

Impact of a cyclonic mesoscale eddy on the structure of the planktonic community at the submesoscale range

Esther Velasco Senovilla

Año 2017

Tutores: Javier Arístegui Ruiz y Pablo Sangrà Inciarte.



Trabajo Fin de Título para la obtención del título: Máster Interuniversitario en Oceanografía.



Impact of a cyclonic mesoscale eddy on the structure of the planktonic community at the submesoscale range

Universidad de las Palmas de Gran Canaria Máster Interuniversitario en Oceanografía

By: Esther Velasco Senovilla.

Directed by: Javier Arístegui Ruiz and Pablo Sangrà Inciarte.

Grupo de Oceanografía Biológica y Grupo de Oceanografía Física del Instituto de Oceanografía y Cambio Global.

Proyect: RODA (Remolinos Oceánicos y Deposición Atmosférica)

Esther Velasco Senovilla

Javier Arístegui Ruiz

Las Palmas de Gran Canaria, 2017

CONTENTS

Abstra	act	3				
1. Introduction						
2. Mat	2. Materials and methods					
	2.1. Study area and sampling	7				
	2.2. Analyses of plankton samples	8				
	2.3. Nutrient analysis					
	2.4. Data analysis	8				
	2.4.1. Hydrographic data	8				
	2.4.2. Conversion of planktonic cell numbers to biomass	9				
	2.4.3. Heterotrophic – autotrophic balance	9				
3. Res	3. Results					
	3.1. Signature of mesoscale structure in the hydrographic fields	10				
	3.2. Chlorophyll and nitrates	13				
	3.3. Structure of planktonic community	14				
4. Discussion						
5. Conclusions						
6. References						
Anexo	Anexo I					

Abstract

Mesoscale and submesoscale features of associated with the eddy field located downstream of the island of Gran Canaria are studied to assess their impact on the structure and distribution of the planktonic community. This study shows hydrographic and biological information based on XBT (Expendable Bathythermographs) and biogeochemical Rosette-CTD casts at a high resolution (near submesoscale) crossing a cyclonic eddy and its marginal frontal regions. Along the transect 4 main features were monitored: the margin of a large anticyclonic eddy, a large cyclonic eddy (affected by a filament from the North Africa Upwelling System), the sharp front between the two eddies, and a small submesoscale anticyclonic eddy. The "Vertical Oceanic Pump" (VOP) in the zone is typified by two main mechanisms, eddy-pumping, generated by the cyclonic eddy, and ASC (ageostrophic secondary circulation), produced at the fronts. Both processes affect the physicochemical nature of the water column, encompassing nutrient distribution. The planktonic community, which includes bacteria, cyanobacteria (Synechococcus and Prochlorococcus), autotrophic picoeukaryotes, and heterotrophic and autotrophic nanoflagellates show a heterogeneous distribution close to the submesoscale range. The analysis suggests that physical forcing (eddy pumping and ASC) is the main reason for the distribution of organisms, together with the filament, which introduces upwelled waters modifying the concentration of nutrients and organisms. The greatest accomplishment of this study compared with other eddy field studies, is that we have used a smaller scale resolution to look in detail and understand the physical forcing on the planktonic community distribution, and hence in the VOP associated with mesoscale features. Our results suggest that processes at submesoscale have a large effect on biogeochemical processes in the ocean, where eddies and frontal structures are dominant.

1. Introduction

Mesoscale eddies are ubiquitous features of the world ocean (Chelton et al., 2007) and may occupy at any time the 25 % of the ocean sea surface (Chaigneau et al., 2009). There are three types of mesoscale eddies: cyclones, anticyclones and intrathermocline eddies (ITE), which are a particular type of anticyclones. Their radius is of the order of the first baroclinic Rossby radius of deformation, O (50 km), being thus geostrophycally adjusted. Therefore, due to the thermal wind balance cyclonic circulation in cyclonic eddies leads to the doming of the isopycnals whereas anticyclonic circulation in anticyclonic eddies leads to the bowl shape of the isopycnals (eg. Sangrà et al., 2007). In the particular case of ITE the subsurface intensification of the anticyclonic circulation leads to dome-shaped isopycnals in the upper layer and bowl-shaped in the lower layers (e.g. Gordon 2002).

The "Vertical Oceanic Pump", VOP (sensu Klein and Lapeyre, 2009), has been defined as those physical processes, mainly at the submesoscale range (10 km), that drive intense nutrient fluxes into the euphotic layer, enhancing primary production and vertical carbon fluxes, thus having a great impact on the marine carbon cycle. As mesoscale eddies are ubiquitous features, the study of the VOP in these structures is of particular importance. Those processes that tend to destroy the thermal wind balance are counteracted by the establishment of vertical velocities that tend to restore this balance setting up the ageostrophic secondary circulation (), which is critical for the VOP (see review by Mahadevan, 2016). Several mechanisms associated with the ASC inside mesoscale eddies have been proposed (see review by McGillicuddy, 2016). Of particular interest for this study are the "eddy pumping" mechanism (Falkowski et al., 1991; Gaube et al., 2014) and frontogenesis resulting from eddy-eddy interaction (Pollard and Treguier, 1992; Mahadevan and Tandom, 2006, Omand et al., 2015).

"Eddy pumping" is used to define the upwelling and downwelling generated during the intensification of eddies (Falkowski et al., 1999). When cyclonic (anticyclonic) eddies intensify, the isopycnals are uplifted (downlifted) inducing an upwelling (downwelling) at the eddy centre, with associated vertical velocities up to 0.8-0.9 m d-1 (Gaube et al., 2014). This may lead to a surface enhancement of chlorophyll in cyclones and a depression and downward transport of chlorophyll in anticyclones (McGillicuddy et al., 1998; Siegel et al., 1999, 2008, 2011; Gaube et al., 2014; Basterretxea et al., 2002). Eddy pumping mainly occurs during the early life stages of eddies, but sometimes also during eddy-eddy interactions (Flierl and McGillicuddy, 2002) as it is the case for this study. In cyclonic eddies the upward flux of nutrient would enhance phytoplankton growth rates, increasing phytoplankton biomass and chlorophyll (Gaube et al., 2014). In contrast, in anticyclones the downlifting of the pycnocline would restrict the upward flux of nutrients into the euphotic zone reducing primary production (Gaube et al., 2014), which would be mostly based on small-size phytoplankton with low biomass and chlorophyll.

Eddy-eddy interactions may lead also to frontogenesis, resulting on convergent strain fields that occur both at the mesoscale and submesoscale ranges (Omand et al., 2015). The strain field will act destroying the thermal wind balance, establishing the ASC in order to restore this balance (Mahadevan and Tandon, 2006). In an early work, Pollard and Reguier (1992) investigated the ASC in a mesoscale front during frontogenesis. They observed upwelling in the

warm (anticyclonic) side of the front and downwelling in the cold (cyclonic) side associated with the balance of potential vorticity. Mahadevan and Tandon (2006) also predicted this clockwise vertical circulation facing downstream of ASC for submesoscale fronts. Vertical velocities may attain 1-10 m d⁻¹ in mesoscale fronts with values as high as 100 m d⁻¹ in submesoscale fronts (Mahadevan and Tandon, 2006). Nagai et al. (2008) modelled the distribution of chlorophyll related to this frontal ASC predicting a subduction in the cold (cyclonic) side and an enhancement in the warm (anticyclonic) side. The isopycnal subduction of chlorophyll along the cold side of the front was clearly observed by Fielding at al. (2001) along the Almería-Oran Front confirming Nagai et al.'s predictions. Recently Omad et al. (2015) observed strong subduction of particulate organic carbon (POC) related to eddy-eddy interactions at the submesoscale range. They hypothesized that this eddy driven subduction of POC could contribute as much as half of the total export of POC during the spring bloom of temperate and subpolar regions.

There is growing evidence that the whole phytoplankton community does not respond in the same way to physical forcing at different scales (e.g., Rodríguez et al., 2001; Clayton et al., 2013; 2014; Sangrà et al., 2014; MacGillicuddy, 2016). Rodriguez et al. (2001) showed that the size structure of the phytoplankton community is controlled by the strength of vertical velocities. Their observations indicate that the relative proportion of large cells increases with the magnitude of the upward velocity. Sangrà et al. (2014) also observed in a non nutrientlimited environment that phytoplankton size spectra strongly correlates with turbulence, being the larger phytoplankton size classes more abundant in high-turbulence environments. In a study along the Kuroshio Front Clayton et al. (2014) described the complexity of the phytoplankton community structure, shaped by a combination of the large scale biogeographical variability of the region, mesoscale mixing of populations and finer scale modification of the light and nutrient environment. Particularly, instabilities at the front drove small-scale physical motions that modified the planktonic community more rapidly than either acclimation or resource uptake could respond.

