Carbon active fluxes in the Northeast Atlantic subtropical gyre

Oceans are a climate key regulation system and also an active reservoir of carbon which increases the general interest for the study of the oceanic carbon cycle. In the actual context of CO_2 emissions and its influence on the climate change, estimates of carbon transported from the atmosphere to deep waters by diel vertical migration becomes critical. Indeed, migrant organisms play a determining role in the vertical downward flux of particulate and dissolved matter in the water column. This work contributes to increase the knowledge and understanding of the active export fluxes due to diel vertical migrants (DVMs) in subtropical waters. It is highlighted that the feeding impact as well as the metabolic flux of diel migrants should be seriously considered, as it can be equivalent to the gravitational flux in subtropical waters. The downward carbon transport in subtropical waters does not end with the sinking of the organic carbon produced in the shallower layers. In fact, the process is much more complex, and part of the production is shunted to the mesopelagic zone by DVMs. The results suggest a pivotal role of epipelagic zooplankton and DVMs in the biological pump and give insights into the fate of a bloom event. Also, the productive pulse due to the late winter bloom is likely to enhance the gut flux and should also be considered. In the large area influenced by the Canary Current, the high productivity gradient and the complex hydrodynamic have a deep impact in terms of abundance, metabolic activity and composition on the epipelagic ecosystem. The mesoscale variability, seasonality and probably the food availability and diet of the migrant community play an important role in the transport and fate of the organic matter annually produced in the subtropical ocean. Also, the lunar cycle effect on the active flux described for subtropical oligotrophic waters represents an important and unaccounted flux of carbon to the mesopelagic zone that deserves further research.

2013 S. Putzeys Carbon active fluxes in the Northeast Atlantic subtropical gyre

UNIVERSIDAD DE LAS PALMAS DE GRAN CANARIA

Tesis Doctoral

Carbon active fluxes in the Northeast Atlantic subtropical gyre

Sébastien Putzeys

2013

Las Palmas de Gran Canaria

UNIVERSIDAD DE LAS PALMAS DE GRAN CANARIA

IOCAG Instituto Universitario de Oceanografía y Cambio Global

Departamento de Biología
Instituto de Oceanografía y Cambio Global
Universidad de Las Palmas de Gran Canaria

D. Jose Manuel Vergara Martín SECRETARIO DEL DEPARTAMENTO DE BIOLOGÍA DE LA UNIVERSIDAD DE LAS PALMAS DE GRAN CANARIA,

CERTIFICA,

Que el Consejo de Doctores del Departamento en su sesión de fecha ..... tomó el acuerdo de dar el consentimiento para su tramitación, a la tesis doctoral titulada **"Flujos activos de carbono en el giro subtropical del Atlántico Noreste**" (**Carbon active fluxes in the Northeast Atlantic subtropical gyre**) presentada por el doctorando D. Sébastien Putzeys y dirigida por los Doctores D. Santiago Hernández-León y Dña. Lidia Yebra Mora.

Y para que así conste, y a efectos de lo previsto en el Artº 73.2 del Reglamento de Estudios de Doctorado de esta Universidad, firmo la presente en Las Palmas de Gran Canaria, a ……

de.....de dos mil trece

UNIVERSIDAD DE LAS PALMAS
DE GRAN CANARIA

Departamento de Biología

Programa de Doctorado en Oceanografía

Órgano responsable del Programa:

Bienio 2001 -2003

Título de la tesis:

“Carbon active fluxes in the Northeast Atlantic subtropical gyre”

Flujos activos de carbono en el giro subtropical del Atlántico Noreste

Tesis Doctoral presentada por D. Sébastien Putzeys para obtener el grado de Doctor por la Universidad de Las Palmas de Gran Canaria

