermocline nutrients and now latitude biological productivity, Nature, 427, 56-60.

Silva, N., N. Rojas, and A. Fedele (2009), Water masses in the Humboldt Current System: Properties, distribution, and the nitrate deficit as a chemical water mass tracer for Equatorial Subsurface Water off Chile, Deep Sea Res. Part II, 56(16), 1004-1020, doi:10.1016/j.dsr2.2008.12.013.

Sobarzo, M., L. Bravo, D. Donoso, J. Garcés-Vargas, and W. Schneider (2007), Coastal upwelling and seasonal cycles that influence the water column over the continental shelf off central Chile, Prog. Oceanogr., 75, 363-383.

Sommer, U. (1994), Are marine diatoms favored by high Si:N ratios? Mar. Ecol. Prog. Ser.115 (3), 309-315.

Stoecker, D. K., D. E. Gustafson, and P. G. Verity (1996), Micro- and mesoprotozooplankton at 140°W in the equatorial Pacific: heterotrophs and mixotrophs, Aquat. Microbiol. Ecol., 10, 273-282.

Strathman, R. R. (1967), Estimating the organic carbon content of phytoplankton from cell volume or plasma volume, Limnol. and Oceanogr., 12, 411-418.

Strub, P., J. Mesías, V. Montecino, and J. Rutllant (1998), Coastal ocean circulation off western South America. In The Sea. Robinson, A.; Brink, K. (Eds.), John Wiley and Sons, Inc., N.Y., USA, 1998, Volume 11, p. 273-313.

Thomsen, S., T. Kanzow, G. Krahmann, R. J. Greatbatch, M. Dengler, and G. Lavik (2016), The formation of a subsurface anticyclonic eddy in the Peru-Chile Undercurrent and its impact on the near-coastal salinity, oxygen, and nutrient distributions, J. Geophys. Res. Oceans, 120, doi: 10.1002/2015JC010878.

Trainer, V. L., B. M. Hickey, and R. A. Horner (2002), Biological and physical dynamics of domoic acid production off the Washington U.S.A. coast, Limnol. Oceanogr., 47, 1438-1446.

Trainer, V. L., S. S. Bates, N. Lundholm, A. E. Thessen, W. P. Cochlan, N. G. Adams, and C.G. Trick (2012), Pseudo-nitzschia physiological ecology, phylogeny, toxicity, monitoring and impacts on ecosystem health, Harmful Algae, 14, 271-300.

Vergara, O. A., V. Echevin, H. H. Sepúlveda, F. Colas, and R. A. Quiñones (2016), Modelling the seasonal dynamics of the Peru-Chile Undercurrent off Central Chile (30–40°S), Continental Shelf Res., 123, 61-79, doi: http://dx.doi.org/ 10.1016/ j.csr.2016.04.001.

Verity, P. and M. Sieracki (1993), Use of color image analysis and epifluorescence microscopy to measure plankton biomass. In: Kemp, P., Sherr, E., Cole, J. (Eds.), Handbook of Methods in Aquat. Microb. Ecol.. Lewis Publisher, Boca Raton, pp. 327-338.

Wang, Y., R. M. Castelao, and Y. Yuan (2015), Seasonal variability of alongshore winds and sea surface temperature fronts in Eastern Boundary Current Systems, J. Geophys. Res. Oceans, 120, 2385-2400, doi:10.1002/2014JC010379.

Zubkov, M. V., M. A. Sleigh, P. H. Burkill, and R. J. G. Leakey (2000), Picoplankton community structure on the Atlantic Meridional Transect: a comparison between seasons, Progr.Oceanogr.,45,369-386.

***Every failure teaches a man***
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# General discussion and Future perspectives

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***Dickens***

## 7.0. General discussion and future perspectives

Until today, numerous studies on microbial communities in upwelling systems (EBUSs) have been published, but too few comparative studies between different EBUSs or between regions in the same EBUS (Mackas et al., 2006) are available. The latter are dominated by comparative studies based on satellite color information, using surface chlorophyll-a (Chl-a) concentration as a proxy for phytoplankton biomass and, in turn, as a basis to model net primary production (NPP) (Carr, 2001; Behrenfeld and Falkowski, 1997; Marra et al., 2003; Kahru et al., 2009; Lachkar and Gruber, 2012). In addition, EBUS studies based on in situ data which include spatio-temporal changes in microbial community structure are still few given a logistic limitation. The results in this thesis have the advantage of being based on a combination of satellite imagery and field observations in order to characterize the structure of microbial communities and its variability in association with environmental factors in regions of two EBUSs having different oceanographic characteristics. Moreover, this thesis uses statistical multivariate analysis rather than the traditional univariate analysis to analyze spatial and/or temporal changes in community structure and in the exploration of the environmental factors that influence such changes.

Comparative studies of EBUSs have shown that while they all are highly productive, there are differences in the levels of biomass and NPP between them and within them, but the mechanisms that cause these differences are not clear (Lachkar and Gruber, 2012; Messié and Chavez, 2015). Differences in the structure of microbial communities are even less well known or understood, making this one of the foci of this thesis. Among the environmental factors that affect phytoplankton biomass and/or NPP, as identified in previous comparative studies, a distinction has been made between local forcing (eg. regional/local winds - coastal upwelling) and remote forcing (large scale circulation; depth of the thermocline) (Carr, 2001; Carr and Kearns, 2003). Along with this, Patti et al. (2008) concluded that the greatest variance in surface Chl-a levels in EBUSs can be explained by nitrate concentration and shelf width. On the other hand, Rossi et al. (2008, 2009) found a negative relationship between the magnitude of lateral stirring (horizontal mixing) and surface Chl-a in EBUSs. In terms of NPP, Lachkar and Gruber (2012) showed that, along with the recognized positive influence of coastal upwelling on NPP, there are three factors that have an inhibitory effect: strong mesoscale activity via eddies, narrow continental platforms, and a deep mixing layer. On this basis, these authors stated that the Atlantic EBUSs are generally more productive and more sensitive to favorable upwelling winds given that the inhibitory factors have a lesser impact in comparison with EBUS systems in the Pacific. More recently, Messié and Chavez (2015) have indicated that macronutrient supply is the dominant regulating factor off NW Africa and also in other EBUSs ,but only during some seasons and some sub-regions within them, with light regulation during wintertime and evidence of iron limitation (except NW Africa) in all EBUSs. Results generated in this thesis on the structure of microbial communities allow us to contrast them with findings generated in previous comparative EBUS studies on the mechanisms involved in biomass or NPP variability in these communities. In what follows, three of the factors that, a priori, are considered most relevant in structuring the microbial communities in the EBUSs of the Canary (Cape Ghir) and the Humboldt (Concepción) systems are analyzed separately.

## 7.1. The role of coastal upwelling on the structure of microbial communities in EBUSs

The high productivity levels that characterize EBUS have been attributed to coastal upwelling events (continuous or seasonal patterns), which normally contribute to the injection towards the surface layer of colder waters, rich in nutrients and with high $CO_2$ concentrations, low in pH and in $O_2$ concentrations in the coastal zone (Huyer, 1983, 1990; Brink, 1991; Lentz, 1992; Lentz and Fewings, 2012). Results of the present study confirm that, at the annual scale, local wind favorable to upwelling is important in both the Cape Ghir (NW Africa) and the Concepción (central-southern Chile) systems. However, there are important differences between both systems regarding seasonality, intensity and magnitude of wind-driven upwelling. In C. Ghir, satellite wind data in this study and in previous studies, indicate that coastal upwelling is continuous throughout the year (Barton et al., 1998; Pelegrí et al., 2005a; Lauthuilière et al., 2008; Arístegui et al., 2009). Despite this continuity, the annual cycle presents an intensification of upwelling favorable winds during winter (December to February) compared to the rest of the year, including occasional episodes of relaxation during autumn (September/October). Wind stress values reported in this thesis (monthly averages) fluctuate between 0.2 and 0.5 N $m^{-2}$, and the upwelling index between 40 and 300 $m^3$ $s^{-1}$ for 100 m along the coast. These average values are consistent with previously reported low wind speeds and a lower oscillation in magnitude in this region compared with other EBUSs (Chavez and Messié, 2009), even though there is a significant daily variation (an order of magnitude) in terms of the upwelling index (Cropper et al., 2014). A novel result of this thesis is that different upwelling phases are distinguished off C. Ghir, including weak, moderate, and strong upwelling phases.

In the system off Concepción, results of this study confirm that coastal upwelling is highly seasonal, with an intensification of upwelling favorable winds during spring-summer months (September to March), winds unfavorable to upwelling during autumn-winter months (June-August), and occasional episodes of relaxation during summer-autumn months (January to April). Wind stress values during the annual cycle (monthly averages) fluctuate between 0.1 to 1.1 N $m^{-2}$, and the upwelling index between -330 and 430 $m^3$ $s^{-1}$ for 100 m along the coast. When comparing these values only for the upwelling period (spring and summer), the upwelling index varies between -150 and 430 $m^3$ $s^{-1}$ for 100 m along the coast (Anabalón, unpublished data). Based on these data, three distinct upwelling phases can be distinguished in this system: moderate and strong upwelling, and no-upwelling phases. However, Anabalón et al. (2016) did not report such differences since the method of calculation was different (an upwelling index average of 7 days, including dates before and during the sampling) and does not include the monthly trend reported above. Overall, the Concepción system presents a wider range of variation in terms of upwelling intensity compared to C. Ghir, even though both systems are located at similar latitudes.