The Canary Islands region spans the coastal transition zone (CTZ) between the rich eutrophic waters of the NW Africa upwelling system and the poor oligotrophic waters of the North Atlantic Subtropical Gyre (Barton et al., 1998; 2000; Arístegui et al., 2003). It is almost unique in terms of the high mesoscale and submesoscale variability resulting both from the topographic perturbation of the prevailing winds and currents by the islands of the archipelago and from baroclinic instabilities developed along the offshore boundary region of the NW African coastal upwelling system. Mesoscale eddies are continuously shed downstream the islands of the archipelago (Arístegui et al., 1994; 1997; Jiménez et al., 2008; Piedeleu et al., 2009), being at the origin of the main pathway of long lived eddies of the northeast subtropical Atlantic, coined as the "Canary Eddy Corridor" by Sangrà et al. (2009). On the other hand, upwelling filaments and eddies, resulting from instabilities along the coastal upwelling jet, may exchange chemical and biological properties between the shelf waters and the open ocean, contributing largely to the coastal-ocean export of organic matter (Arístegui et al., 2004; García-Muñoz, 2004; 2005; Pelegrí et al., 2005) Eventually, these upwelling-source features may interact with island-generated eddies leading to a complex hydrographic environment that

shapes the distribution and activity of planktonic communities (Barton et al., 2004; Arístegui and Montero, 2005; Sangrà et al., 2005).

Many studies have investigated the impact of mesoscale eddies on chlorophyll distribution and a few of them also on the phytoplankton composition and higher trophic levels (see review in McGillicuddy, 2016). However, to the best of our knowledge none of these studies have addressed the variability of the phytoplankton community composition at a submesoscale approach, in spite of the generally accepted view that processes at small scales govern carbon fluxes in the ocean (e.g. Mahadevan, 2016). With the aim of contributing to understand this gap in knowledge we conducted an interdisciplinary survey of a mesoscale cyclonic eddy placed southeast of Gran Canaria, close to the transition zone between the upwelling and the eddy field downstream the Archipelago (Figure 1), in the frame of the RODA ("Remolinos Oceánicos y Deposición Atmosférica") project, during August 2006. One of the main goals of the study was to look at the impact of the ASC and its interacting structures on the variability of the phytoplankton community structure at a spatial scale close to the submesoscale.

This paper shows, firstly, the materials and methods employed during the cyclonic eddy system monitoring on board the BIO Hespérides, laboratory and data analysis (section 2). Following, results (section 3), are presented both from a hydrographical and biological perspective. Next, we discuss how meso and submesoscale features cause vertical motions in the water column causing variability in the structure of the planktonic community (section 4), before including a summary with the main conclusions (section 5).



Figure 1: Sea surface temperature (SST) image from NOAA-15 for 17 August 2006. Study area (blue box), upwelling filaments (red straight arrows), the transect conducted with CTD (black line), mushroom structure (mark with white dots), the cyclonic eddy (C, surrounded with blue dots), the anticyclonic eddy (A) and the filament (F) are labelled.

2. Materials and methods

2.1. Study area and sampling

The data analysed throughout this work was obtained from RODA-1 cruise aboard B.I.O Hespérides within the project "RODA - Oceanic eddies and atmospheric deposition in the Canary Current (Subtropical East Atlantic): monitoring biological and biogeochemical effects, and carbon fluxes to the deep ocean".

In order to map the eddy field downstream the islands we sampled a 70 x 80 nautical mile grid by means of 62 casts of XBTs (disposable bathythermographs down to 1000 m depth), from the 11th to 14th August 2006 (Figure 2). After locating the eddies' emplacement, we sampled a high resolution biogeochemical transect crossing the frontal system between an anticyclonic-cyclonic-anticyclonic eddy system, along 48 hours. This monitoring can be considered near-synoptic. The sampling consisted of 20 stations (named 64 to 83), separated each other by 5 nautical miles (at submesoscale resolution). A single cast was performed at each of the stations lasting about 1 hour. Temperature, salinity, and fluorescence were recorded on site down to 2000 metres deep using a SeaBird 911 Plus, CTD (conductivity, temperature, and depth) system, mounted on a General Oceanics rosette sampler, equipped with 24 12L Niskin bottles. 36 water samples were analysed for salinity and about 50 readings were done with a digital reversible thermometer to calibrate the CTD.



Figure 2: Topography corresponding to the isotherm 16°C. (a) XBT grid from cruise RODA-1, 11-14 August 2006. Red dots indicate XBT stations. (b) Transect from cruise RODA-1, 14-16 August 2006. Red dots indicate station locations numbered in the order of sampling.

Water samples for inorganic nutrients, chlorophyll a and planktonic organisms were collected from the Niskin bottles at the same stations of the CTD casts, at 5, 25, 50, 75, 100, 150 and 200 metres; plus an extra one depth at the chlorophyll maximum (DCM), which was situated between 45 and 88 m along the section.

2.2. Analyses of plankton samples.

The abundances of bacteria, picoeukaryotes (small photosynthetic eukaryotic cells <3-4 μ m, named hereafter "Eukaryotes-1"), and the cyanobacteria *Prochlorococcus* and *Synechococcus* were determined by means of flow cytometry. Subsamples (2 ml) were collected in microvials, fixed with paraformaldehyde (1% final concentration), refrigerated at -4°C for half an hour, quickly frozen in liquid nitrogen and stored at -80°C. Samples were analysed on board with a FACSCalibur (Becton&Dickinson) flow cytometer. Previous to the analysis, bacteria were stained with SYTO-13 (Molecular Probes Inc.), at a dilution rate of 1:10 to a final concentration of 2.5 μ M. Total cell abundances, as well as the proportion of high (HNA) and low (LNA) nucleic-acid content bacteria, were identified by their signatures in side scatter (SSC) vs green fluorescence (FL1) plots (Gasol et al., 1999; Arístegui et al., 2004).

The identification and enumeration of autotrophic Eukaryotes-1 and cyanobacteria in samples was based on the interactive analyses of multiple bivariate scatter plots of SSC, and red (FL3) and orange (FL2) fluorescence.

The analyses were run at a low speed (<30 μ l/min) for bacteria and at high speed (80-100 μ l/min) for phytoplankton, reaching 10000 events per acquisition. A greenish yellow suspension (Polyscience Inc) formed by 1 μ l latex beads (~10⁵ beads ml⁻¹ for phytoplankton and ~10⁶ beads ml⁻¹ for bacteria) was added as an internal standard. The flow rate was determined volumetrically after every 10 samples run.

Autotrophic and heterotrophic nanoplankton were analysed by epifluorescence microscopy, with an inverted microscope (ZEISS AXIOVERT 35) with 1000x resolution. Samples (100 ml) were preserved with glutaraldehyde (1 % final concentration) and stored under cold (4°C) and dark conditions. Within a few days after the sampling date, subsamples (20-50 ml) were filtered through 0.6 μ m black polycarbonate filters, and stained with DAPI (4,6-diamidino-2-phenylindole; Porter and Feig, 1980) at a final concentration of 5 μgml^{-1} (Sieracki et al., 1985). To differentiate between heterotrophic (HNF) and autotrophic nanoflagellates (>4 μ m; hereafter named "Eukaryotes-2"), the samples were analysed under UV, green and blue light filters. The enumeration included at least 100 cells of each group per sample.

2.3. Nutrient analysis.

Discrete samples for the determination of the concentrations of dissolved inorganic nitrate + nitrite were collected on falcon tubes and kept frozen until their analysis at the laboratory. A Bran+Luebbe AA3 analyzer was used, following standard spectrophotometric methods (Hansen and Koroleff 1999).

2.4. Data analysis.

We applied Fortran and excel to perform the different data analyses. Besides, we used the Surfer software (version 10) program to interpolate data in space (kriging method), apart from producing the final plots.

2.4.1. Hydrographic data.

In order to estimate the potential density (σ_t) the CTD data were used according to the algorithms integrated in the data processing module. Chlorophyll data were obtained directly from the profiling Wetlab fluorometer, using the conversion factor provided by the

manufacturer. The fluorometer, as well as the CTD probes, were calibrated at the factory just prior to the cruise.

SLA (sea level anomaly) data and biogeochemical profiles were used to identify the size of the different structures, as well as the eddies' radius. These were estimated thanks to data interpolation, so the values are approximations.

The temperature anomaly was obtained using as reference the values of a profile located outside the Eddy (station 83) and then it was subtracted from each of the temperature profiles.

The geostrophic velocity field was estimated from the data of temperature and salinity profiles, using the equation of geostrophic balance

$$-fv = -\frac{1}{\rho}\frac{\partial p}{\partial x}$$
$$fu = -\frac{1}{\rho}\frac{\partial p}{\partial y}$$

where f is the Coriolis parameter, ρ is the density and $\partial p/\partial x$ and $\partial p/\partial x$ are horizontal pressure gradients. To solve the geostrophic balance, it is necessary to apply the hydrostatic relation: $\partial p/\partial z = -\rho g$, where $\partial p/\partial z$ is vertical pressure gradient and g is gravity.

Together with the geostrophic velocity obtained in the jet in the front between cyclonic and anticyclonic eddies, the Rossby number was calculated from the following equation

Rossby number =
$$u/f \cdot L$$

where u is the velocity of the jet (expressed in ms⁻¹), f is the Coriolis parameter and L is the length of the jet (expressed in ms⁻¹).