Dirigida por el Dr. D. Santiago Hernández-León

Dra. Dña. Lidia Yebra Mora

El Director **El Co-Director** **El Doctorando**

En Las Palmas de Gran Canaria el

ACKNOWLEDGMENTS · AGRADECIMIENTOS

À mes Parents

A mis Padres

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ABSTRACT

Oceans are a climate key regulation system and also an active reservoir of carbon which increases the general interest for the study of the oceanic carbon cycle. In the actual context of CO_2 emissions and its influence on the climate change, estimates of carbon transported from the atmosphere to deep waters by diel vertical migration becomes critical. Indeed, migrant organisms play a determining role in the vertical downward flux of particulate and dissolved matter in the water column. This work contributes to increase the knowledge and understanding of the active export fluxes due to diel vertical migrants (DVMs) in subtropical waters. It is highlighted that the feeding impact as well as the metabolic flux of diel migrants should be seriously considered, as it can be equivalent to the gravitational flux in subtropical waters. The downward carbon transport in subtropical waters does not end with the sinking of the organic carbon produced in the shallower layers. In fact, the process is much more complex, and part of the production is shunted to the mesopelagic zone by DVMs. The results suggest a pivotal role of epipelagic zooplankton and DVMs in the biological pump and give insights into the fate of a bloom event. Also, the productive pulse due to the late winter bloom is likely to enhance the gut flux and should also be considered. In the large area influenced by the Canary Current, the high productivity gradient and the complex hydrodynamic have a deep impact in terms of abundance, metabolic activity and composition on the epipelagic ecosystem. The mesoscale variability, seasonality and probably the food availability and diet of the migrant community play an important role in the transport and fate of the organic matter annually produced in the subtropical ocean. Also, the lunar cycle effect on the active flux described for subtropical oligotrophic waters represents an important and unaccounted flux of carbon to the mesopelagic zone that deserves further research.

THESIS PREVIEW

This work, entitled “Carbon active fluxes in the Northeast Atlantic subtropical gyre” is part of a series of studies carried out in the frame of the research projects BREDDIES (REN2001-2650/ANT), MESOPELAGIC (CICYT, MAR97-1036), COCA (REN2000-1471-C02-02 MAR) and CONAFRICA (CTM2004-02319/MAR) performed by the Biological Oceanographic Laboratory, within the IOCAG (Instituto Universitario de Oceanografía y Cambio Global, Universidad de Las Palmas de Gran Canaria). Dr. Santiago Hernández-León has lead and supervised this thesis together with Dr. Lidia Yebra Mora.

This thesis is divided in two parts. First, it has been written integrally in English and structured in Introduction, Methodology, Results, Discussion, Conclusions and Future research. This thesis has been organized according to the rules to obtain the *Doctor Europeus* Mention (BOULPGC. Art. 1 Chapter 4, to 5 of November 2008). The second part of the thesis has been written in Spanish and, in this way, it contains the 50 pages in Spanish required by the Regulation of Elaboration, Court, Defense and Evaluation of Doctoral Thesis of the University of Las Palmas of Gran Canaria (BOULPGC. Art. 2 Chapter 1, 5th of November 2008). In addition, it follows the structure demanded by this Regulation: Introduction, Objectives, Original contributions, Methodology, Results, General Discussion, Conclusions and Future Research.

I· INTRODUCTION

1.1 The Carbon dioxide, importance and problematic

Carbon dioxide (CO_2), although its concentration in the atmosphere is low (0.3%), acts retaining the infrared radiation in the low layers of the atmosphere (Figure 1.1). Carbon dioxide combined with the aqueous vapor and other gases present in the atmosphere are responsible for the so-called "greenhouse effect", fundamental to the preservation of a suitable temperature for the life on Earth.