Results presented in this study suggest that the intensity of upwelling in the Cape Ghir and the Concepción systems directly influence the structure of microbial communities at the annual scale (Morales and Anabalón, 2012; Anabalón et al., 2014, 2016). However, the two systems are very different in terms of community structure. In C. Ghir, diatoms are, for the most part, not a dominant component of the phytoplankton, but instead, mixed functional groups (autotrophs + mixotrophs) are favored. In addition, significant differences in composition, abundance, and biomass of microbial communities were found in association with different upwelling phases, suggesting that the organisms quickly respond to oceanographic changes. These results are similar to those reported by Crespo et al. (2012) for the upwelling system of the Iberian Peninsula, with an absence of diatoms, dominance of nanoflagellates, and the presence of mixed functional groups. In contrast, in the upwelling system off Concepción, diatoms are the dominant component in terms of biomass during the upwelling period, in coincidence with previous results for this region (Gonzalez et al., 1987, 2007; Anabalón et al., 2007; Sánchez et al., 2012) and for other EBUSs (Kudela et al., 2009; Du et al., 2009). It should be noted that, in the Concepción system, the autotrophic nanoflagellates are a dominant component during the non-upwelling season (up to 60% of total Chl-a), but they are also important during the upwelling period (up to 40% of total Chl-a) (Anabalón et al. 2007; Böttjer and Morales, 2007).

At a larger time-scale, it has been recently suggested that specific sub-regions (poleward regions) within some of the main EBUSs, including the Humboldt and the

Benguela systems, have experienced an intensification of coastal upwelling during the last 60 years (Sydeman et al., 2014). In association with this, the impacts of upwelling wind increase on planktonic communities are a subject of investigation in most recent years. For example, Lachkar and Gruber (2011b) proposed that a potential intensification of upwelling would lead to an increase in NPP in the Canary system in comparison with the California system, although Gómez-Letona et al. (2017) found no evidence of NPP changes in the Canary System during the 1998-2015 period, in agreement with the lack of evidence for wind intensification in this EBUS (García-Reyes et al., 2015). On the other hand, Lachkar and Gruber (2012) proposed that wind intensification could produce an increase in the offshore transport of plankton and/or in the water column turbulence, both processes having a negative impact on the biomass of micro-phytoplankton and NPP in the coastal zone of EBUSs. Without doubt, to resolve low-frequency changes in the structure and dynamics of microbial communities, a wide spatial and a long temporal coverage are required to better identify and predict them. Nevertheless, using a relatively short in situ time series off Concepción (St. 18), results presented in this thesis (Anabalón et al., 2016) indicate an intensification of upwelling favorable winds during the 2006–2009 compared with the 2002–2006 period. This change was associated with a decrease in the abundance and biomass of some of the dominant diatom genera during the 2006–2009 period, without changes in the dominance of diatoms. In summary, changes in the patterns of coastal upwelling favorable winds in EBUS, at different time scales, can be directly reflected as positive or negative impacts on microbial community structure.

## 7.2. The role of the mesoscale activity on the structure of microbial communities in EBUSs

A recent study compares mesoscale activity in different EBUSs and the results indicate that such activity (in terms of eddy kinetic energy) is, in general, stronger in the Pacific than in the Atlantic EBUSs (Lachkar and Gruber, 2012). In addition, each EBUS presents regional differences in mesoscale activity. In the Canary system, the central sub-region (33°30'– 28°N), which includes C. Ghir, presents a higher mesoscale activity compared with the northern (28–21ºN) and southern (36–33°30'N) sub-regions (Nieto et al., 2012). Satellite data presented in this thesis for the C. Ghir system (Anabalón et al., 2014) do show intense mesoscale activity, including the presence of jets, meanders, fronts, eddies, and filaments in the CTZ, an observation which coincides with results from previous studies in the region (Hagen et al., 1996; Hernandez-War and Nykjaer, 1997; Barton et al., 1998; Nieto et al., 2012). In particular, the recurrent filament generated off C. Ghir, which has a highly variable length (30 to 300 km; Hagen et al., 1996; Hernandez-War and Nykjaer, 1997; Barton et al., 1998), was weak during the sampling program in this thesis and, therefore, its effect on community structure could not be evaluated. However, previous studies have indicated the importance of this filament in terms of the exportation of organic matter from the coast to the open ocean and/or of the cross-shore Chl-a distribution (Head et al., 1996; Van Camp et al., 1991; Neuer et al., 2002; Freudenthal et al., 2001, 2002;

Arístegui and Harrison, 2002; García-Muñoz et al., 2005; Pelegrí et al., 2005a, 2005b; Santana-Falcon et al., 2016).

In the Concepción system, observations during this study (Morales et al., 2017) suggest that mesoscale activity contributes to exchanges between coastal and oceanic microbial communities, represented by diatoms, as a result of interactions between an upwelling front and a mesoscale eddy. These interactions and their effects on the microbial communities are an example of the fact that mesoscale activity in EBUSs is not restricted to the export from the coastal zone to the ocean, as it is usually being posed (Gruber et al., 2011), but there is an effective exchange in both. In addition, it is feasible that mesoscale processes have an inhibitory effect on NPP in the coastal zone (Gruber et al., 2011; Lachkar and Gruber 2011a, 2012), but, at the same time, they contribute to increase NPP in the CTZ and open ocean (Falkowski et al., 1991; McGillicuddy et al., 1998).

## 7.3. The role of nutrients

Nutrients in the water column play a very important role in both, the Cape Ghir and the Concepción systems, according to the results presented in this thesis (Morales and Anabalón, 2012, Anabalón et al., 2016). However, there are significant differences between the two systems regarding the concentration of nutrients in the surface layer (0-30 m depth). The maximum average values of $NO_3$ and $SiOH_4$ in this layer were 5 and 2.6 µM, respectively, while in Concepción they were 15 µM in both cases. These values are consistent with the results of previous studies that have characterized nutrient levels in the Canary (Codispoti et al., 1982; Arístegui et al., 2006; Chavez and Messié, 2009) and Humboldt (Herrera and Escribano, 2006; Lachkar and Gruber, 2012) EBUSs. Along with this, the proportionsbetween nutrients (Si/N and N/PO4) obtained in this study indicate that C. Ghir has both a Si and N deficit, in concordance with previous studies in neighboring areas (Treguer and Le Corre, 1978; Fanning, 1992; Romero et al., 2002; Codispoti et al., 1982; Arístegui et al., 2006; Chavez and Messié, 2009). On the contrary, no nutrient deficit in the coastal area of the Concepción system (St. 18) was detected during the annual cycle but Si-deficit might occur in the CTZ, an aspect which has been reported here for the first time in this sub-region.

In the case of Cape Ghir, the lack of diatom dominance can be explained, in part, by nutrient levels (Si and/or $NO_3$) in the upwelled waters, associated with nutrient-poor waters of the North Atlantic water mass (NAW) (Harrison et al., 1977; Levasseur and Therriault, 1987). In the region of study, Si-deficit is strongly associated with changes in the structure of diatom assemblages (composition, abundance, and biomass), as observed in this study and in previous studies (Treguer and Le Corre, 1978; Fanning, 1992; Romero et al., 2002). However, a potential Si-limitation by itself does not explain these differences since changes in the composition of diatom assemblages are expected to arise from differences in both N and Si assimilation rates or requirement levels at specific taxa levels in the case of EBUSs (Kudo, 2003; Van Ruth et al., 2012). In addition, suboptimal conditions imposed by a nutrient deficit directly affect the intracellular Chl-a concentration and the C:Chl-a proportion (Harrison et al., 1977; Gilpina et al., 2004). This appears to be the case during our study since low Chl-a concentrations and high C:Chl-a values were detected during the samplings off C. Ghir

(Anabalón et al., 2014). A Si- or N-deficit could explain the prevalence of mixed functional groups (autotrophs/mixotrophs) in this system (Anabalón et al., 2014). In this sense, the classic vision of species succession in upwelling systems agrees with a reported lower affinity for N-uptake in dinoflagellates in comparison with diatoms when the environmental levels of N are low (Smayda, 1997; Collos et al., 2005). In fact, dinoflagellate blooms in upwelling areas have been associated with conditions such as a decrease in nutrient levels after a relaxation phase of upwelling (Fraga et al., 1988; Pitcher and Boyd, 1996; Probyn et al., 2000; Sordo et al., 2000; Langlois, 2001). On the other hand, Wilkerson and Dugdale (2008) suggest that the nutrient more frequently involved in limiting the growth of phytoplankton in coastal upwelling systems is N, although clearly Si can shape the dynamics of the community by limitation or co-limitation in the case of diatoms (Kudela, 2008).