2.4.2. Conversion of planktonic cell numbers to biomass.

Plankton abundances were transformed to biomass following the conversion factors obtained by MF Montero et al. (unpublished data) for coastal and oceanic waters of the Canary Islands region, after measuring biovolumes of each functional group of plankton. The following conversion factors were applied: 18 $fgC \cdot cel^{-1}$ for bacteria, 43 $fgC \cdot cel^{-1}$ for *Prochlorococcus*, 120 $fgC \cdot cel^{-1}$ for *Synechococcus*, 500 $fgC \cdot cel^{-1}$ for autotrophic Eukaryotes-1 and 3000 $fgC \cdot cel^{-1}$ for autotrophic Eukaryotes-2, as well as for heterotrophic nanoflagellates (HNF).

2.4.3. Heterotrophic – autotrophic balance.

In order to evaluate the influence of oceanographic processes on plankton community structure and biomass, we looked at the ratio between autotrophic (A) and heterotrophic (H) biomasses. H was estimated as the sum of the bacteria and HNF biomasses. A was obtained summing up the biomasses of *Synechococcus*, *Prochlorococcus*, Eukaryotes-1 and Eukaryotes-2.

3. Results

3.1. Signature of mesoscale structure in the hydrographic fields

As already mentioned, as part of our sampling strategy, we first conducted an XBT grid in order to first locate a mesoscale eddy (Figure 2a). Once located, we then crossed the structure with a high resolution CTD transect in order to get the vertical fields at near submesoscale resolution, and collect water samples for biogeochemical analysis. Figure 2b shows the 16°C isotherm topography as obtained from the XBT grid. We may clearly recognize the 3D signature of a mesoscale cyclonic eddy as indicated by the doming of the isotherm at the centre of the grid. The CTD transect crossed the centre of the eddy between stations 72 and 68 where the 16°C isotherm shoals almost 100 m respect to the far field (Figure 2b). We may also observe a relative cold tongue stretching from the southeast corner centred at station 76 of the CTD transect that corresponds to the signature of an upwelling filament. It is also important to notice the strong gradient of the isopleths in the southwest corner, which is the result of the interaction of the cyclonic eddy with an anticyclone, as detailed below.

Figure 1 shows the sea surface temperature (SST) field in our domain of interest just one day before the CTD transect crossing the cyclonic eddy (August 17) as obtained from remote sensing. We may recognize the signature of several mesoscale structures that interact with the sampled eddy. North of Cabo Bojador there is an upwelling filament that stretches offshore embracing the cold core cyclonic eddy. The tip of this filament is located inside of our observational domain interacting with the eddy as revealed from the 16°C topography (Figure 2b). South of Cabo Bojador there is a second upwelling filament that ends in a mushroom-like structure which is associated with the occurrence of a dipolar system of anticyclonic and cyclonic eddies. Probably this dipole is at the origin of the filament. The warm core anticyclonic eddy of this dipole interacted with the surveyed cold core cyclonic eddy and the frontal boundary between both eddies was crossed by the southern end of the CTD transect as shown in Figure 2b.

Figure 3a depicts the vertical section of potential temperature along the CTD transect. As typical for the summer season, horizontal averaged vertical potential temperature field is characterized by a seasonal thermocline below a relatively shallow mixed layer and by the permanent subtropical thermocline in deeper layers. Besides, there is large variability of the temperature field along the transect related with the signature of several mesoscale and submesoscale structures. The signature of the cyclonic eddy is evident through the doming of the isotherms between stations 67 and 76, being the eddy centre located at station 70. Potential temperature anomaly shows that it is a depth structure reaching 500 m depth (Figure 3b). It introduces a negative anomaly about -4°C in the seasonal thermocline upper layer. The eddy radius, as calculated from the vertical anomaly section, is about 40 km which is of order of the climatological first baroclinic radius of deformation for the region, $Rd \sim$ 40 km (Chelton et al., 1998), being thus a mesoscale structure. At the surface layers (first 200 m) an upwelling filament centred at station 76 is embedded in the eddy. Its width is about 20 km well below 2*Rd* being thus, a submesoscale structure. North of the filament the isotherms show a bowl shape centred at station 81 (Figure 3a). This introduces a positive potential temperature anomaly about + 2°C

and 300 m depth. This relatively shallow warm core structure may be associated with a submesoscale anticyclonic eddy of 20 km radius well below *Rd*. Finally, at the southern end of the transect we may recognize the occurrence of a strong frontal region between station 65 and 69 resulting from the interaction of the cyclonic eddy with an anticyclonic eddy, as observed in the SST field (Figure 1). The width of this structure is about 35 km well below 2 *Rd* being thus, also of the submesoscale type.



Figure 3: (a) Vertical distribution of potential temperature (in °C) along stations 64-83, during the first 500 m. Red arrows on the top axis indicate stations position. The bold black line shows the core of the thermocline. Circled station on the top axis indicate the filament core at station 76. The locations of the cyclonic eddy (CE), the front (Fr) and the anticyclonic eddies (AE) are indicated with segments on the top axis. (b) Differential temperature anomaly during the first 1000m. Higher values mark the core of the eddies, negative for cyclonic and positive for anticyclonic.

From this point onwards the terms cold/cyclonic and warm/anticyclonic will be used interchangeably, following those used by Arístegui et al. (1994)

The above-mentioned large mesoscale and submesoscale variability is also reflected on the vertical sections of salinity and potential density (Fig. 4a and 4b, respectively). Despite this variability which is focused mainly in the first 100m, we can observe a salinity decrease with depth (Fig. 4a). Due to the upwelling and downwelling of isopleths associated with the cyclonic and anticyclonic eddies, we find more saline water at similar depths in the core of anticyclones (e.g. stations 64-65 and 80-81; Figure 4a).



Figure 4: Vertical sections of salinity (a) and potential density (b) during the first 500 m. See Fig. 3a for the features. Red arrows on the top axis indicate stations position.

The vertical profile of potential density along the transect is shown in figure 4b. The pattern of potential temperature (Fig. 3a) and potential density (Fig. 4b) are similar. Isopycnal depression coincides with the anticyclonic eddy and isopycnal elevation with the cyclonic eddy. Values lower than 25.2 kgm^{-3} in the surface layer (< 25 m) are found in the core of warm eddies. Therefore, potential density depends more on temperature than on salinity. It must be remarked that isopycnals are not straight lines or subtle curves but sharp lines, which may be related to secondary ageostrophic velocity. This will be argued in further detail in the discussion.

The balance between horizontal pressure gradient force and Coriolis force is illustrated in the geostrophic velocity plot of Figure 5. The criterion used determines that geostrophic velocity is positive (negative) if the current moves north or east (south or west). It has to be considered that the average geostrophic velocity in the Canary Current is $0.2 m s^{-1}$ (Sangrà, 1995; Pelegrí et al., 2005). Following the south-north transect we observe a strong jet between sta. 65-68, which coincides with the front between the anticyclonic and cyclonic eddies, reaching negative values up to $1 m s^{-1}$. This value is of the same order of the highest ones registered in the ocean. The estimated Rossby number (R_o) is 0.48, which is a typical value in submesoscale processes, where R_o is close to 1 (Mahadevan, 2016). The highest positive geostrophic velocity is found between sta. 79-81 reaching values up to $0.5 m s^{-1}$, while a strong negative geostrophic velocity



is observed between sta. 81-82. The presence of these two countersign velocity cores gives evidence of the location of an anticyclonic structure northeast of the sampling region.

A great variation is observed when analysing the distribution of geostrophic velocity with depth. The wind thermal equation justifies this variation showing that the geostrophic movement variation in the vertical axis depends on the horizontal distribution in the density field; in this case, the study area is a barocline mass field, related to mesoscale structures, that's why it is logical the variation of the distribution of geostrophic velocity with depth.

Figure 5: The colour filled contour plot shows geostrophic velocity. The positive values indicate flux toward north, and negative values towards south; thin black lines are isopycnals $(kg \cdot m^{-3})$. See Fig. 3a for the features. Red arrows on the top axis indicate stations position.

3.2. Chlorophyll and nitrates.

The combined distribution of the Chlorophyll field (Chl a) with isopycnals along the transect (Fig. 6) shows that chlorophyll concentration follows a pattern related to potential density distribution. The highest Chl a concentrations are found below the mixed layer (ML), which oscillates between 10 m and 25 m approximately.