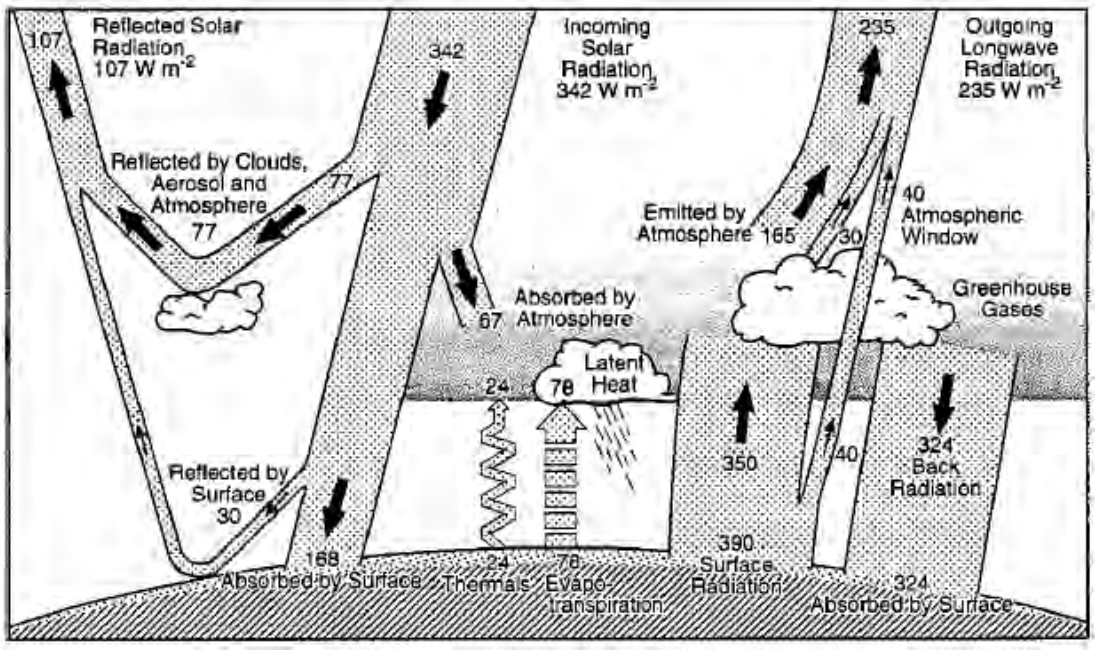

Figure 1.1. Mean energetic balance on the planet (Units in $W \cdot m^{-2}$, Kiehl and Trenberth, 1997).

However, the exploitation and burnout of fossil fuels with the purpose of sustaining industrial activities and transport release great amounts of carbon dioxide towards the atmosphere. This emission is nowadays one of the major preoccupations of the humanity and also the greater aggression than undergoes the planet since carbon dioxide, as a greenhouse effect gas, induced the so-called "climate change". Climate change is closely linked to the increase of carbon dioxide concentration in the atmosphere and to the consequent increase of the greenhouse effect. This is due to the drastic modification of the atmospheric CO_2 concentration caused by the emissions derived from the anthropogenic activities during the last century (Figure 1.2).

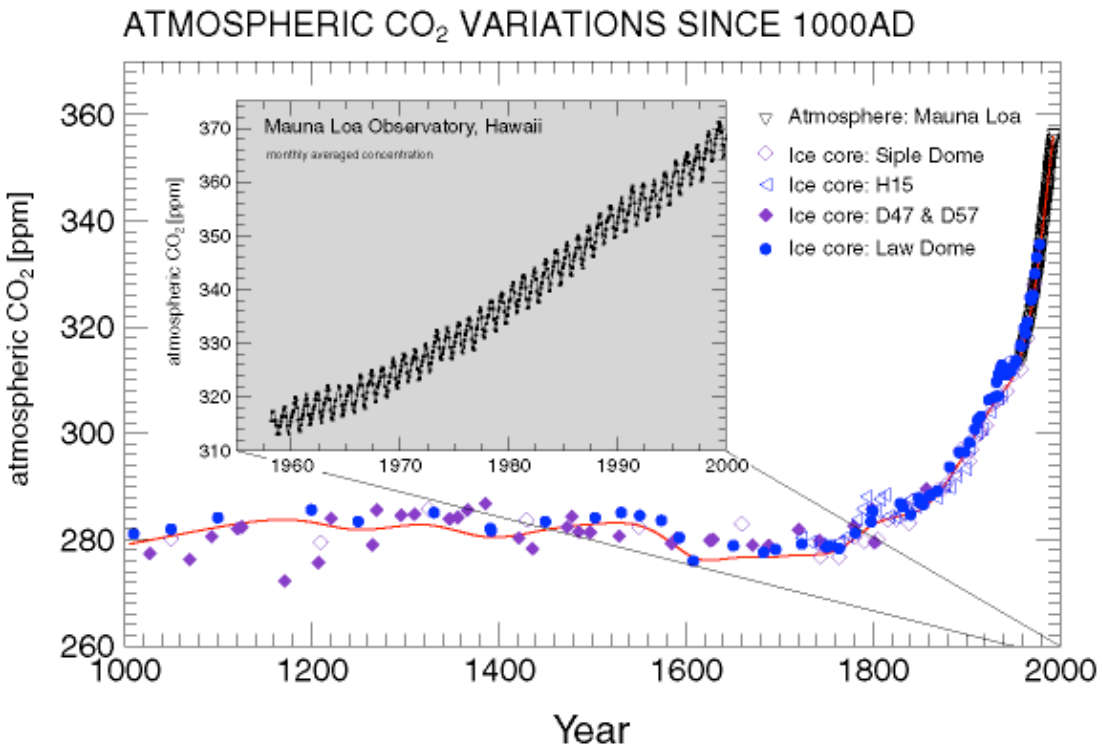

Figure 1.2. Evolution of carbon dioxide levels (Sarmiento and Gruber, 2002).

Data from glaciers indicate that CO_2 levels in the atmosphere have changed throughout history. However, in the pre-industrial period (1000-1800) the CO_2 concentration remained at 280 ppmv (590 Pg C, Etheridge *et al.*, 1996), but increased dramatically since then and reached the 366 ppmv in 1998 (775 Pg C, Holmén, 2000) and surpassed the 380 ppmv in 2004 (Varotsos *et al.*, 2007). Nowadays, the concentration of CO_2 in the atmosphere according to the National Oceanic and Atmospheric Administration (NOAA) is 393 ppmv (August 2012, Figure 1.3).