In the Concepción system, the results of the present study suggest that changes in community structure during the annual cycle appear to be associated with factors other than changes in nutrient concentration in the coastal zone, however, they do play an important role at the interannual scale (Anabalón et al., 2016). Changes in the proportions of nutrients (Si/N and N/P) in the period 2002–2009 were associated with changes in the structure of micro-phytoplanktonic assemblages during the upwelling, productive period. A decrease in Si and a mild to moderate increase in $NO_3$ was detected during the period 2006–2009, which resulted in a significant reduction (up to 100%) of the Si/N proportion and a moderate increase in the N/P proportion. According to Gilpin et al. (2004), changes in Si/N influence the growth dynamics of diatoms and can eventually lead to Si-limitation. Therefore, it is likely that the observed changes in diatom biomass, as total and specific taxa, could have been stimulated by recent changes in Si/N in the coastal zone (Anabalón et al., 2016). These changes could be explained to a large extent by differences in the assimilation rates of nutrients in different species. For example, the genera *Chaetoceros* and *Thalassiosira* have a cell Si/N proportion which is similar to that in the environment, but their rates of absorption during the growth phase are different, being almost constant at Si/N values of 0.5 during exponential growth in *Chaetoceros* and of 1.5 in *Thalassiosira* (Kudo, 2003).

Results in this thesis indicate that a change in the Si/N proportion between the 2002–2006 and 2006–2009 periods seems to have had a greater impact on the diatom genera *Skeletonema* and *Leptocylindrus*, resulting in a greater reduction of their abundances during the latest period, while the impact on *Chaetoceros* and *Thalassiosira* was lower. This decline could be partially explained by differences in the physiological response of the dominant taxa to changes in the availability of Si. For example, the cosmopolitan species *Skeletonema costatum* appears to be more sensitive to Si-deficit than other dominant taxa, such as *Chaetoceros* spp.; however, if there is a severe Si-limitation, all taxa could decrease rapidly in abundance (Harrison and Davis, 1979; Yamamoto and Tsuchiya, 1995; Nelson and Dortch, 1996). Unfortunately, existing estimates of species-specific rates of absorption and/or assimilation of nutrients are very few and often inconsistencies are observed, which can be attributed to differences in the nutrient history of cells and/or to intra-specific differences in nutrient requirements (Glibert et al., 2018). In the case of EBUSs, structural changes in planktonic communities, as well as the development of harmful algal blooms, are themes very strongly linked to a characterization of the physiological aspects associated with nutrient utilization and, therefore, should be appropriately considered.

## 7.4. Other environmental factors that influence the structure of microbial communities in EBUSs

The main oceanographic factors that control changes in the composition, abundance, and biomass of microbial communities were analyzed in the present study. The results indicate that, in both study areas, several factors are involved, in addition to the existence of strong correlations between environmental factors (Anabalón et al., 2014; 2016). The main factors identified for the study areas, at the annual and/or intra-annual levels, were different but included those previously described by others to explain variability in phytoplankton biomass and/or NPP, that is, wind-driven upwelling and eddy kinetic energy. Factors such as shelf width and mixed layer affecting NPP were not included in this study but certainly play an important role. A factor that has not been explicitly considered in previous studies of these EBUSs, or in other EBUSs, is the proportion of nutrients. In addition, it has not been taken into account in the changes of these proportions the influence that can have anthropogenic nutrient contributions to the coastal zone in all EBUSs. In this sense, Yévenes et al. (2015) reported an increase in the average annual discharge of N in the rivers located in the Concepción system, derived from anthropogenic activity, which can explain significant changes in the Si/N and N/P ratios in the coastal zone. In the California system, it has been observed that wastewater effluent, riverine runoff, submarine groundwater discharge, and atmospheric deposition are important sources of nutrients (N) at the local level and, therefore, influence coastal productivity (Reifel et al., 2013; Howard et al., 2014; Lecher et al., 2015).

Previous studies suggest that a narrow continental shelf may inhibit NPP because nutrient retention is lower than in wide platforms (Austin and Lentz 2002; Marchesiello and Estrade 2009). Off Concepción, the platform is comparatively wider than that off Cape Ghir, therefore, the latter would have a lower retention capacity in the coastal zone. In addition, previous studies suggest that a wide continental shelf tends to minimize nutrient losses in the vertical dimension by trapping them in the sediments, either in organic or inorganic form (Dermarcq and Faure, 2000; Liu and Weisberg, 2007; Lachkar and Gruber, 2012). On this same point, iron concentration is another important nutrient in EBUSSs, except for NW Africa (Messié and Chavez, 2015), and it is associated with shelf width, with wide platforms retaining a larger amount of river-derived iron in coastal systems (Chase et al., 2007). However, freshwater inputs by rivers are generally very low in EBUSs and probably play a minor role in structuring microbial communities when integrating throughout the region in each EBUS (Mackas et al., 2006).

### 7.5. Closing Remarks

Results presented in this thesis point out to a series of aspects which need to be considered in future studies of microbial communities in EBUSs, besides the impact of wind-driven upwelling. In terms of forcing, nutrient levels are a relevant factor structuring microbial communities at the annual scale in some cases (C. Ghir) but not in others (Concepción). In combination with this, the proportion between nutrients was also a relevant factor but at different time scales in the systems analyzed (seasonal in C. Ghir and interannual in Concepción). At the mesoscale level, this thesis contributed to identify the combined effect of eddy-front interaction in the CTZ on microbial community structure, concluding that an active coastal oceanic exchange is generated and should be considered in evaluating the spatial/temporal changes in EBUSs communities. In terms of microbial community structure, most studies in EBUS have focused on the gross level (eg. total Chl-a and/or primary production), without considering community composition. In this thesis, evidence is provided that community changes can be detected at low taxonomic levels (eg. species, genus) and not at the gross level. This finding supports the view that microbial community changes in response to environmental changes require a better characterization of taxa or functional group composition, even if this process is time-consuming and the fact that taxonomist are today a scarce resource. On the other hand, satellite approaches to phytoplankton community composition have advanced in recent years but, for the most part, the level of detection is still gross (eg. functional groups). In addition, results of this thesis indicate that caution is required in using fixed C:Chl-a conversion factors since these ratios are subject to large variations within species and functional groups, so that the proportion between autotrophs/mixotrotrophs and heterotrophs can be highly dependent on the values chosen. In the same context, our analyses also detected the need to standardize the criteria used in the estimation of biovolumen as to calculate biomass (eg. number of measurements included; minimum number of cells considered). Overall, in situ time series of microbial communities are an essential component to understand the structure and dynamics of microbial communities in EBUSs and to predict the impact of large-scale processes, such as climate change.

## 7.6 REFERENCES

Anabalón, V., Morales, C.E., Escribano, H.R., Varas, M.A., 2007. The contribution of nano- and micro-planktonic assemblages in the surface layer (0–30 m) under different hydrographic conditions in the upwelling area off Concepción, central Chile. Prog. Oceanogr. 75, 396–414.

Anabalón, V., Arístegui, J., Morales, C.E., Andrade, I., Benavides, M., Correa-Ramirez, M.A., Espino, M., Ettahiri, O., Hormazabal, S., Makaoui, A., Montero, M.F., Orbi, A., 2014. The structure of planktonic communities under variable coastal upwelling conditions off Cape Ghir (31°N) in the Canary Current System (NW Africa). Prog. Oceanogr. 120, 320–339.

Anabalon, V., Morales, C. E., Gonzalez, H. E., Menschel, E., Schneider, W., Hormazabal, S., Valencia L., Escribano, R., 2016. Micro-phytoplankton community structure in the coastal upwelling zone off Concepción (central Chile): Annual and inter-annual fluctuations in a highly dynamic environment. Prog. Oceanogr. 149, 174–188.

Arístegui, J., Harrison, W.G., 2002. Decoupling of primary production and community respiration in the ocean: implications for regional carbon studies. Aquat. Microb. Ecol., 29, 199-209.

Arístegui, J., Álvarez-Salgado, X.A., Barton, E.D., Figueiras, F.G., Hernández-León, S., Roy, C., Santos, A.M.P., 2006. Oceanography and fisheries of the Canary Current Iberian region of the Eastern North Atlantic. In: Robinson, A., Brink, K.H. (Eds.), The Global Coastal Ocean: Interdisciplinary Regional Studies and Syntheses, The Sea: Ideas and Observations on Progress in the Study of the Seas, vol. 14. Harvard University Press, pp. 877–931.

Arístegui J., Barton E.D., Álvarez-Salgado, X.A., Santos A.M.P., Figueiras, F.G., Kifani, S., Hernández-León, S., van Mason, E., Machú, E., Demarcq, H., 2009. Sub-regional ecosystem variability in the Canary Current upwelling. Prog. Oceanogr. 83, 33-48.

Austin, J. A., Lentz, S.J., 2002. The Inner Shelf Response to Wind-Driven Upwelling and Downwelling. J. Phys. Oceanogr. 32, 2171–2193. doi:10.1175/1520-0485

Barton, E.D., Arístegui, J., Tett, P., Cantón, M., García-Braun, J., Hernández-León, S., Nykjaer, L., Almeida, C., Almunia, J., Ballesteros, S., Basterretxea, G., Escánez, J., García-Weill, L., Hernández-Guerra, A., López-Laatzen, F., Molina, R., Montero, M.F., Navarro-Pérez, E., Rodríguez, J.M., van Lenning, K., Vélez, H., Wild, K., 1998. The transition zone of the Canary Current upwelling region. Prog. Oceanogr. 41, 455–504.