The deep chlorophyll maximum (DCM) is found at an average of 50-75 m along the transect. However, it can be appreciated that the front has an effect on its distribution, since the concentration at the stations in its western side is lower at those depths and the DCM is found down to 88 m. The Chl a distribution reaches 200 m depth at sta. 65 due to subduction at the front between the cyclonic and anticyclonic eddy along stations 64-68. Chl a levels are rather high in the centre of the cyclonic eddy at a depth of 50 m, reaching maximum values close to 2 mgm^{-3} at sta. 69, with no Chl a beyond 100 m depth between stations 68-72. Following the rise and downs of the pycnocline, the nutricline shallows in the core of the cyclonic eddy and deepens in the core of the two anticyclonic eddies (Fig. 7), largely affecting the distribution of Chl a and phytoplankton groups. Indeed, the DCM shallows and increases in concentration over the nitracline at the core of the cyclonic eddy (compare Figs. 6 and 7). The nutrients distribution is also related to secondary vertical circulation besides eddy pumping, as will be argued in further detail in the discussion.



Figure 7: Vertical profile of nitrate concentration, from 0 to 200 m. Solid black lines shows isopycnals $(kg \cdot m^{-3})$, the bold red line indicates the core of the thermocline. Red arrows on the top axis indicate stations position. See Fig. 3a for the features.

3.3. Structure of the planktonic community

The highest bacteria accumulations (Fig. 8) are found at the convergence regions between the cold eddy and the two warm eddies, placed both north and south of the cyclone, presumably where organic matter accumulates. LNA bacteria (Fig. 8b) are particularly abundant at station 66 where the sharpest convergence zone is found, displaying up to 6 times more cells/ml than at any other station, even at deep layers. HNA bacteria, however, are more abundant at the upwelling filament region (stations 75-76). Although some of these HNA cells could belong to the cyanobacteria *Prochlorococcus*, most of them would be true opportunistic heterotrophic



Figure 6: The colour filled contour plot shows Chlorophyll concentration $(mg \cdot m^{-3})$; thin black lines are isopycnals $(kg \cdot m^{-3})$. The bold red line shows the mixed layer depth (MLD). See Fig. 3a for the features. Red arrows on the top axis indicate stations position.



bacteria, with large genomes, taking benefit of the filament waters with higher organic matter content.

Figure 8: Vertical distribution of (a) HNA bacteria abundance (cell ml^{1}), (b) LNA bacteria abundance cell ml^{1}) and (c) total bacteria biomass (pg $C \cdot ml^{-1}$). The bold blue line shows mixed layer depth (MLD). Thin black lines are isopycnals (kg $\cdot m^{-3}$). See Fig. 3a for the features, red arrows on the top axis indicate stations position.

Synechococcus and Prochlorococcus (Fig. 9a and 9b, respectively) show similar distributions with higher biomasses mostly in the mixed layer and at the margins of the cyclonic eddy, where nutrient concentrations are lower. This supports previous reported observations that cyanobacteria may uptake DOM as a primary energy source, in combination with photosynthesis. The differences between their niches may be due to that Synechococcus has a greater resistance to survive in a high light and Prochlorococcus has a greater ability to support low irradiance (Agustí, 2004). Small autotrophic eukaryotes (Euk-1, $<4\mu$ m) (Fig. 9c), display a similar cross-section distribution as Prochlorococcus, with highest biomass at the margins of the cyclonic eddy, but following the 26 kg m⁻³ isopycnal at deeper layers; thus contributing to the DCM. Only at the core of the cyclonic eddy, where the isopycnals rise and nitrate concentrations are higher, Euk-1 drop in abundance, being replaced by larger autotrophic eukaryotes (Euk-2, >5 μ m) (Fig. 9d) with, presumably, higher nutrient saturation rates. Indeed, Euk-2 dominate in the region of influence of the cyclonic eddy and the upwelling filament, where the pycnocline shallows and the nutrient concentrations are higher, largely contributing to the DCM. It is interesting to note the low concentrations of most phytoplankton groups at the offshore boundary of the coastal jet (stations 79-80; where the offshore geostrophic velocity is highest), although this pattern is not so clear observed in Chl a. It could be that large phytoplankton from the coastal upwelling, not counted in our study, would be transported offshore at the convergent front of the upwelling filament, contributing to the DCM. In any case, these cells would not be very actively growing since nutrients concentrations were low at these stations. The distribution of heterotrophic nanoflagellates (HNF) (Fig. 9e) coincided with the that of the Euk-2, probably indicating that the latter group is mixotrophic. The highest biomass is observed

in the cold-core (where bacteria biomass is the lowest) and the filament, while the lower biomass is found at the anticyclonic eddy.



Figure 9: Distribution of the picoplankton and nanoplankton biomasses along the transect, all units are $pgC \cdot ml^{-1}$. (a) Synechococcus, (b) Prochlorococcus, (c) Euk-1, (d) Euk-2 and (e) HNF. See Fig. 3a for the features. Thin black lines are isopycnals, bold black line shows the core of the thermocline; red arrows on the top axis indicate stations position.

Table 1

Mean values of autotrophic (A) and heterotrophic (H) biomasses and H/A ratios along the transect averaged over the 5-200 m depth and at the DCM. All units are in mg $C \cdot m^{-3}$.

	Chl a	Bacteria	HNF	н	Syn	Pro	Euk -1	Euk-2	А	H/A
MEAN ± SD (5 -200 m)	0.18 ± 0.4	5.8 ± 3.8	5.2 ± 2.2	11.0	0.4 ± 0.5	1.9 ± 2.0	0.7 ± 1.0	4.6 ± 2.6	7.6	1.4
DCM MEAN ± SD	0.99 ± 0.4	6.4 ± 2.8	6.8 ± 2.0	13.2	0.3 ± 0.2	2.4 ± 1.3	1.9 ± 0.9	6.8 ± 2.5	11.4	1.2

The average ratio of heterotrophic to autotrophic biomass (H/A) is of ~1.4 (Table 1) in the first 200 m and 1.2 at the DCM, which indicates that, heterotrophic organisms dominate over autotrophs, probably due to a high load of organic matter being remineralized by bacteria. According to Gasol et al. (1997) we may conclude that this value is characteristic of transition waters between coastal waters and the open ocean. Bacteria biomass (5.8 mg C m⁻³) and HNF

biomass (5.2 mg C m⁻³) contribute about the same to heterotrophic biomass pool, while the large autotrophic eukaryotes (Euk-2) are the major contributors to the autotrophic biomass pool. The mesoscale variability has a strong impact in the H/A balance of the region as we can see in Figure 10. Autotrophy predominated only at the DCM depth in the cyclonic eddy, near the front and around sta. 72. At the western front of the eddy, we may observe a large H/A ratio, due to the great concentration of bacteria (compare Figs. 8c and 10). Likewise, at stations 77-81 there is a heterotrophic predominance, where phytoplankton is low due to the scarcity of nutrients (compare Figures 7 and 10).

The carbon to chlorophyll a ratio (C/Chla) varies when computing it for the whole water column or just for the DCM. Average values in the upper 200 m yield a ratio of 43 mgC/mgChla, while at the DCM the ratio is about 11 mgC/mgChla. These values must be considered with caution, since the Chl a was derived from the fluorescence of the CTD sensor calibrated to Chl a in the factory. Moreover, phytoplankton larger than 10-20 μ m ("microplankton") was not counted, and could modify the carbon content of the ratio. Nevertheless, the C/Chla reflect a 4-fold variability,



Figure 10: Vertical distribution of the H/A balance along stations 64-83, in the upper 200 m. Red tones indicate heterotrophic predominance and green tones denote autotrophic predominance. Thin black lines are isopycnals and red arrows on the top axis indicate stations position. See Fig. 3a for the features.

frequently found when comparing surface phytoplankton populations to those living at deeper layers, forming the DCM, which are photo-adapted to low light conditions.

4. Discussion

A great heterogeneity of structures was found in the transect studied to the south of Gran Canaria during the summer of 2006. Apart from finding the cyclonic mesoscale eddy, which was the aim of the study, we found a front, with a large anticyclonic eddy, an upwelling filament and a fourth structure that can be linked to an anticyclonic submesoscale eddy. All of these features affected the distribution of the planktonic community.

A shoaling of the isopycnal surfaces and nutricline (Fig. 7) is observed in the cyclonic eddy together with an increase in the chlorophyll concentration in its core (Fig. 6). These characteristics are typical of a cyclonic eddy in its early stages of formation, or either may imply that the doming is intensified by eddy-eddy interactions. The latter mechanism is known as "eddy pumping" (Gaube et al., 2014), although it could be confused with "eddy trapping" since their characteristics are similar (displaying anomalies like in a monopole eddy) (McGillicuddy, 2016). However, in the later case, eddies trap the fluid inside (d'Ovidio et al., 2013; Flierl, 1981; Provenzale, 1999; McGillicuddy, 2016), showing traces of physical, chemical, and biological properties from the water where it was originated. Thus, in the case of eddy trapping, anomalies are present from its initial formation (McGillicuddy, 2016). However, in the eddy pumping isopycnals are vertically disturbed by the forcing of the eddy to reach a near-geostrophic balance (Sangrà et al., 2007). Besides, the eddy trapping seems unlikely ought to the origin of the eddies in the archipelago (induced by islands' perturbation or by baroclinic instabilities in the coastal jet of the NW Africa upwelling system). As a consequence of the isopycnals doming in the cyclonic eddy, nutrient-rich cold water core is injected in the core of the eddy (see figure 3b). This cold water, however, do not make a significant contribution to the heat budget of the area (Holte et al., 2013; Mahadevan, 2014).