On the other hand, carbon dioxide is vital for the growth of autotrophic organisms. In addition, carbon is the element that allows the transport of the primary energy, solar or chemical, through the trophic webs in the biosphere. In the atmosphere, the hydrosphere and the lithosphere, the carbon circulates as matter and energy, as much through the organisms (biosphere) than through the inert matter (necromass). The carbon flux through the system lithosphere-ocean-atmosphere-biosphere, as well as the biological, geological, physical and chemical processes that regulate this flux, determines and characterizes the complex cycle of organic and inorganic compounds of carbon.

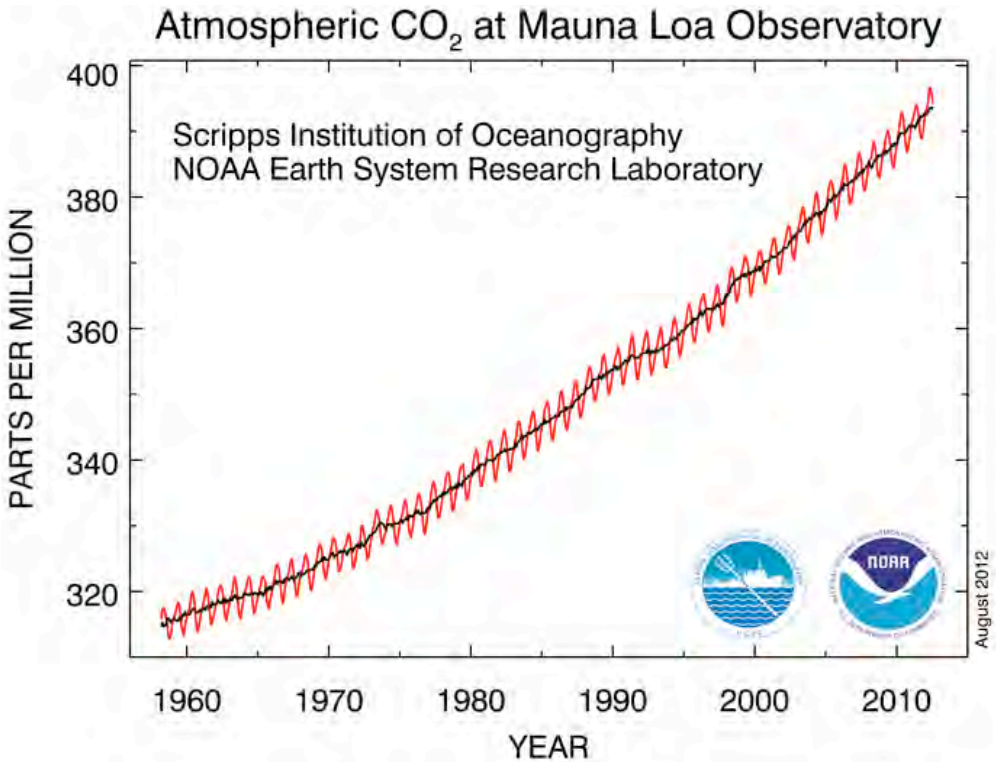

Figure 1.3. Evolution of carbon dioxide levels (from NOAA, http://www.esrl.noaa.gov/).

In this cycle, some carbon species get accumulated throughout the system creating the great reservoirs of carbon, which are: the lithosphere, the ocean, the atmosphere and the biosphere (Figure 1.4). The carbon cycle, of importance for the regulation of Earth climate and with large implications for the support of life, has been and continues to be widely studied (Falkowski *et al.*, 2000). It is defined as a succession of transformations that undergoes carbon throughout time. Indeed, besides the space dimension, the carbon cycle comprises two cycles that follow different time scales:

▪ The biological cycle that includes the carbon exchanges (CO_2) between the living organisms and the atmosphere (Field *et al.*, 1998; Joos *et al.*, 1999). This cycle is relatively fast and it is considered that the renovation of atmospheric carbon takes place every 20 years.

▪ The biogeochemical cycle that regulates the carbon transfer between the atmosphere, the hydrosphere and the lithosphere (oceans and grounds), which is longer than the biological cycle due to geologic mechanisms. The retention of carbon in this case is from thousands to millions of years (Falkowski *et al.*, 2000).