Behrenfeld, M.J., Falkowski, P.G., 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. Limnol. Oceanogr. 42, 1–20. http://dx.doi.org/10.4319/lo.1997.42.1.0001.

Böttjer, D., Morales, C.E., 2007. Nanoplanktonic assemblages in the upwelling area off Concepción (36°S), central Chile: abundance, biomass, and grazing potential during the annual cycle. Prog. Oceanogr. 75, 415–434.

Brink, K.H., 1991. Coastal-trapped waves and wind-driven currents over the continental shelf. Annu. Rev. Fluid Mech. 23, 389–412.

Carr, M., Kearns, E., 2003. Production regimes in four eastern boundary current systems. Deep Sea Res. Part II 50, 3199–3221.

Carr, M., 2001. Estimation of potential productivity in Eastern Boundary Currents using remote sensing, Deep Sea Res., 49, 59–80, doi:10.1016/S0967-0645(01)00094-7.

Chase, Z., Strutton, P. G., Hales, B., 2007. Iron links river runoff and shelf width to phytoplankton biomass along the US West Coast, Geophys. Res. Lett., 34, 4 pp., L04607, doi:10.1029/2006GL028069, 2007.

Chavez, F.P., and Messié, M., 2009. A comparison of eastern boundary upwelling systems. Prog. Oceanogr. 83, 80–96.

Codispoti, L.A., Dugdale, R.C., Minas, H.J., 1982. A comparison of the nutrient regimes off North-west Africa, Peru and Baja California. Rapports et Proces-verbaux des Réunions. Conseil International pour l'Éxploration de la Mer 180, 184–201.

Collos, Y., Vaquer, A., and Souchu, P. (2005). Acclimation of nitrate uptake by phytoplankton to high substrate levels. J. Phycol. 41, 466–478.

Crespo, B.G., Espinoza-González, I.O., Teixeira, I.G., Castro, C.G., Figueiras, F.G., 2012. Structure of the microbial plankton community in the NW Iberian margin at the end of the upwelling season. J. Marine Syst. 95, 50–60.

Cropper T. E., Hanna, E., Bigg G. R., 2015. Spatial and temporal seasonal trends in coastal upwelling off Northwest Africa, 1981-2012. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **86***,* 94–111. doi:10.1016/j.dsr.2014.01.007

Demarcq, H. and Faure, V., 2000. Coastal upwelling and associated retention indices derived from satellite SST. Application to octopus vulgaris recruitment, Ocean. Acta 23, 391–408.

Du, X. and Peterson, W., 2009. Seasonal cycle of phytoplankton community composition in the coastal upwelling system off central oregon in 2009 Estuaries and Coasts 37 299–311

Nelson, D.M., Dortch, Q., 1996. Silicic acid depletion and silicon limitation in the plume of the Mississipi River: evidence from kinetic studies in spring and summer. Mar. Ecol. Prog. Ser. 136, 163–178.

Falkowski, P. G., Ziemann, D., Kolber, Z., Bienfang, P. K., 1991. Role of eddy pumping in enhancing primary production in the ocean, Nature, 352, 55–58, doi:10.1038/352055a0.

Fanning, K.A., 1992. Nutrient Provinces in the Sea: Concentration Ratios, Reaction Rate Ratios, and Ideal Covariation. J. Geophys. Res. 97 (C4), 5693 – 5712.

Fraga, S., Anderson, D. M., Bravo, I., Reguera, B., Steidinger, K. A., Yentsch, C. M., 1988. Influence of upwelling relaxation on dinoflagellates and shellfish toxicity in Ria de Vigo, Spain. Estuarine, Coastal and Shelf Science. 27:349–361.

Freudenthal, T., Neuer, S., Meggers, H., Davenport, R., Wefer, G., 2001. Influence of lateral particle advection and organic matter degradation on sediment accumulation and stable nitrogen isotope ratios along a productivity gradient in the Canary Islands region. Marine Geology 177, 93–109.

Freudenthal, T., Meggers, H., Henderiks, J., Kuhlmann, H., Moreno, A., Wefer, G., 2002. Upwelling intensity and filament activity off Morocco during the last 250,000 years. Deep-Sea Res. I 49, 3655–3674.

García-Muñoz, M., Arístegui, J., Pelegrí, J., Antoranz, A., Ojeda, A., Torres, M., 2005. Exchange of carbon by an upwelling filament off cape ghir (NW africa). J. Marine Syst. 54:83–95

Garcia-Reyes, M., Sydeman, W.J., Schoeman, D.S., Rykaczewski, R.R., Black, B.A., Smit, A.J., Bograd. S.J., 2015. Under pressure: climate change, upwelling, and ecosystem boundary upwelling ecosystems Front.Mar. Sci., 2 (2015), p. 109, 10.3389/ fmars.2015.00109

Gilpina, L.C., Davidson, K., Roberts, E., 2004. The influence of changes in nitrogen: silicon ratios on diatom growth dynamics. J. Sea Res. 51, 21–35.

Glibert, P.M., Al-Azri, A., Allen, J.I., Bouwman A.F., Beusen, A. H. W., Burford M. A., Harrison P. J., Zhou M., 2018. Key questions and recent research advances on harmful algal blooms in relation to nutrients and eutrophication. In: Glibert PM, Berdalet E, Burford M et al (eds) Global ecology and oceanography of harmful algal blooms. Springer, Cham, pp 229–259

González, H.E., Bernal, P., Ahumada R.,1987. Desarrollo de dominancia local en la taxocenosis de fitoplancton de Bahía de Concepción, Chile, durante un evento de surgencia. Rev. Chilena Hist. Nat., 60, pp. 19-35

González, H.E., Menschel, E., Aparicio, C., Barría, C., 2007. Spatial and temporal variability of microplankton and detritus, and their export to the shelf sediments in the upwelling area off Concepción, Chile (~36ºS), during 2002–2005. Prog. Oceanogr. 75, 435–451.

Gómez-Letona, M., Ramos, A.G., Coca J., Arístegui, J., 2017. Trends in Primary Production in the Canary Current Upwelling System—A Regional Perspective Comparing Remote Sensing Models. Front. Mar. Sci., 14 November 2017. https://doi.org/10.3389/fmars.2017.00370

Gruber, N., Frenzel, H., Marchesiello, P., McWilliams, J.C., Nagai, T., Plattner, G., 2007. On the role of eddies for coastal productivity and carbon export to the open-ocean. Geophysical Research Abstracts 9, 07743.

Gruber, N., Lachkar, Z., Frenzel, H., Marchesiello, P., Münnich, M., McWilliams, J.C., Nagai, T., Plattner, G.K., 2011. Eddy-induced reduction of biological production in eastern boundary upwelling systems. Nat. Geosci. 4 (11), 787–792.

Hagen, E., Zulicke, C., Feistel, R., 1996. Near-surface structures in the Cape Ghir filament off Morocco. Oceanologica Acta 19, 577–598.

Harrison, P.J., Davis, C.O., 1979. The use of outdoor phyto-plankton continuous cultures to analyze factors influencing species selection. J. Exp. Mar. Biol. Ecol. 14, 19–23.

Harrison, P.J., Conway, H.L., Holmes, R.W., Davis, C.O., 1977. Marine diatoms grown in chemostats under silicate or ammonium limitation. III. Cellular chemical composition and morphology of *Chaetoceros debilis*, *Skeletonema costatum*, and *Thalassiosira gravida*. Mar. Biol. 43, 19– 31.

Head, E.J.H., Harrison, W.G., Irwin, B.I., Horne, E.P.W., Li, W.K.W., 1996. Plankton dynamics and carbon flux in an area of upwelling off the coast of Morocco. Deep-Sea Res. I 43, 1713–1738.

Hernández-Guerra, A., and Nykjaer, L., 1997. Sea surface temperature variability off north-west Africa: 1981–1989. Int. J. Rem. Sens. 18, 2539–2558.

Herrera, L., Escribano, R., 2006. Factors structuring the phytoplankton community in the upwelling site off El Loa River in northern Chile. J. Marine Syst. 61, 13–38.

Howard, M.D.A., Sutula, M., Caron, D.A., Chao, Y., Farrara, J.D., Frenzel, H., Jones, B., Robertson, G., McLaughlin, K., Sengupta, A., 2014. Anthropogenic nutrient sources rival natural sources on small scales in the coastal waters of the Southern California Bight. Limnol. Oceanogr. 59, 285–297.

Huyer, A. 1983. Coastal upwelling in the California Current System. *Prog. Oceanogr.* 12, 259–284. doi: 10.1016/0079-6611(83)90010-1

Huyer, A., 1990. Shelf circulation. In: Le Mehaute, B., Hanes, D.M. (Eds.), The Sea, Vol 9: Ocean Engineering Science. Wiley, pp. 423–466.

Kahru, M., Kudela, R., Manzano-Sarabia, M., and Mitchell, B. G., 2009. Trends in primary production in the California Current detected with satellite data, J. Geophys. Res., 114, C02004, doi:10.1029/2008JC004979.