The water pumping was caused by the eddy pumping from the superficial area to the euphotic layer providing nitrate (McGillicuddy et al., 1999; Lévy, 2008) and therefore nitracline is raised. Although the highest concentration of nutrients is usually found between 500 and 1000 m, as a result of remineralization in the deeper layers and surface consumption (Lévy, 2008), in this study nitrate concentration (Figure 7) has been raised to thermocline limits. The growth of phytoplankton can be stimulated through this nutrient injection (Bibby et al., 2008; Cotti-Raush et al., 2016). It can be compared to Falkowski et al. (1991)'s results, where an increase of 3.5 times in vertically integrated primary production was observed in comparison to adjacent waters, in a cyclonic eddy in Hawaii (Arístegui et al., 1994).

Chlorophyll concentration can increase as a result of in situ growth of phytoplankton (Aristegui et al., 1997), not always being a direct indicator of biomass since its variation can be the result of other phenomena such as photoadaptation (Laws and Bannister, 1980; Cullen, 1982; Geider, 1987; Falkowski and LaRoche, 1991; Behremfield et al., 2005, 2008; Gaube et al., 2014). Our data seem to indicate that chlorophyll distribution is directly linked to biomass (compare Figures 6 and 9). This implies that high photosynthesis rates are stimulated by high nutrient concentrations in the euphotic layer (Chenillat et al., 2015), and therefore eddy pumping affects the abundance of phytoplankton (Falkowski et al., 1991), especially those with a bigger size: Euk-2 and HNF (Figs. 9d and 9e, respectively). This follows McGillicuddy (2016),

who states that upwellings favour the relative abundance of larger phytoplankton, based on Rodriguez et al. (2001), who observed the relation between vertical velocity and the sizeabundance spectrum in the northeast of the Alboran Sea. The input of nutrients in the euphotic layer in the centre of the cyclone provides an adequate environment for the proliferation of Euk-2, without light or nutrient limits.

On the other hand, different hydrographic profiles suggest that the front is a submesoscale structure caused by frontogenesis of the cyclonic eddy and the anticyclonic eddy (at the west of the transect) as different water densities converge because of the mesoscale flow field (Lévy et al., 2012; Gaube et al., 2014). This type of instability is usually accompanied by ageostrophic secondary circulation (ASC). The high Rossby number associated with the front (0.48) is an indicator of great relative vorticity which generates a loss of geostrophic balance. Hence, the development of ageostrophic secondary circulation (Mahadevan and Tandon, 2006), restores geostrophic and thermal wind balance (Mahadevan, 2016). Vertical velocities are difficult to appreciate as they are 3 or 4 orders of magnitude smaller than mesoscale horizontal velocities (Mahadevan and Tandon, 2006).

According to the ageostrophic circulation theory (Woods, 1985; Hoskins et al., 1985; Pollar y Regier, 1992) and to the scheme by Pollar and Regier (1992), we modified the latter adapting it to our own case study (Fig. 11). In the cyclonic (anticyclonic) side relative vorticity (ζ) is positive (negative) and as long as eddy convergence is kept, it will result in vertical shear. Vorticity diminishes in the anticyclonic side as it approaches the front. Conversely, in the cyclonic side it increases. This happens as $R_o \sim 1$, thus the relative vorticity growth is asymmetrical, being more positive than (cyclonic) negative (anticyclonic), as it is an area where there is convergence, which makes cyclonic vorticity to increase and anticyclonic vorticity to diminish



Figure 11: Frontogenesis and ASC. The confluence moves water toward the front. On the cyclonic (anticyclonic) side the vorticity increases (decreases), so the separation of isopycnals increases (decreases). Vertical circulation takes place as indicated in the figure because the surface is fixed. Figure adapted from Pollar and Regier (1992).

(Bluestein, 1993; Mahadevan y Tandon, 2006). To preserve potential vorticity, defined as (ζ +f) / h (f as Coriolis parameter and h the thickness of an isopycnal layer) (Willians and Follows, 2003; Lévy, 2008), vertical velocities appear resulting in the increase in the isopycnal layer thickness. The direction of these velocities is upwards occupying a bigger area (Mahadevan and Tandon, 2006; Mahadevan, 2016), in the anticyclonic side where warm and light waters are found,

whereas in the cyclonic side, which is formed by colder and heavier waters, velocities have a more intense downward direction (Mahadevan and Tandon, 2006; Mahadevan, 2016). Velocity will be null on the surface and will increase with depth down to the point where confluence decreases. Circulation through the front will happen on the surface on the anticyclonic side towards the cyclonic one, and in deeper layers in the opposite direction. This secondary circulation also occurs towards the other side of the cyclone.

The upward vertical advection of nutrients that appear in the euphotic layer through the sharp isopycnal surfaces of the front is the result of the ASC (Klein and Lapeyre, 2009; Lévy at al., 2001, Mahadevan and Archer, 2000; Spall and Richards, 2000; Mahadevan, 2016), so the nutrient upwelling is determined by the depth reached by the submesoscale vertical velocity in the water column (Lévy et al., 2012). Figure 7 shows that the curves which correspond to isopycnals and nutrients traverse in the front area and therefore nutrients are high through them, which remarks that the nutrient profile is determined by eddy pumping and ageostrophic secundary circulation. This alteration in the submesoscale dynamic on the typical nutrient profile can cause phytoplankton growth (Lévy et al., 2012), as well as an increase in the production of organic matter (Willians and Follows, 2003).

However, our results are not really in good agreement with the scheme previously shown (Fig. 10). The organism disposition (Fig. 9) and Chl a distribution (Fig. 6) at the front could suggest that the ageostrophic secondary circulation in the downwards flow does not take place crossing the isopycnals, but along them. Chlorophyll a is distributed following isopycnals; DCM is found at greater depths than in the rest of the profile. Regarding the distribution of Euk-1, most accumulate in the isopycnals along the front. Thus, this circulation also results in a downwards secondary transport of phytoplankton trough the flow (Fielding et al., 2001), being this a good indicator of the existence of active subduction at the front (e.g. Fielding et al., 2001; Nagai et al., 2008). Nagai et al. (2008), using a Semi-Geostrophic circulation model coupled to a planktonic ecosystem model, showed that patches of phytoplankton can present zigzag across frontal structures, due to isopycnal subduction of water rich in phytoplankton on the denser side of the front and upwelling of nutrient-poor water on the lighter side of the front. This zigzag pattern of distribution can be observed in the distribution of Euk-1 across the front (Figure 9c). In contrast, the larger flagellates, Euk-2 (Figure 9d), could overcome subduction and remain core of the cyclonic eddy where more nitrate is available.

Convergent frontal regions between eddies have been reported in the Canary Islands region to accumulate dissolved (DOM) and particulate (POM) organic matter, as well as concentrate bacteria (Arístegui and Montero, 2005; Baltar et al., 2010). Here, we found that beside heterotrophic bacteria, cyanobacteria (*Synechococcus* and *Prochlorococcus*) are also distributed in the margins of the eddy (Figures 8 and 9), being the highest concentration of *Prochlorococcus* found in the anticyclonic side of the front (Figure 9b). Generally, large particles and organic matter aggregates are assumed to sediment easily (Oman et al., 2015). However, in regions of upwards flow, the residence time in the surface waters increases, resulting in a decrease in their sinking rates (Rodriguez et al., 2001). In our study, HNA and LNA bacteria are also concentrated in the margins of the eddy but, unlike cyanobacteria and HNA bacteria, LNA bacteria are found down to 1000 m depth at stations 65-66 (Figure 8b only shows the upper 200 m). We believe that these bacteria are growing attached to particles, which sink fairly fast in spite of the ASC, due to their aggregation and gain of ballast at the convergent front. In this way, the front would acts as a major mechanism of the Vertical Ocean Pump (VOP), enhancing the flux of carbon to the dark ocean.

The upwelling filament, as observed in the satellite image (Fig. 1), stems from the coastal jet of the coastal upwelling system. It recirculates around the cyclonic eddy, presumably transporting organic matter and chlorophyll as observed in previous studies (Arístegui et al., 1997; 2004; Arístegui and Montero, 2005). Like at the front between the cyclonic and anticyclonic eddies, ageostrophic circulation can also be produced in the submesoscale filament. According to the theory proposed by McWilliam et al. (2009) a cold water filament consists of two opposite fronts because it supplies denser water with positive vorticity, producing a central downwelling with a double cell with upwards flow in both less dense sides. The interaction of the filament in the mesoscale field is quite complex, so our data cannot support a firm conclusion on this and we can only hypothesize. Considering that the filament has been trapped by the cyclonic mesoscale eddy – a cold filament inside a cold core – applying the theory proposed by McWilliams et al. (2009) would be problematic. In addition to that, it should be taken into account that, as previously mentioned, in the cyclonic eddy there is a downwards secondary circulation, which moves horizontally both to the left (front) and to the right (where the filament is).