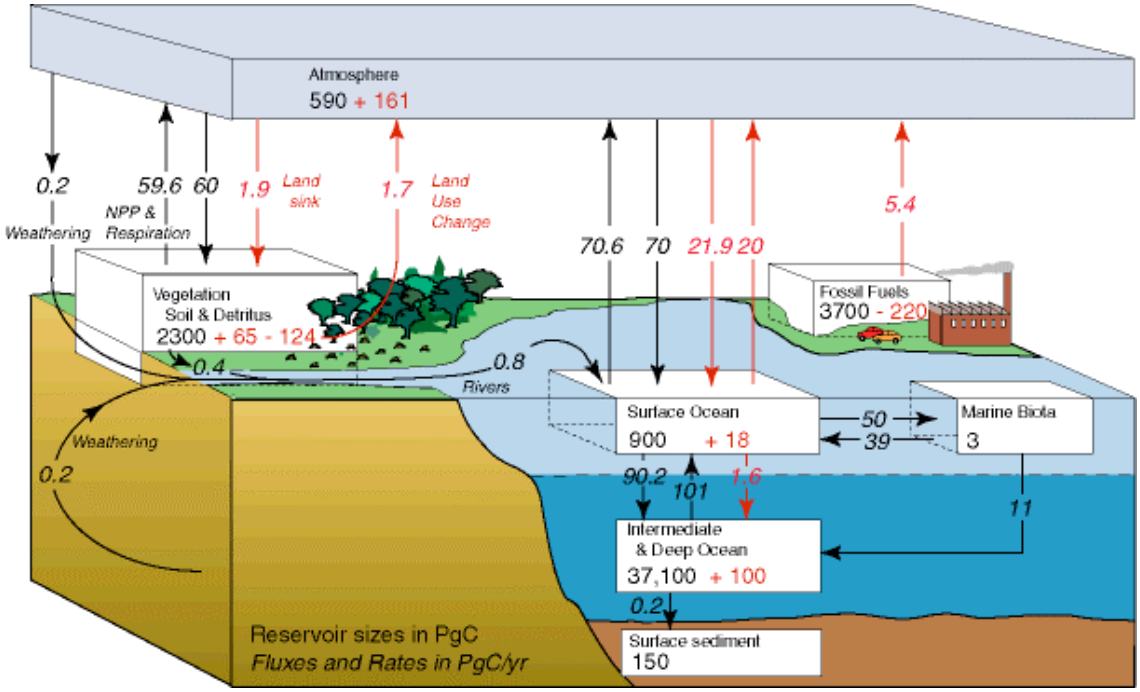

Figure 1.4. Global cycle of carbon, main reservoirs and flows. Arrows show the fluxes (in petagrams of carbon per year, 1 Pg C = 10^{15} gC) between the atmosphere and its two primary sinks, the land and the ocean, averaged over the 1980s. Anthropogenic fluxes are in red; natural fluxes in black. The net flux between reservoirs is balanced for natural processes but not for the anthropogenic fluxes. Within the boxes, black numbers give the preindustrial sizes of the reservoirs and red numbers denote the changes resulting from human activities since preindustrial times. For the land sink, the first red number is an inferred terrestrial land sink whose origin is speculative; the second one is the decrease due to deforestation. Numbers are slight modifications of those published by the Intergovernmental Panel on Climate Change. NPP is net primary production. (Sarmiento and Gruber, 2002).

1.2 The CO_2 cycle in the ocean

The study of the carbon cycle in the ocean has a great importance as it plays a fundamental role in the climatic system. It is not only due to the heat exchange and transport of waters masses, but also due to its impact in the biogeochemical cycle of carbon over the entire planet. The ocean is the major active reservoir of carbon surpassing by an order of magnitude the continental biosphere and the atmosphere. Its capacity to exchange CO_2 with the atmosphere and specially the carbon storage in its deep layers provides a key role in the control of atmospheric carbon dioxide content. Thus, the interface atmosphere-ocean is the nexus between the greenhouse effect and

oceanography. A better knowledge of the carbon cycle in the oceanic system can only be reached if we determine the fate of anthropogenic carbon dioxide removed from the atmosphere by the ocean. Consequently and due to the increasing interest to know the factors that could modulate the greenhouse effect, international research programs have been developed during the last years, such as JGOFS (Joint Global Ocean Flux Study) or GLOBEC (Global Ocean Ecosystem Dynamics), followed by IMBER (Integrated Marine Biogeochemistry and Ecosystem Research) since 2007. These programs attempt to increase our knowledge on the structure and functioning of the global oceanic ecosystem. They also attempt to identify the response of the ecosystem to the global climate change.