Kudela R. M, and Peterson T. D., 2009. Influence of a buoyant river plume on phytoplankton nutrient dynamics: what controls standing stocks and productivity? J. Geophys. Res. 114:C00B11.10.1029/ 2008JC004913

Kudo, I., 2003. Change in the uptake and cellular Si:N ratio in diatoms responding to the ambient Si:N ratio and growth phase. Mar. Biol. 143, 39–46.

Lachkar, Z., and Gruber, N., 2011. What controls biological productivity in coastal upwelling systems? Insights from a comparative modeling study, Biogeosciences, 8, 9901–9941, doi:10.5194/bgd-8- 9901-2011.

Lachkar, Z., Gruber, N., 2012. A comparative study of biological production in eastern boundary upwelling systems using an artificial neural network. Biogeosciences 9, 293–308.

Langlois, G.W., 2001. Shellfish Biotoxin Monthly Report. Technical Report, California Department of Health Services. pp. 1, 13.

Lauthuilière, C., Echevin, V., Lévy, M., 2008. Seasonal and intraseasonal surface chlorophyll-a variability along the northwest African coast. J. Geophys. Res. 113, C05007. http://dx.doi.org/10.1029/ 2007JC004433.

Lecher, A.L., Mackey, K., Kudela, R., Ryan, J., Fisher, A., Murray, J., Paytan, A., 2015. Nutrient loading through submarine groundwater discharge and phytoplankton growth in Monterey Bay, CA. Environ. Sci. Technol. http://dx.doi.org/10.1021/acs. est.5b00909 (150519131048004).

Lentz, S.J., 1992. The surface boundary layer in coastal upwelling regions. J. Phys. Oceanogr. 22, 1517–1539.

Lentz, S.J., Fewings, M.R., 2012. The wind- and wave-driven inner-shelf circulation. Ann. Rev. Mar. Sci. 4, 317–343. http://dx.doi.org/10.1146/ annurev-marine-120709-142745.

Levasseur, M.E., Therriault, J.C., 1987. Phytoplankton biomass and nutrient dynamics in a tidally induced upwelling: the role of the NO3:SiO4 ratio. Mar. Ecol. Progr. Ser. 39, 87–97.

Liu, Y. and Weisberg, R., 2007. Ocean currents and sea surface heights estimated across the West Florida Shelf, J. Phys. Oceanogr., 37, 1697–1713.

Mackas, D., Strub, P.T., Thomas, A.C., Montecino, V., 2006. Eastern ocean boundaries pan-regional view. In: Robinson, A.R., Brink, K.H. (Eds.), The Sea. Harvard Press Ltd., Boston, pp. 21–60, Chapter 2.

Marchesiello, P. and Estrade, P., 2009. Eddy activity and mixing in upwelling systems: a comparative study of Northwest Africa and California regions, Int. J. Earth Sci., 98, 299–308, doi:10.1007/s00531-007-0235-6.

Marra, J., Ho, C., and Trees, C., 2003. An alternative algorithm for the calculation of primary productivity from remote sensing data, Technical LDEO-2003-1.

McGillicuddy, D.J., Robinson, A.R., Siegel, D.A., Jannasch, H.W., Johnson, R., Dickeys, T., McNeil, J., Michaels, A.F., Knap, A.H., 1998. Influence of mesoscale eddies on new production in the Sargasso Sea. Nature 394, 263–266. http://dx.doi.org/ 10.1038/28367.

Messié, M., and F. Chavez, 2015, Seasonal regulation of primary production in eastern boundary upwelling systems,. Prog. Oceanogr., 134,1–18.

Morales, C. E. and V. Anabalón (2012), Phytoplankton biomass and microbial abundances during the spring upwelling season in the coastal area off Concepción, central-southern Chile: Variability around a time series station, Prog. Oceanogr., 92, 81-91.

Morales, C.E., Anabalon, V., Bento, J.P., Hormazabal, S., Cornejo, M., Correa-Ramirez, M.A., Silva, N., 2017. 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). J. Geophys. Res. Ocean, 122, 8944–8965.

Morel, F.M.M., 2008. The co-evolution of phytoplankton and trace element cycles in the oceans. Geobiology 6 (3):318-324. doi: 10.1111/j.1472-4669.2008.00144.x.

Nelson, D.M., Dortch, Q., 1996. Silicic acid depletion and silicon limitation in the plume of the Mississipi River: evidence from kinetic studies in spring and summer. Mar. Ecol. Prog. Ser. 136, 163–178.

Neuer, S., Freudenthal, T., Davenport, R., Llinás, O., Rueda, M.J., 2002. Seasonality of surface water properties and particle flux along productivity gradient off NW Africa. Deep Sea Res. II 49, 3561–3567.

Nieto, N., Demarcq, H., McClatchie, S., 2012. Mesoscale frontal structures in the Canary Upwelling System: new front and filament detection algorithms applied to spatial and temporal patterns. Remote Sens. Environ. 123, 339– 346.

Obata, A., Ishizaka, J., Endoh, M., 1996. Global verification of critical depth theory for phytoplankton bloom with climatological in situ temperature and satellite ocean color data, J. Geophys. Res., 101, 20657–20667.

Patti, B., Guisande, C., Vergara, A.R., Riveiro, I., Maneiro, I., Barreiro, A., Bonanno, A., Buscaino, G., Cuttitta, A., Basilone, G., Mazzola, S., 2008. Factors responsible for the differences in satellite-based chlorophyll a concentration between the major global upwelling areas. Estuarine, Coastal and Shelf Science 76, 775–786.http://dx.doi.org/10.1016/ j.ecss.2007.08.005.

Pelegrí J, Arístegui J, Cana L, Gonzalez-Davila M, Hernandez-Guerra A, Hernandez-Leon S, Marrero-Dıaz A, Montero M, Sangra P, Santana-Casiano M., 2005a. Coupling between the open ocean and the coastal upwelling region off northwest africa: water recirculation and offshore pumping of organic matter. J. Marine Syst. 54(1-4):3–37

Pelegrí J, Marrero-Dıaz A, Ratsimandresy A, Antoranz A, Cisneros-Aguirre J, Gordo C, Grisolıa D, Hernandez-Guerra A, Laiz I, Martınez A, Parrilla G, Perez-Rodrıguez P, Rodrıguez-Santana A, Sangra P., 2005b. Hydrographic cruises off northwest africa: the canary current and the cape ghir region. J. Marine Syst. 54(1-4):39–63

Pitcher, GC.; Boyd, AJ., 1996. Across-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., editors. Harmful and Toxic Algal Blooms. Intergovernmental Oceanographic Commission of UNESCO. p. 243-246.

Platt, T., Bird, D. F., Sathyendranath, S. 1991. Critical Depth and Marine Primary Production, Proc. Roy. Soc. Lnd., 246, 205–217, doi:10.1098/rspb.1991.0146, 1991.

Probyn TA, Pitcher GC, Monteiro PMS, Boyd AJ, Nelson G. 2000. Physical processes contributing to harmful algal blooms in Saldanha Bay, South Africa. South African J. Marine Sci. 22:285–297.

Reifel, K. M., Corcoran, A. A., Cash, C., Shipe, R. and Jones, B. H., 2013. Effects of a surfacing effluent plume on a coastal phytoplank- ton community. Contin. Shelf Res., 60, 38–50.

Romero, O.E., Lange, C.B., Wefer, G., 2002. Interannual variability (1988–1991) of siliceous phytoplankton fluxes off northwest Africa. J. Plankton Res. 24, 1035–1046.

Sánchez, G. E, Lange, C.B., González, H. E., Vargas, G., Muñoz, P., Cisternas, C., Pantoja S., 2012. Siliceous microorganisms in the upwelling center off Concepción, Chile (36°S): Preservation in surface sediments and downcore fluctuations during the past ~150 years. Prog. Oceanogr., 92-95, 50-65.

Smayda, T.J., 1997. What is a bloom? A commentary. Limnol. Oceanogr., 1132–1136.

Sordo, I., Barton, E.D., Cotos, J.M., Pazos, Y., 2001. An inshore poleward current in the NW of the Iberian Peninsula detected from satellite images, and its relation with G. catenatum and D. acuminata blooms in the Galician rias. Estuarine Coastal and Shelf Science 53, 787–799.

Sverdrup, H. U., 1953. On conditions for the vernal blooming of phytoplankton, Journal du Conseil – Conseil Permanent International Pour L'exploration de la Mer, 287–295.

Sydeman, W.J., García-Reyes, M., Schoeman, D.S., Rykaczewski, R.R., Thompson, S.A., Black, B.A., Bograd, S.J., 2014. Climate change and wind intensification in coastal upwelling ecosystems. Science 345, 77–80.

Treguer, P., Le Corre, P., 1978. The ratios of nitrate phosphate, and silicate during uptake and regeneration phases of the Moroccan upwelling regime. Deep-Sea Res., 26A, 163-184.

Van Camp, L., Nykjaer, L., Mittelstaedt, E., Schlittenhakdt, P., 1991. Upwelling and boundary circulation off Northwest Africa as depicted by infrared and visible satellite observations. Progr. Oceanogr. 26, 357–402.