On the one hand, we can consider that in the west side of the filament, the upwards flow occurs near station 75, as nutrient isolines seem to indicate (Fig.7). The cell in the east side would correspond to the front between the cold filament (downwelling) and the submesoscale anticyclonic eddy, formed by warm, lighter waters (upwelling). Horizontal circulation will take place on the surface from the anticyclonic side towards the filament and in deeper layers in the opposite direction. This cell may be deduced from the nitrate and chlorophyll distributions (Fig. 6 and 7), since both properties ascends in the anticyclonic side across isopycnals.

On the other hand, we can interpret the double cell as an inner structure of the cyclonic eddy, since it has been trapped by itself. Thereby, in the west cell, the upward flow at station 75 only includes water from the filament and the cell closes at the surface towards the filament and at a greater depth in the opposite direction. In the eastern side, the upward flow happens around stations 77-79 (which belong to the anticyclonic submesoscale eddy formed by warmer and lighter waters) so the upwards flow is formed by the sum of the flow originated in the cyclone and the flow originated in the filament, due to the ageostrophic circulation. Horizontal circulation will take place on the surface of the anticyclonic side towards the cyclonic one and in deeper layers in the opposite direction, acting similarly as that of the strong front studied to the west of the transect. Likewise, chlorophyll distribution is affected by the cyclonic-anticyclonic (submesoscale) front, raising the DCM in depth.

Considering all these mechanisms, the content in organic matter, chlorophyll and planktonic organisms found in the filament area will not only depend on the origin of filament waters, but also on futher modifications that take place along the filament development (Arístegui et al.,

2004) including processes associated with eddy interactions at the submesoscale, like agesotrophic circulation.

Bacteria (Fig. 8) and *Prochlorococcus* (Fig. 9b) prevail in surface waters above the nitracline, probably because of the high content in organic matter, since they do not rely exclusively on "new" inorganic nutrients (e.g. nitrate). Euk-1 (Fig. 9c) are accumulated in the area below the thermocline, probably –as explained above- because they are transported downwards (where nutrients are more abundant) by subduction of superficial water (compare figures 7 and 9c). ASC could however decrease Euk-1 inside the cyclone by exporting cells out of the euphotic zone (Fig. 9c, Mahadevan, 2016). HNF (Figure 9e), which distribution is determined by the presence of their prey (small bacteria and cyanobacteria), are also concentrated around the filament.

The submesoscale anticyclonic eddy (stations 78-82) presented a rather superficial core. Isopycnals (Fig. 4b) show a depression in its core, as the result of its formation, which, like in the cyclonic eddy, seems to have been formed by eddy pumping (McGillicuddy, 2016) but in the opposite way. Anticyclones in their early formation stages are usually associated with a decrease in primary production (Sweeney et al., 2003; Cotti-Raush et al., 2016). During wind-eddy intensification, apart from a downward pumping of nutrients, phytoplankton can also be transported below the euphotic zone (Gaube et al., 2014). In our study, we can appreciate how Euk-1 and Euk-2 are located below the thermocline (Figures 9c and 9d, respectively).

Anticyclonic eddies may sequester DOC and POC by accumulation from adjacent waters, deepening of the mixed layer, and downward transport towards deeper waters in their cores (Arístegui and Montero, 2005). In our case, the mixed layer varies very little and despite this we may observe at the core of the submesoscale anticyclonic eddy (station 81) a relative peak of Chl a as deep as 100 m depth. Like in the case of the frontal regions between the cyclonic eddy with the large anticyclone and the filament, bacteria and cyanobacteria (particularly *Prochlorococcus*) accumulate in the core of the submesoscale anticyclonic eddy, probably at because organic matter is higher at this site (Arístegui et al., 1997).

5. Conclusions

In summary, the small-scale resolution of our sampling provides new insights in the study of the impact of mesoscale structures in the dynamic of nutrients, chlorophyll, and planktonic communities (Klein et al., 2008; Klein y Lapyere, 2009). We were able not only to assess the upwelling/downwelling processes associated with eddy pumping but also the effect of ageostrophic secondary circulation (ASC), which dominates small-scale circulation patterns at the frontal regions with adjacent structures (Nagai et al., 2008).

Planktonic organisms behave differently depending on physical forcing, due to its diverse characteristics such as size, motility, feeding, prey availability, etc. Bacteria and cyanobacteria were both dependent on organic matter concentration. Bacteria – presumably growing attached to sinking particles resulting from aggregation and gain in buoyancy - were found as deep as 1000 m depth in the cyclonic–anticyclonic convergent front. Cyanobacteria distributions, were determined both by the concentration of DOM, and its tolerance to light conditions, more than

by nutrient concentration. Small autotrophic eukaryotes (Euk-1) were located forming a DCM at the margins of the cyclonic eddy, and its distribution was determined by ASC at the front. Larger autotrophic eukaryotes (Euk-2) were mainly placed in the centre of the cyclonic eddy, where nutrient concentrations are higher. HNF were determined by the availability of food, and thus were located at frontal regions, where bacteria and cyanobacteria prevailed.

Even though the study is limited to a single transect and therefore, our conclusions may be interpreted with caution, we can hypothesize that the structure of the planktonic community is modified along the Canary Eddy Corridor compared to its original structure, when eddies are generated.

Due to the great presence of meso and submesoscale features in the ocean and its impact on the planktonic community, studies at small-scale resolution should be prioritised, and broadened to the study of other organisms that can be affected by their presence.

The main difficulty of this type of research is the need to carry out a high-resolution sampling in a short period of time. Combination of traditional oceanographic casts together with new high-resolution monitoring (e.g. undulating vehicles, buoys, gliders, etc.) would yield a powerful approach to address the coupling between physical ad biogeochemical processes at the submesoscale, and thus to assess the impact of these structures in the VOP and the carbon cycle in the ocean.

6. References

- Agustí, A., 2004. Viability and niche segregation of *Prochlorococcus* and *Synechococcus* cells across the Central Atlantic Ocean. Aquatic Microbial Ecology, 36, 53-59.
- Arístegui, J., Barton, E. D., Montero, M. F., García-Muñoz, M., Escánez, J., 2003. Organic carbon distribution and water column respiration in the NW Africa-Canaries Coastal Transition Zone. Aquatic Microbial Ecology, 33 (3), 289-301.
- 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 and upwelling filament (Cape Juby, NW Africa). Progress in Oceanography, 62, 95-113.
- Arístegui, J., Montero, M.F., 2005. Temporal and spatial changes in plankton respiration and biomass in the Canary Islands region: the effect of mesoscale variability. Journal of Marine Systems, 54, 65-82.
- Arístegui, J., Sangrà, P., Hernández-León, S., Cantón, M., Hernández-Guerra, A., Kerling, J.L., 1994. Island-induced eddies in the Canary Islands. Deep-Sea Research I, 41, 1509-1525.
- Arístegui, J., Tett, P., Hernández-Guerra, A., Basterretxea, G., Montero, M.F., Wild, K., Sangrà,
 P., Hérnandez-León, S., Cantón, M., García-Braun, J.A., Pacheco, M., Barton, E.D., 1997.
 The influence of island-generated eddies on chlorophyll distribution: a study of mesoscale variation around Gran Canaria. Deep-Sea Research I, 44, 71-96.
- Baltar, F., Arístegui, J., Gasol, J.M., Lekunberri, I., Henrndl, G. J., 2010. Mesoscale eddies: hotspots of prokaryotic activity and differential community structure in the ocean. The ISME Journal 4, 975-988