1.3 The carbon pumps

The CO_2 exchanges between the ocean and the atmosphere are highly dependent on surface water temperature, atmospheric circulation, and currents as well as on the respiration and photosynthesis processes. Two important mechanisms influence the carbon cycle in their organic and inorganic forms. These two processes are known as the physical pump (also called solubility pump) and the biological pump (Raven and Falkowski, 1999). Both mechanisms are responsible for the absorption of atmospheric carbon dioxide and its incorporation to the oceanic system.

1.3.1 The physical pump

The physical pump is related to the physical and thermodynamical processes that allow the capture and storage of atmospheric carbon. The solubility pump is made up of two elements. The first element is the solubility of carbon dioxide in the air-sea interphase, being larger the solubility when coldest is the water. Besides depending on the temperature, the storage capacity depends on the alkaline reservoir and on the amount of CO_2 already present in the ocean. The wind speed, together with the water mixing and the evaporation, which cools down the ocean superficial layer, contribute to the

atmosphere-ocean exchanges.

The second element is related to the general circulation of the ocean, which is called thermohaline circulation. The deep waters are formed by sinking of water masses at high latitudes in favorable conditions for the carbon dioxide solubility. These deep water masses contain a high concentration of dissolved inorganic carbon. This process allows polar dense cold waters to transfer atmospheric CO_2 to the deep ocean where it is trapped for centuries. The sinking of polar waters has therefore a key role in the carbon drain.

The CO_2 solubility in water together with the general circulation of the oceans are able to pump carbon from the atmosphere towards the interior of the ocean. The deep waters circulate until equatorial warmer latitudes. There they emerge to the surface and, when their temperature increase, the solubility of CO_2 diminishes. In this way, the equatorial waters release great amounts of carbon dioxide to the atmosphere, being thus CO_2 sources. Upwellings, and in our particular case the North African upwelling, also act as CO_2 sources.

The alkaline reservoir is regulated by the chemical reactions of carbon dioxide with seawater. These reactions are in a balance of several ionic and non-ionic species collectively known as dissolved inorganic carbon. These species are: free dissolved carbon dioxide (CO_2), carbonic acid (H_2CO_3), bicarbonate (HCO^{3-}) and carbonate (CO_3^{2-}).

$$CO_2 + 2\ H_2O \leftrightarrow H_2CO_3 \leftrightarrow HCO^{3-} + H^+$$

$$HCO^{3-} \leftrightarrow CO_3^{2-} + H^+$$

This chemical equilibrium, also called alkalinity or carbonate system, depends on factors such as the pH, which in turn depends on the balance of positive (Na^+, K^+, Mg^{2+}, Ca^{2+}) and negative ions (CO_3^{2-}, Cl, SO_4^{2-}, Br^-) in the water. Thus an alteration of the pH can lead to a major or minor atmospheric carbon dioxide uptake in order to balance the air-sea equilibrium. Therefore, the higher is the imbalance of positive charge in the water, the greater is the solubility of carbon dioxide. This balance can be modified by chemical processes like the dissolution/precipitation of $CaCO_3$, or by biological activity like photosynthesis, respiration or calcification. Each of these processes has

different effects on the alkalinity, and together they exert a large influence in the global carbon cycle.

1.3.2 The biological pump

The biological pump corresponds to the transfer of primary production towards sub-superficial waters by sedimentation of particulate organic carbon (POC, the passive or gravitational flux) and also due to the diel vertical migration of planktonic organisms (the active flux). The biological pump is responsible for the transport of atmospheric carbon through the biological systems. Once incorporated into the biological system, carbon circulates among the different levels of the food web and its fate depends on biological activities like growth, ingestion, respiration, excretion and mortality.

The biological pump is based on the ability of autotrophic organisms, mainly phytoplankton, to synthesize complex organic molecules such as glucids, lipids, protids and from simple mineral compounds as carbon dioxide, ammonium, phosphate and nitrate. This synthesis needs a huge amount of energy that is provided to the ecosystem by the solar radiation. Photosynthetic pigments ensure the capture of solar radiation. These pigments turn the solar radiation into organic forms of energy (eg. ATP, NADPH) that organisms can use to perform the photosynthetic reaction. Written in a generalized way and taking into account the Redfield ratio (Redfield, 1934; C:N:P=106:16:1) photosynthesis follows the equation:

$$106\ CO_2 + 16\ HNO_3 + H_3PO_4 + 122\ H_2O \xrightarrow{\text{ATP / NADPH}} (CH_2O)_{106}(NH_3)_{16}H_3PO_4 + 138\ O_2$$