Van Ruth, P.D., Qin, J.G., Branford, A.J., 2012. Size dependent competition in centric diatoms as a function of nitrogen and silicon availability. Open J. Marine Sci. 2, 33–42.

Wilkerson F. and Dugdale R. C., 2008. Coastal Upwelling. In: Nitrogen in the marine environment (eds) D G Capone, D A Bronk, M R Mulholland and E J Carpenter (Springer) doi: 10.1016/B978-0-12-372522-6.00007-4

Yamamoto, T., and Tsuchiya, H., 1995. Physiological response of Si-limited Skeletonema costatum to silicate supply with salinity decrease. Bull. Plankton Soc. Japan 42, 1–17.

Yévenes, M., Figueroa, R., Parra, O., Farias, L., 2015. Inter-annual variability of dissolved inorganic nitrogen in the Biobío River, Central Chile: an analysis base on a decadal database along with 1-D reactive transport modeling. Hydrol. Earth Syst. Sci. – Discussion 12, 705–738.

# CONCLUSIONS

***Mata ki te vai-kava***
*Los ojos que miran al mar*
***Idioma y cultura rapa niu***

# CONCLUSIONS

1. At the seasonal to annual scale, wind-driven upwelling was identified as a common forcing of microbial community structure in both EBUSs. In the C. Ghir EBUS, where upwelling is recurrent during the year, different upwelling phases (mainky weak to moderate) contributed to changes in microbial community structure. In the Concepción EBUS, where upwelling is highly seasonal, the annual cycle of upwelling strongly influenced microbial community structure.

2. In the C. Ghir EBUS, the microplankton (mainly diatoms and auto/mixotrophic dinoflagellates) made the highest contributions to photoautotrophic carbon (C) biomass but the nanoplankton (mainly flagellates and dinoflagellates) made the largest contributions to total chlorophyll-a (Chl-a) in most cases. A mixed composition of functional groups of autotrophs/mixotrophs in the coastal and CTZ in this area is probably the result of nutrient contents in the upwelled waters. In the Concepción EBUS, total Chl-a and C-biomass was dominated by the microplanktonic fraction (mainly photoautotrophic diatoms) during the upwelling period. Increases in total mean abundance and biomass of phytoplankton were attributed to a few dominant diatom taxa, with a change of at least one order of magnitude between spring-summer upwelling compared to the autumn-winter non-upwelling season.

These changes were associated with annual changes in surface temperature and salinity, whereas macro-nutrient concentrations remained relatively high during the year.

3. At the interannual scale in the EBUS of Concepción, total micro-phytoplankton abundance and biomass decreased during the upwelling season of the 2006–2009 period compared with the 2002–2006 period, notably due to lower abundances of the diatom genera *Skeletonema* and *Leptocylindr*us, but the relative dominance of a few diatom taxa was maintained. The 2006–2009 period was characterized by higher upwelling intensity, colder and higher salinity waters, and changes in nutrient concentrations and ratios compared with the first period. The dominant genera *Chaetoceros* and *Thalassiosira* persisted during both periods, suggesting that they rapidly adapt to changing environmental conditions.

4. In the CTZ of both EBUSs, where meso- and sub-mesoscale activity plays an important influence on microbial community structure, significant differences between coastal and CTZ community structures were detected. In the case of the Concepción EBUS, the interaction between an upwelling front and an anticyclonic subsurface eddy was found to contribute to an active exchange of coastal and oceanic microbial components, as exemplified by taxa of microplanktonic diatoms. These results suggest that, not only there is an advection or loss of phytoplankton from the coastal via mesoscale activity in EBUSs, but that there is also an input of oceanic taxa towards the coast whenever submesoscale dynamics allow for coastal-oceanic exchanges of waters.

5. owing to the inherent oceanographic variability of ebuss and to the recurrence of microbial community patterns in them, they are expected to have a higher resilience than other ocean systems. today, however, it is still difficult to predict with certainty how the ebuss will respond to potential long-term changes in the mean magnitude of upwelling favorable winds at mid-latitudes. under a scenario of upwelling wind intensification in the ebus off central-southern chile, as suggested recently, increasing offshore advection and higher water column turbulence could negatively influence the development and the retention of phytoplankton blooms in the coastal zone. associated with this, colder atmospheric conditions and drought development would negatively impact the continental input of nutrients to the coastal zone in mid-latitude ebuss, which can induce significant changes in the microbial community structure and, probably, can modify the trophic structure and carbon flux in the system. in contrast, the absence of evidence for wind intensification in the canary system implies that no large changes in microbial community are to be expected, unless regional or basin-scale processes associated with changes in ocean circulation promote them.

***Kikin kawsakuyqa gallarimun***
***chay yachannay tukukusganpin***
*La libertad comienza allí donde*
*se acaba la ignorancia*
***Idioma y Cultura quechua***

# SUMMARY IN SPANISH

***Kikin kawsakuyqa gallarimun***
***chay yachannay tukukusganpin***
*La libertad comienza allí donde*
*se acaba la ignorancia*
***Idioma y Cultura quechua***

# RESUMEN EN CASTELLANO

Entre los sistemas pelágicos, los sistemas de surgencia de borde oriental (EBUSs: Eastern Boundary Upwelling System) son reconocidos por sus altos niveles productivos y de biomasa de fitoplancton en la zona costera (Chavez and Messié, 2009; Arístegui et al., 2009; Capone and Hutchins, 2013). Sin embargo, la estructura de las comunidades microbianas en EBUSs y su variabilidad espacio-temporal son aspectos que permanecen pobremente caracterizados en algunas regiones de los principales EBUSs, principalmente a causa de las escasas series de tiempo in situ existentes (Arístegui et al., 2009; Demarcq, 2009; Chavez and Messié, 2009; Hutchings et al., 2009; García-Reyes et al., 2015). Las estructuras comunitarias del fitoplancton en los EBUS de Canarias y Humboldt son, entre todas, las menos conocidas en términos de una caracterización detallada de sus componentes (más allá de Chl-a total) y de sus variaciones espaciales y temporales. Sobre esta base, esta tesis se enfoca en dos sub-regiones de estos EBUSs, una que representa el sistema EBUS del Atlántico, con surgencia costera semipermanente (Cabo Ghir, ~31ºN), y otra que representa el sistema EBUS del Pacífico, con surgencia costera estacional (Concepción). El enfoque principal es entender los cambios espaciales y temporales a los que están sujetas las comunidades microbianas planctónicas (pico- a micro-plancton) en estos EBUSs, especialmente en cuanto a los efectos que tienen sobre ellas la surgencia costera y la actividad

de mesoescala. En la escala temporal, se enfatizan las dinámicas estacionales-anuales en ambos sistemas, además de la interanual en el sistema de Concepción; en la escala espacial, se incluyen las variaciones en la zona de surgencia costera y en la zona de transcición costera (ZTC). Los resultados de este estudio son relevantes para comprender el funcionamiento de los EBUS en términos de la dinámica trófica y el ciclo del carbono a escala regional-global, y para predecir las respuestas de estos ecosistemas a los efectos del cambio climático, tales como la posible intensificación de los vientos favor costera la surgencia en algunas regiones de los EBUS

En **primer capítulo** [*The structure of planktonic communities under variable coastal upwelling conditions off Cape Ghir (31°N) in the Canary Current System (NW Africa)*] se enfocó en los efectos de las variaciones espaciales (transecta costa-océano con 7 estaciones) y temporales (5 cruceros entre Diciembre 2008 y Octubre 2009) en las condiciones oceanográficas sobre la estructura de comunidades planctónicas (grupos funcionales, tamaño y composición de taxa, abundancia y biomasa de carbono). El objetivo específico de este capítulo fue caracterizar las variaciones estacionales en las condiciones oceanográficas de la zona surgencia costera y la ZTC frente a Ghir y su influencia sobre las variaciones en la estructura de comunidades microbianas.

Los resultados obtenidos indican que variaciones espaciales en las condiciones de surgencia y en la estructura de comunidades planctónicas (grupos funcionales, tamaño y composición de taxa, abundancia y biomasa de carbono) fueron significativas. Un análisis multivariado de las variables ambientales permitió tanto la separación espacial de las estaciones, basada principalmente en diferencias en la concentración de nutrientes, y una distinción temporal de fases de surgencia, basada principalmente en diferencias en la temperatura superficial del mar y el número de días favorables a la surgencia. Estos grupos también fueron representativos de la variabilidad espacio-temporal en las comunidades planctónicas, lo que sugiere que las condiciones de surgencia influyen directamente en su estructura. Para la mayoría de los cruceros, el microplancton (principalmente diatomeas y dinoflagelados auto-mixotróficos) presentó las más altas contribuciones en biomasa de carbono fotoautótrofo (C), pero el nanoplancton (principalmente flagelados y dinoflagelados) realizó las mayores contribuciones al total de Chl-a. Las proporciones medias de biomasa entre heterótrofos y autótrofos (desde pico- a microplancton) fueron, en su mayoría, ≤1 (pirámide normal), como se espera para zonas costeras productivas, solo cuando se consideró la contribución de la mixotrofía. Una composición mixta de grupos funcionales de autótrofos - mixótrofos en la zona de estudio es probablemente el resultado de el contenido de nutrientes en las aguas surgentes dado que se detectó en algunos cruceros una potencial limitación por silicatos o nitratos junto con una proporción C:Chl-a relativamente alta en el microfitoplancton. Los cambios temporales en los taxones de diatomeas con diferentes requerimientos de nutrientes también sugieren una fuerte influencia de los nutrientes. Las cocnetraciones de nutrientes comparativamente más bajos en esta zona están vinculados a los patrones de circulación regional, una plataforma relativamente estrecha (menor tiempo de residencia de las aguas surgentes), un nivel relativamente más alto de actividad de mesoescala que en zonas aledañas, y con intensidades de viento débiles a moderadas la mayor parte del año.