- 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-Well, L.,
 Hérnandez 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. Progress in Oceanography, 41, 455–504.
- Barton, E. D, Arístegui, J., Tett, P. and Navarro-Pérez, E. 2004. Variability in the Canary Islands area of filament-eddy exchanges. Progress in Oceanography, Vol. 62, pp. 71-94.
- Barton, E. D., Basterretxea, G., Flament, P., Mitchelson-Jacob, E. G., Jones, B., Arístegui, J., Herrera, F., 2000. Lee region of Gran Canaria. Journal of Geophysical Research: Oceans, 105 (C7), 17173-17193.
- Basterretxea, G., E.D. Barton, P. Tett, P. Sangrá, E. Navarro, y J. Arístegui. 2002. Eddy and DCM response to wind-shear in the lee of Gran Canaria. Deep-Sea Research I, 49: 1087-1101
- Behrenfeld, M., Boss E., Siegel D., Shea, D., 2005. Carbon-based ocean productivity and phytoplankton physiology from space, Global Biogeochem. Cycles, 19, 1–14
- Behrenfeld, M., Halsey, K., Milligan, A., 2008. Evolved physiological responses of phytoplankton to their integrated growth environment. Philosophical Transactions of the Royal Society B, 363, 2687–2703.
- Bibby, T.S., Gorbunov, M.Y., Wyman K.W., Falkowski, P.G., 2008. Photosynthetic community responses to upwelling in mesoscale eddies in the subtropical North Atlantic and Pacific Oceans. Deep-Sea Research I, 55, 1310-1320.
- Bluestien, H.B., 1993. Synoptic-Dynamic Meteorology in Midlatitudes. Observations and Theory of Weather Systems, vol 2. Oxford University Press, USA.
- Chaigneau, A., Eldin, G., Dewitte, B., 2009. Eddy activity in the four major upwelling systems from satellite altimetry (1992 2007). Progress in Oceanography, 83 (1), 117-123.
- Chelton, D. B., Deszoeke, R. A., Schlax, M.G., 1998. Geographical variability of the first baroclinic Rossby Radius of Deformation. Journal of physical oceanography, 28, 433-460.
- Chelton, D. B., Schlax, M.G., Samelson, R.M., de Szoeke, R.A., 2007. Global observations of large oceanic eddies. Geophysical Research Letters, 34, L15606, 1-5.
- Chenillat, F., Franks, P. J. S., Rivière, P., Capet, X., Grima, N., Blanke, B., 2015. Plankton dynamics in a cyclonic eddy in the Southern California Current System. Journal of Geophysical Research: Oceans, 120, 1-23.
- Clayton, S., Dutkiewicz, S., Jahn, O., Follows, M.J., 2013. Dispersal, eddies, and the diversity of marine phytoplankton. Limnology and Oceanography: Fluids Environments, 3, 182-197.
- Clayton S., Nagai T., Follows M.J., 2014. Fine scale phytoplankton community structure across the Kuroshio Front. Journal of Plankton Research, 36, 1017–30
- Cotti-Rausch, B.E., Lomas, M.W., Lachenmyer, E.M., Goldman, E.A., Bell, D.W., Goldberg, S.R., Richardson, T.L., 2016. Deep-Sea Research I, 110, 106-122.
- Cullen, J.J., 1982. The deep chlorophyll maximum: Comparing vertical profiles of chlorophyll a. Canadian Journal of Fisheries and Aquatic Science, 39, 791-803.
- D'Ovidio, F., De Monte, S., Della Penna, A., Cotté, C., Guinet, C., 2013. Ecological implications of eddy retention in the open ocean: a Lageangian approach. Journal Physics A, 46, 254023
- Falkowski, P.G., LaRoche, J., 1991. Acclimation to spectral irradiance in algae. Journal of Phycology, 27, 8-14.
- Falkowski, P.G., Ziemman, D., Kolber, Z., Bienfang, P.K., 1991. Role of eddy pumping in enhancing primary production in the ocean. Nature, 352, 55-58.

- Fielding, S., Crisp, N., Allen, J.T., Hartman, M.C., Rabe, B., Roe, H.S.J., 2001. Mesoscale subduction at the Almeria–Oran front: Part 2. Biophysical interactions. Journal of Marine Systems, 30, 287–304
- Flierl, G.R., 1981. Particle motions in large-amplitude wave fields. Geophysical & Astrophysical Fluid Dynamics, 18, 39-74.
- Flierl, G.R., McGillicuddy D.J. Jr., 2002. Mesoscale and submesoscale physical-biological interactions. In The Sea, Vol. 12: Biological-Physical Interactions in the Sea, ed. Ar Robinson, JJ McCarthy, BJ Rothschild, pp. 113-85. New York: Wiley & Sons.
- García-Muñoz, M., Arístegui, J., Montero, M.F., Barton, E.D., 2004. Distribution and transport of organic matter along a filament-eddy system in the Canaries- NW Africa coastal transition zone region. Progress in Oceanography, 62 (1-4), 115-129.
- García-Muñoz, M., Arístegui, J., Pelegrí, J.L., Antoranz, A., Ojeda, A., Torres, M., 2005. Exchange of carbon by an upwelling filament off Cape Ghir (NW Africa). Journal of Marine Systems, 54, 83-95.
- Gasol, J.M., del Giorgio, P.A., Duerte, C.M., 1997. Biomass distribution in marine planktonic communities, 43(6), 1353-1361.
- Gasol, J.M., Zweifel, U.L., Peters, F., Furhman, J.A., Hagstrom, A., 1999. Significance of size and nucleic acid content heterogeneity as measured by flow cytometry in natural planktonic bacteria. Applied Enviromental Micrbiology, 65, 4475-4483.
- Gaube, P., McGillicuddy Jr., D.J., Chelton, D.B., Behrenfeld, M.J., Strutton, P., 2014. Regional variations in the influence of mesoscale eddies on near-surface chlorophyll. Journal of Geophysical Research: Oceans, 119, 8195-8220.
- Geider, R., 1987. Light and temperature dependence of the carbon to chlorophyll a ratio in microalgae and cyanobacteria: Implications for physiology and growth in the ocean. New Phytologist, 106, 1-34.
- Gordon, A.L., Giulivi, C.F., Lee, C.M., Furey, H.H., Bower, A., Talley, L., 2002. Japan/East Sea Intrathermocline Eddies. Journal of Physical Oceanography, 32, 1960–1974.
- Hansen, H. P., Koroleff, F., 2007. Determination of nutrients. Methods of Seawater Analysis, Third Edition, 159-228.
- Holte, J., Straneo, F., Moffat, C., Weller, R., Farrar, J. T., 2013. Structure and surface properties of eddies in the southeast Pacific Ocean. Journal of Geophysical Research: Oceans, 118(5), 2295-2309.
- Hoskins, B.J., McIntyre, M.E., Robertson, A.W., 1985. On the use and significance of isentropic potential vorticity maps. Quarterly Journal of the Royal Meteorological Society, 111 (470), 877-946.
- Jiménez, B., Sangrà, P., Mason, E., 2008. A numerical study of the relative importance of wind and topographic forcing on oceanic eddy shedding by tall, deep water islands. Ocean Modelling, 22(3), 146-157.
- Klein, P., Hua, B.L., Lapyere, G., Capet,X., Legentil, S., Sasaki, H., 2008. Upper ocean turbulence from high 3-D resolution simulations. Journal of Physical Oceanography, 38, 1748-1763.
- Klein, P., Lapyere, G., 2009. The oceanic vertical pump induced by mesoscale and submesoscale turbulence. Annual Review of Marine Science, 1, 351-375.
- Laws, E., Bannister, T., 1980. Nutrient and light limited growth of Thalassiosira fluviatilis in continuous culture, with implications for phytoplankton growth in the ocean. Limnology and oceanography, 25, 457-476.

- Lèvy, M., 2008. The modulation of biological production by oceanic mesoscale turbulence. Lecture Notes in Physics, 744, 219-261.
- Lèvy, M., Ferrari, R., Franks, P.J.S., Martin, A.P., Rivière, P., 2012. Bringing physics to life at the submesoscale. Geophysical Research Letters, 39, L14602, 1-13.
- Lèvy, M., Klein, P., Treguier, A.M., 2001. Impacts of sub-mesoscale physics on production and subduction of phytoplankton in an oligotrophic regime. Journal of Marine Research, 59, 535-565.
- Mahadevan, A., 2014. Eddy effects on biogeochemistry. Nature, 506 (7487), 168.
- Mahadevan, A., 2016. The impact of submesoscale physics on primary productivity of plankton, Annual Review of Marine Science, 8, 161–184
- Mahadevan, A., Archer, D., 2000. Modelling the impact of fronts and mesoscale circulation on the nutrient supply and biogeochemistry of the upper ocean. Journal of Geophysical Research: Oceans, 105, 1209-1225.
- Mahadevan, A., Tandon, A., 2006. An analysis of mechanisms for submesoscale vertical motion at ocean fronts. Ocean Modellling, 14, 241–56
- McGillicuddy Jr., D.J., 2016. Mechanisms of physical-biological-biogeochemical interaction at the oceanic mesoscale. Annual Review of Marine Science, 8, 125-159.
- McGillicuddy, D.J., Johnson, R., Siegel, D.A., Michaels, A.F., Bates, N.R., Knap, A.H., 1999. Mesoscale variations of biogeochemical properties in the Sargasso Sea. Journal of Geophysical Research: Oceans, 104, 13381-13394.
- McGillicuddy, D. J., Robinson, A. R., Siegel, D. A., Jannasch, H. W., Johnson, R., Dickey, T. D., McNeil, J., Michaels, A.F., Knap, A. H., 1998. Influence of mesoscale eddies on new production in the Sargasso Sea. Nature, 394(6690), 263-266.
- McWilliams, J.C., Colas, F., Molemaker, M.J., 2009. Cold filamentary intensification and oceanic surface convergence lines. Geophysical Research Letters, 36, L18602, 1-5.
- Nagai, T., Tandon, A., Gruber, N., McWilliams, J.C., 2008. Biological and physical impacts of ageostrophic frontal circulations driven by confluent flow and vertical mixing. Dynamics of Atmospheres and Oceans, 45, 229–251.
- Omand, M.M., D'Asaro, E.A., Lee, C.M., Perry, M.J., Briggs, N., Cetinié, I., Mahadevan, A., 2015: Eddy-driven subduction exports particulate organic carbon from the spring bloom. Science, 348, 222–223
- Pelegrí, J.L., Arístegui, J., Cana, L., González- Dávila, M., Hérnandez-Guerra, A., Hérnandez-León, S., Marrero-Díaz, A., Montero, M.F., Sangrà, P., Santana-Casiano, M., 2005. Coupling between the open ocean and the coastal upwelling region off northwest Africa: water recirculation and offshore pumping of organic matter. Journal of Marine Systems, 54, 3-37.
- Piedeleu, M., Sangrà, P., Sánchez-Vidal, A., Fabrés, J., Gordo, C., Calafat, A., 2009. An observational study of oceanic eddy generation mechanisms by tall deep-water islands (Gran Canaria). Geophysical Research Letters, 36, L14605, 1-5.
- Pollard, R.T., Regier, L.A., 1992. Vorticity and vertical circulation at an ocean front. Journal of physical oceanography, 22, 609-625.
- Porter, K.G., Feig, Y.S., 1980. The use of DAPI for identifying and counting aquatic microflora. Limnology and Oceanography, 25, 943-948.
- Provenzale, A., 1999. Transport by coherent barotropic vortices. Annual Review Fluid Mechanics, 31, 55-93.