Thus, the photosynthesis is the base of almost all the trophic food web since it originates organic matter also called biomass. Through photosynthesis, a portion of the atmospheric CO_2 is stored into the biomass and can be used to fuel higher trophic levels of the pelagic food web (Chisholm, 1992). The photosynthetic activity removes carbon dioxide from the surface layers and determines the levels of dissolved inorganic carbon in surface waters and the exchange of carbon between the ocean and the atmosphere. The annual amount of carbon uptake is estimated to be

approximately 2.2 Pg C·yr^{-1} (Takahashi *et al.*, 2002). In this way the ocean acts, in general, like a drain for the atmospheric carbon dioxide. However, Del Giorgio and Duarte (2002) showed that oceanic respiration (55 to 76 Gt C·yr^{-1}) represents a major source of CO_2 in the biosphere, comparable to the estimated 70 to 80 Gt C·yr^{-1} contributed by soil respiration. There are indications that open-ocean respiration is at least as large as soil respiration, the uncertainty in the magnitude of the former is also much larger, and its importance as a source of CO_2 to the atmosphere is as yet unclear. Del Giorgio and Duarte (2002) also comment that consideration of oceanic respiration may help explain the distribution of CO_2 sources regions in the ocean. In particular, the role of the subtropical ocean as a source of CO_2 to the atmosphere is consistent with evidence that respiration in the photic layer exceeds primary production. These authors concluded that "we cannot claim to grasp the global carbon cycle when we do not know whether the biota of the world's ocean is a net source or sink for carbon".

The trophic food web in the ocean is complex (Figure 1.5) and the organic matter produced in the surface layer circulates between the different elements of the food web. However, part of the biomass generated by the autotrophs is lost in the deep ocean due to the gravity. The microbial loop theory showed the existence of more trophic levels between primary producers and consumers (Azam *et al.*, 1983). The microbial loop (Figure 1.5) is responsible for a quick recycling of the dissolved organic carbon and nutrients in the eutrophic layer through the circuit bacteria- flagellate-microzooplankton to the main food web chain and other trophic levels (e.g. Williams, 1981; Azam *et al.*, 1983) giving rise to regenerated production (Dugdale and Goering, 1967; Eppley and Peterson, 1979). The flux of organic carbon is known as gravitational flux (POC flux) and represent the first element of the biological pump. Honjo *et al.* (2008) showed the POC flux varies from 25 (Pacific Warm Pool) to 605 (divergent Arabian Sea) mmolC m^{-2}·yr^{-1}. The oceanic region exhibiting the highest POC flux over a significantly large region is the area of the North Pacific Boreal Gyres where the average POC flux is 213 mmol m^{-2}·yr^{-1}. The POC flux is particularly high in large upwelling margins, including the divergent Arabian Sea and off Cape Verde.

One of the data sets showing the lowest flux over a significant region/basin is the POC flux 39 mmol $m^{-2} \cdot yr^{-1}$ in the North Pacific subtropical/tropical gyres (Honjo *et al.*, 2008).

The carbon ingested by each trophic level will be excreted and partly defecated (30% of total ingested carbon) and the rest will be respired or incorporated into the organisms as growth. Altogether a 70% of the ingested carbon is assimilated. The second element of the biological pump is the active flux. This flux is composed by i) the gut flux, ii) the respiratory flux, iii) the excretion flux, and finally iv) the flux due to mortality. This work focuses toward the active carbon fluxes in the water column and more specifically on the gut and respiratory fluxes mediated by diel migrant meso-zooplanktonic organisms.