El **segundo capítulo** (*Phytoplankton biomass and microbial abundances during the spring upwelling season in the coastal area off Concepción, central-southern Chile: Variability around a time series station*) se centró en la variabilidad espacial de las condiciones oceanográficas en la zona de surgencia (data colectada mensualmente en la St. 18 y en tres curceros incluyendo 8 estaciones localizadas sobre la plataforma continental y el quiebre de la plataforma en el área alrededor de St. 18) y su asociación con la estructura de comunidades planctónicas (Chl-a tamaño fraccionado y abundancia microbiana) en la capa superficial durante la época de surgencia (primavera de 2004, 2005 y 2006) en el sistema de Concepción. El objetivo específico del estudio fue evaluar la representatividad de la serie de tiempo St. 18 como típica del sistema de surgencia costera en la región centro-sur de Chile en términos de la variabilidad oceanográfica y de la estructura de las comunidades microbianas durante la época de surgencia.

Los resultados muestran que la variabilidad espacial (submesoescala) en Chl-a y los componentes microbianos en la zona de surgencia costera no fue significativa, pero la dispersión de los datos alrededor de los valores medios fue alta. La estructura de la columna de agua (temperatura y salinidad) en la capa superficial explicó una fracción significativa (25-65%) de la variabilidad espacial en la mayoría de los componentes planctónicos; sus respuestas a la variabilidad oceanográfica fueron lineales en algunos casos y no-lineales en otros. En su mayor parte, la St. 18 representa adecuadamente las condiciones oceanográficas medias y la estructura de las comunidades planctónicas en las aguas costeras frente a Concepción durante la primavera. Sin embargo, la variabilidad espacial debe tenerse en cuenta en las interpretaciones de los cambios temporales en esta estación fija, así como en las evaluaciones del flujo de carbono en el sistema así como en los procesos de exportación desde este sistema de surgencia.

El **tercer capítulo** (*Micro-phytoplankton community structure in the coastal upwelling zone off Concepción (central Chile): Annual and interannual fluctuations in a highly dynamic environment*) se enfocó en analizar la variabilidad anual e interanual en la estructura de comunidades microfitoplanctónicas en el sistema costero de Concepción y su asociación con las fluctuaciones oceanográficas (7 años de series de tiempo in situ St. 18: 2002-2009). El objetivo específico del estudio fue caracterizar la variabilidad oceanográfica estacional e interanual en la zona de surgencia frente a Concepción y su influencia sobre las variaciones en la estructura de comunidades microbianas.

Los resultados indican que, en la escala anual, la abundancia y biomasa media totales son atribuidas a unos pocos taxones dominantes de diatomeas y son al menos un orden de magnitud mayor durante la primavera-verano comparado con el otoño-invierno. Estas variaciones anuales están asociadas a cambios en la surgencia, salinidad y temperatura superficiales, mientras que las concentraciones de macronutrientes se mantuvieron relativamente altas durante todo el año. En la escala interanual, la abundancia y biomasa media totales disminuyeron durante la temporada de surgencia en el período 2006-2009 en comparación con el período 2002-2006, debido principalmente a la menor abundancia de *Skeletonema* y *Leptocylindrus*, pero se mantuvo la dominancia relativa de unos pocos taxones. El período 2006-2009 se caracterizó por una mayor intensidad de la surgencia, aguas más frías, mayor salinidad y cambios en las concentraciones de nutrientes y sus proporciones en comparación con el primer período. Los cambios interanuales en la comunidad del microfitoplancton se asociaron principalmente con cambios en salinidad y temperatura superficiales (cambios en la intensidad de afloramiento), pero también con cambios en las proporciones Si/N y N/P que podrían estar relacionados a otros procesos de aportes derivados del continente.

El **cuarto capítulo** y último *(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))* se enfocó en el análisis de los procesos de mesoescala y submesoescala (como frentes y remolinos) que contribuyen a influenciar la distribución de fitoplancton y el intercambio de diatomeas dominantes en la zona de surgencia costera y aquellas en la ZTC (crucero corto en verano y en la zona de surgencia al N de Punta Lavapié, incluyendo dos transectas perpendiculares a la costa, combinado con datos satelitales para el periodo enero-febrero 2014). El objetivo específico fue evaluar la influencia de la interacción frente-remolino sobre la distribución y estructura de comunidades fitoplanctónicas y sobre los intercambios de diatomeas entre la zona de surgencia costera y la ZTC frente a Concepción.

Los resultados muestran que el crucero se realizó durante un evento de relajación de los vientos y que un frente termohalino (FRN-1) flanqueado por un remolino de mesoescala anticiclónico e intra-termoclina (ITE-1) persistieron durante el período de estudio. Durante el crucero, el ITE-1 contribuyó a una intrusión de aguas oceánicas cálidas hacia la costa (sección sur) y a una advección mar afuera de aguas costeras frías (sección norte), formando este último un filamento frío y de alta concentración de Chl-a. Las biomasas totales de fitoplancton y de diatomeas (muestreos in situ) fueron altas en la capa superficial en FRN-1 y en la subsuperficie en ITE-1, mientras que los valores en la zona costera fueron más bajos y dominadopor células pequeñas. Especies de diatomeas típicas de la zona costera y especies dominantes en aguas oceánicas fueron ambas encontradas en el área de interacción de FRN-1 e ITE-1, sugiriendo que esta mezcla es el resultado de la advección desde y hacia la costa. En general, la interacciones frente-remolino en EBUSs podrían contribuir a incrementar los intercambios cruzados de plancton costero y oceánico, además de sustentar el crecimiento de fitoplancton en el área de quiebre de la plataforma a través de inyecciones verticales localizadas de nutrientes en la zona frontal, combinadas con la advección y el bombeo vertical de nutrientes hacia superficie generadas por ITEs.

**Las conclusiones derivadas de esta tesis son las siguientes:**

1. A la escala estacional a anual, la surgencia costera inducida por vientos fue identificada como un forzante común sobre la estructura de comunidades microbianas en ambos EBUSs. En el EBUS de C. Ghir, donde la surgencia es recurrente durante el año, diferentes fases de surgencia (principalmente débiles a moderadas) contribuyen a los cambios en la estructura microbiana. En el EBUS de Concepción, donde la surgencia es fuertemente estacional, el ciclo anual de la surgencia costera influencia muy significativamente la estructura de comunidades microbianas.

2. En el EBUS de C. Ghir, el microplancton (principalmente diatomeas y dinoflagelados auto/mixotróficos) presentó las más altas contribuciones de biomasa de carbono fotoautótrofo (C), pero el nanoplancton (principalmente flagelados y dinoflagelados) aportó las mayores contribuciones a la Chl-a total en la mayoría de los casos. La composición mixta de grupos funcionales autótrofos/mixótrofos en la zona costera y ZTC en esta área es probablemente el resultado del contenido de nutrientes en las aguas de surgencia. En el EBUS de Concepción, los mayores contribuciones a la Chl-a total fueron de la fracción microplanctónica (principalmente diatomeas fotoautótrofas) durante el periodo de surgencia. Los aumentos en la abundancia y la biomasa media totales de fitoplancton se atribuyeron a unos pocos taxones dominantes de diatomeas, con un cambio de al menos un orden de magnitud entre el periodo de surgencia en comparación con el periodo de no surgencia. Estos cambios estuvieron asociados a cambios anuales en la temperatura y salinidad superficiales, mientras que las concentraciones de macronutrientes se mantuvieron altas durante el año.

3. En escala interanual en el EBUS de Concepción, la abundancia y la biomasa totales de micofitoplancton disminuyeron durante la temporada de afloramiento del período 2006-2009 en comparación con el período 2002-2006, debido principalmente a la menor abundancia de los géneros de diatomeas *Skeletonema* y *Leptocylindrus* , pero se mantuvo el dominio relativo de unos pocos taxones de diatomeas. El período 2006-2009 se caracterizó por una mayor intensidad de surgencia, aguas con alta salinidad, más frías y cambios en las concentraciones y proporciones de nutrientes en comparación con el primer período. Los géneros dominantes *Chaetoceros* y *Thalassiosira* persistieron durante ambos períodos, lo que sugiere que se adaptan rápidamente a las cambiantes condiciones ambientales.