- Rodriguez, J., Tintore, J., Allen, J.T., Blanco, J.M., Gomis, D., Reul, A., Ruiz, J., Rodríguez, V., Echevarría, F., Jiménez-Gomez, F., 2001. Mesoscale vertical motion and the size structure of phytoplankton in the ocean. Nature 410, 360-363.
- Sangrà, P., 1995. Perturbación de un flujo geofísico por un obstáculo: aplicación a la isla de Gran Canaria. Doctoral thesis, Universidad de Las Palmas de Gran Canaria, Spain.
- Sangrà, P., Auladell, M., Marrero-Díaz, A., Pelegrí, J.L., Fraile-Nuez, E., Rodríguez-Santana, A., Martín, J.M., Mason, E., Hernández-Guerra, A., 2007. On the nature of oceanic eddies shed by the Island of Gran Canaria. Deep-Sea Research I, 54, 687-709.
- Sangrà, P., García-Muñoz, C., García, C.M., Marrero-Díaz, Á., Sobrino, C., Mouriño-Carballido, B.,
 Aguiar-González, B., Henríquez-Pastene, C., Rodríguez-Santana, Á., Lubián, L.M.,
 Hernández-Arencibia, M., Hernández-León, S., Vázquez, E., Estrada-Allis, S.N., 2014.
 Coupling between upper ocean layer variability and size-fractionated phytoplankton in a
 non-nutrient-limited environment. Marine Ecology Progress Series, 499, 35-46.
- Sangrà, P., Pascual, A., Rodríguez-Santana, Á., Machín, F., Mason, E., McWilliams, J.C., Pelegrí, J.L., Changming, D., Rubio, A., Arístegui, J., Marrero-Díaz, Á., Hernández-Guerra, A., Martínez-Marrero, A., Auladell, M., 2009. The Canary Eddy Corridor: A major pathway for long-lived eddies in the subtropical North Atlantic. Deep Sea Research Part I: Oceanographic Research Papers, 56(12), 2100-2114.
- Sangrà, P., Pelegrí, J.L., Hernández-Guerra, A., Arregui, I., Martín, J.M., Marrero-Díaz, A., Martínez, A., Ratsimandresy, A.W., Rodríguez-Santana, A., 2005. Life history of an anticyclonic eddy. Journal of Geophysical Research: Oceans, 110(C3), 1-19.
- Siegel, D. A., Court, D.B., Menzies, D.W., Peterson, P., Maritorena, S., Nelson, N.B., 2008. Satellite and in situ observations of the bio-optical signatures of two mesoscale eddies in the Sargasso Sea. Deep Sea Res., Part II, 55(10-13), 1218-1230.
- Siegel, D.A., McGillicudy Jr, D.J., Fields, E.A., 1999. Mesoscale eddies, satellite altimetry, and new production in the Sargasso Sea. Journal of Geophysical research, 104 (C6), 13359-13379.
- Siegel, D.A., Peterson, P., McGillicuddy, D.J., Maritorena, S., Nelson, N.B., 2011. Bio-optical footprints created by mesoscale eddies in the Sargasso Sea. Geophysical Research Letters, 38, L13608, 1-6.
- Sieracki, M.E., Jhonson, P.W., Sieburth, J.McM., 1985. Detection, enumeration, and sizing of planktonic bacteria by image-analyzed epifluorescence microscopy. Applied and Environmental Microbiology, 49(4), 799-810.
- Spall, S.A., Richards, K.J., 2000. A numerical model of mesoscale frontal instabilities and plankton dynamics-I. Model formation and initial experiments. Deep-Sea Research I, 47, 1261-1301.
- Sweeney, E.N., McGillicuddy, D.J., Buesseler, K.O., 2003. Biogeochemical impacts due to mesoscale eddy activity in the Sargasso Sea as measured at the Bermuda Atlantic Timeseries Study (BATS). Deep Sea Research Part II: Topical Studies in Oceanography, 50(22), 3017-3039.
- Williams, R.G., Follows, M.J., 2003. Physical Transport of Nutrients and the Maintenance of Biological Production. In Ocean biogeochemistry: a JGOFS synthesis. Springer, Berlin, 19-51.
- Woods, J. D., 1985. The physics of thermocline ventilation. Elsevier oceanography series, 40, 543-590.

ANEXO I

ACTIVIDADES DESARROLLADAS

El TFM se desarrolló en el ámbito de la oceanografía física y biológica.

Una parte del trabajo consistió en la búsqueda bibliográfica de artículos y comprensión de los mismos. Dado lo amplio del tema los tutores me proporcionaron algunas "reviews" de las que partir.

Los tutores me facilitaron los datos procedentes de la campaña RODA (2006), necesarios para el desarrollo del trabajo. Parte de los datos ya habían sido procesados por lo que el trabajo consistió en su representación (haciendo uso del lenguaje de programación Fortran y del programa Surfer) e interpretación. Los datos de nutrientes me fueron presentados en las gráficas que proporciona el analizador por lo que tuve que medirlos y recalcularlos, para posteriormente representarlos e interpretarlos. También, algunos datos físicos se utilizaron para obtener otros parámetros como el número del Rossby, etc. haciendo uso de Fortran y Excel (se explica en material y métodos).

Finalmente, la redacción del trabajo, actividad que me ha resultado más compleja de lo que esperaba.

FORMACIÓN RECIBIDA

A lo largo de las tutorías con Pablo Sangrà recibí formación sobre Fortran y sobre Surfer.

NIVEL DE INTEGRACIÓN E IMPLICACIÓN DENTRO DEL DEPARTAMENTO Y RELACIONES CON EL PERSONAL

El trabajo fue desarrollado durante un periodo en las instalaciones de la Facultad de Ciencias del Mar y posteriormente a distancia. Durante el primer periodo pude trabajar en el Departamento de Oceanografía física en el que no coincidí con mucha gente, por lo que la integración fue bastante baja. No obstante, debido a que necesité que me enseñaran como se interpretaban los datos obtenidos del analizador de nutrientes acudí al departamento de biología en el IOCAG, que se encuentra en las instalaciones de Taliarte, y el personal fue muy agradable, dispuesto a ayudarme, con interés por mi trabajo, hicieron que me sintiera integrada (a pesar de lo poco que pude acudir).

ASPECTOS POSITIVOS Y NEGATIVOS MÁS SIGNIFICATIVOS RELACIONADOS CON EL DESARROLLO DEL TFT

El desarrollar parte del trabajo a distancia creo que ha resultado algo negativo porque impide una mayor relación con los tutores y gente de los departamentos. No obstante, fue mi decisión. Además, creo que también ha sido negativo partir de datos ya obtenidos por otros investigadores, esto no me ha permitido formarme en campañas oceanográficas y trabajo de laboratorio.

Creo que ha sido positivo el tema escogido, tanto porque a nivel personal me gusta cómo porque creo que es un tema relevante y en el que la investigación debe continuar. Por otro lado, he de agradecer a Pablo Sangrà la paciencia y el tiempo dedicado, aprendí mucho con él, a Javier Arístegui también, pero la relación fue menos cercana.

VALORACIÓN PERSONAL DEL APREDIZAJE CONSEGUIDO A LO LARGO DEL TFT

Creo que he aprendido mucho a lo largo del trabajo, lo amplio del tema escogido me ha permitido desarrollar un conocimiento interdisciplinar del mismo. Además, he aprendido a utilizar el Surfer y a manejar un poco el Frontran, programas que me parecen muy útiles en oceanografía. También he aprendido a emplear artículos científicos y aplicarlos a mis datos. En cuanto al trabajo escrito, cuando empecé no sabía hacer que las ideas fluyeran en el texto de una forma continuada y amena, creo que al final el trabajo está bien desarrollado.

En general creo que el desarrollo del TFM ha sido un proceso en el que he aprendido a ser más organizada, a gestionar mejor los tiempos de trabajo, a ser autocrítica, y autodidacta, en ocasiones.