4. En la ZTC de ambos EBUSs, donde la actividad de mesoescala y submesoescala tiene una influencia importante en la estructura de comunidades microbianas, se detectaron claras diferencias espaciales a estas escalas en la estructura de las comunidades costeras y de la ZTC. En el caso del EBUS de Concepción, la interacción entre un frente costero y un remolino anticiclónico contribuyó a un intercambio activo de componentes microbianos entre la costa y la ZTC, ejemplificado en el caso de taxones de diatomeas microplanctónicas. Estos resultados sugieren que no solo hay una advección o pérdida de fitoplancton costero debido a la actividad de mesoescala en EBUSs, sino que también hay un aporte de taxones oceánicos hacia la costa cada vez que la dinámica submesoescala permite intercambios de aguas costeras y oceánicas.

5. Debido a la variabilidad oceanográfica inherente a los EBUSs y a la recurrencia de patrones en las comunidades microbianas en ellos, se espera que estos sistemas presenten una mayor resiliencia que otros sistemas marinos. A la fecha, sin embargo, aún es difícil predecir con certeza cómo los EBUSs responderán a cambios potenciales en la magnitud

media de los vientos favorables a la surgencia en las latitudes medias. Bajo un escenario de intensificación del viento favorable a la surgencia en el EBUS frente a Chile centro-sur, como se ha sugerido recientemente, un aumento en la advección costa afuera y una mayor turbulencia en la columna de agua podría tener un efecto negativo sobre el desarrollo y la retención de afloramientos de fitoplancton en la zona costera. En asociación con esto, condiciones atmosféricas más frías y de sequía podrían afectar los aportes continentales de nutrientes a la zona costera de EBUSs en latitudes medias, lo que podría inducir cambios significativos en la estructura comunitaria microbiana y, probablemente, podría modificar la estructura trófica y el flujo de carbono en el sistema. En contraste, la ausencia de evidencia sobre intensificación del viento en el sistema de Canarias implica que no es esperable que ocurran grandes cambios en las comunidades microbianas, a menos que procesos de escala regional a cuenca asociados a cambios en la circulación en los océanos los promuevan.

# REFERENCES

Arístegui J., Barton E.D., Álvarez-Salgado, X.A., Santos A.M.P., Figueiras, F.G., Kifani, S., Hernández-León, S., van Mason, E., Machú, E., Demarcq, H., 2009. Sub-regional ecosystem variability in the Canary Current upwelling. Prog. Oceanogr. 83, 33-48.

Capone, D.G., Hutchins, D.A. (2013). Microbial biogeochemistry of coastal upwelling regimes in a changing ocean. Nat. Geosci., 6, 711–717.

Chavez, F.P., Messié, M., 2009. A comparison of eastern boundary upwelling systems. Prog. Oceanogr. 83, 80–96.

Demarcq, H., 2009. Trends in primary production, sea surface temperature and wind in upwelling systems (1998–2007). Prog. Oceanogr. 83, 376–385, http://dx.doi.org/ 10.1016/ j.pocean. 2009.07.022.

García-Reyes M., Sydeman W.J., Schoeman D.S., Rykaczewski R.R., Black B.A., Smit A.J. Bograd S.J.,2015. Under pressure: climate change, upwelling, and ecosystem boundary upwelling ecosystems, Front. Mar. Sci. 2, 109. http://dx.doi.org/10.3389/ fmars. 2015.00109.

Hutchings, L., van der Lingen, C., Shannon, L., Crawford, R., Verheye, H.M.S., Bartholomae, C., van der Plas, A., Louw, D., Kreiner, A., Ostrowski, M., Fidel, Q., Barlow, R., Lamont, T., Coetzee, J., Shillington, F., Veitch, J., Currie, J., Monteiro, P. ,2009. The Benguela Current: an ecosystem of four components. Prog. Oceanogr. doi:10.1016/j.pocean.2009.07.046.

***Fütra che may fey ñi wilüfan zuamkelay***
***chongümalelafiel kakelu ñi pelom***
*Grande es aquel que para brillar no*
*necesita apagar la luz de los demás*
***Idioma y cultura  mapuche***

# ACKNOWLEDGEMENTS

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***iñchiñ tangen-ngenkülelaiñ,***
***iñchiñ may ta mapu ngeiñ***
*La tierra no es nuestra,*
*nosotros somos de la tierra*
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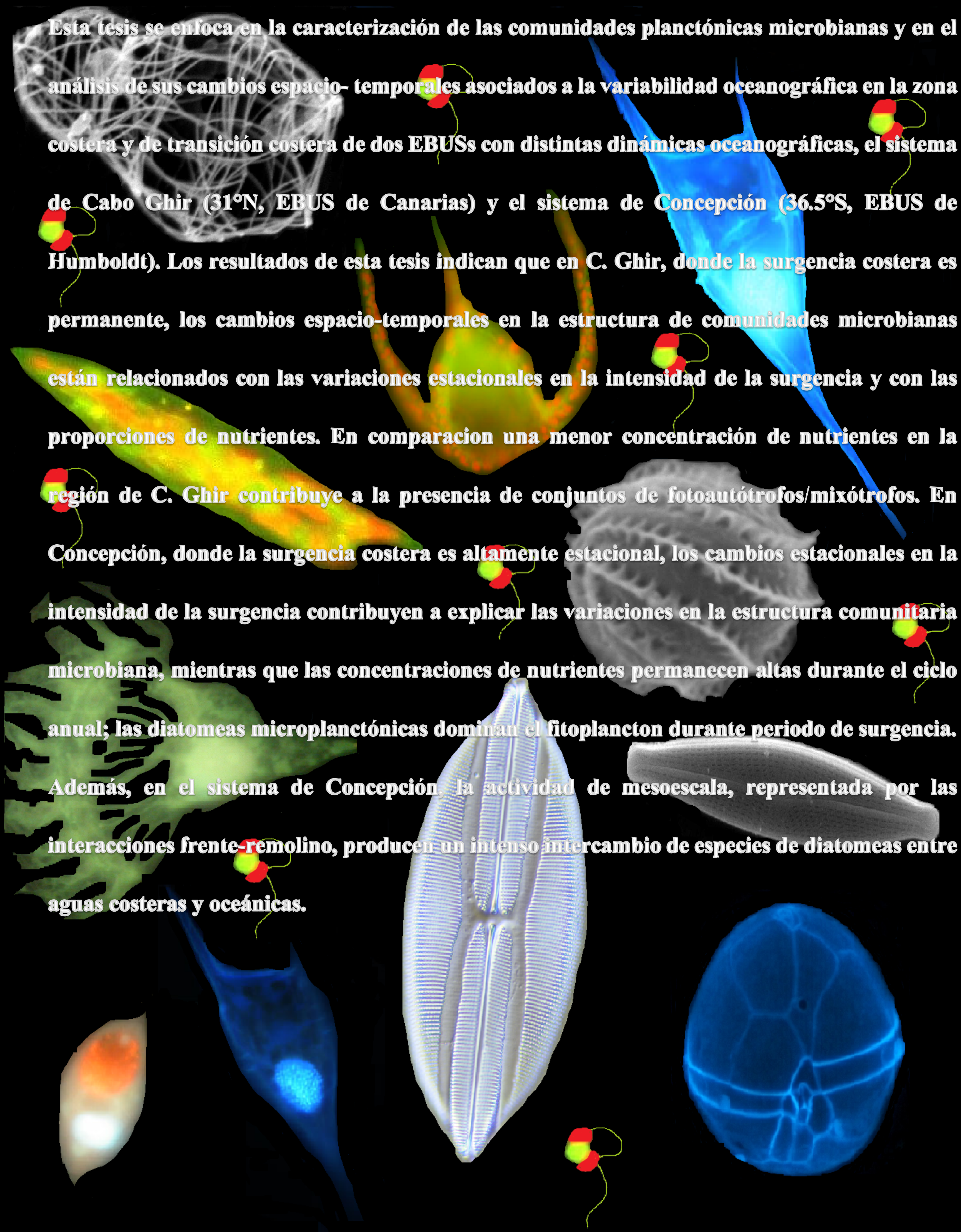

Esta tesis se enfoca en la caracterización de las comunidades planctónicas microbianas y en el análisis de sus cambios espacio- temporales asociados a la variabilidad oceanográfica en la zona costera y de transición costera de dos EBUSs con distintas dinámicas oceanográficas, el sistema de Cabo Ghir (31°N, EBUS de Canarias) y el sistema de Concepción (36.5°S, EBUS de Humboldt). Los resultados de esta tesis indican que en C. Ghir, donde la surgencia costera es permanente, los cambios espacio-temporales en la estructura de comunidades microbianas están relacionados con las variaciones estacionales en la intensidad de la surgencia y con las proporciones de nutrientes. En comparacion una menor concentración de nutrientes en la región de C. Ghir contribuye a la presencia de conjuntos de fotoautótrofos/mixótrofos. En Concepción, donde la surgencia costera es altamente estacional, los cambios estacionales en la intensidad de la surgencia contribuyen a explicar las variaciones en la estructura comunitaria microbiana, mientras que las concentraciones de nutrientes permanecen altas durante el ciclo anual; las diatomeas microplanctónicas dominan el fitoplancton durante periodo de surgencia. Además, en el sistema de Concepción, la actividad de mesoescala, representada por las interacciones frente-remolino, producen un intenso intercambio de especies de diatomeas entre aguas costeras y oceánicas.