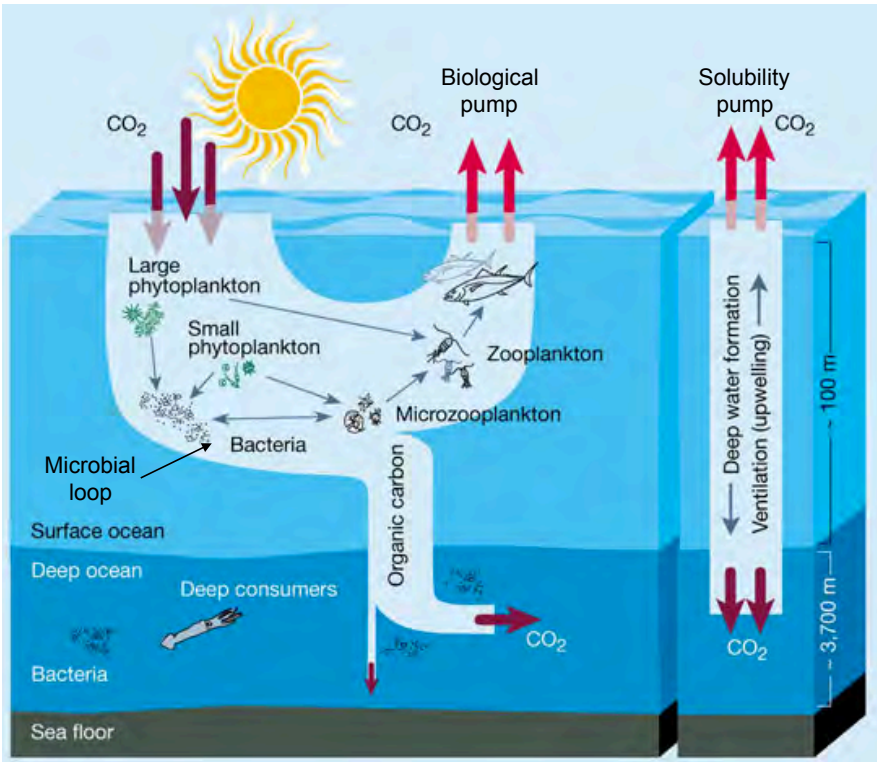

Figure 1.5. Components and internal processes of the biological pump. The CO_2 is transformed by the phytoplankton into organic matter in the photic zone. This organic matter is processed and a part of it sinks to deep waters (modified from Chisholm, 2000).

Besides the effect on organic matter synthesis, the solar radiation has an important physiological impact (both on autotrophs and heterotrophs) and also has ethologic impacts on animals. Various authors have shown the

influence of sun or moon illumination on the behavior of zooplankton (Cushing, 1951; Mc Naught and Hasler, 1964; Ringelberg, 1964; Boden and Kampa, 1967; Forward, 1988; Hernández-León *et al.*, 2001a, 2002, 2004, 2007, 2009, 2010). Due to the importance of the solar illumination and also to its periodicity, animals behavior is cyclic and they present adaptations corresponding to this periodicity, such as synchronism with the biological cycles or with favorable and unfavorable periods.

In the ocean, many zooplanktonic organisms perform vertical migrations (Longhurst, 1976; Youngbluth, 1976; Sameoto, 1984; Laval, 1989; Hernández-León *et al.*, 1999, 2001a, 2001b, 2002, 2004, 2010; Yebra *et al.*, 2005). This phenomenon has been studied by observing differences between day and night vertical profiles of zooplankton. These differences are significant both in terms of biomass and of taxonomic composition. According to their displacement in the water column, the zooplankton can be divided in four groups; (1) the non-migrants, (2) the night migrants toward the surface, (3) occasional migrants and (4) the inverse migrants moving at night toward the deeper layers.

This thesis is focused on the organisms of the second group. These zooplanktonic forms perform daily migration movements. By day they are in the deep scattering layer (500 m depth approximately) of the ocean to avoid being predated (Zaret and Suffern, 1976; Frost, 1988; Dawidowicz *et al.*, 1990). At dusk they ascend toward superficial layers (0-200 m) (Angel, 1985; Fowler and Knauer, 1986; Hernández-León *et al.*, 2001a, 2001b, 2002, 2004; Yebra *et al.*, 2005) to feed on phytoplankton, microplankton or non-migrant zooplankton. The ingestion and afterwards migration implies a transport of organic matter from the surface to the deep layers (Figure 1.5; Angel, 1985; Fowler and Knauer, 1986; Longhurst and Harrison, 1988, 1989; Hernández-León *et al.*, 2001b, 2002, 2004, 2010; Yebra *et al.*, 2005; Steinberg, 2008; Shatova, 2012). When the digestion time is longer than the time that migrants require to go back into deep zones, the gut content is transported to depth where egestion, respiration and excretion take place. This transport of fecal material is called gut flux (Angel, 1985, 1989). Respiration at depth is also a net carbon transport toward the deep layers of the ocean. This transport is

called respiratory flux. The calculations performed by several authors (Longhurst and Harrison, 1988; Longhurst *et al.*, 1989, 1990; Zhang y Dam, 1997; Hernández-León *et al.*, 2001b, 2004; Yebra *et al.*, 2005; Steinberg, 2008) suggest that the respiratory flux due to migrants could represent a significant fraction of the total carbon flux in the ocean. The respiratory flux plus the gut flux are both main components of the active flux and can represent an important part of the biological pump compared to the passive flux (from 0 up to 100% of the POC flux; Longhurst y Harrison, 1988; Longhurst *et al.*, 1989, 1990; Zhang y Dam, 1997; Hernández-León *et al.*, 2001b, 2002, 2004, 2010; Yebra *et al.*, 2005; Steinberg, 2008).

In addition to the respiratory and gut fluxes, there are other active fluxes such as mortality flux due to the dead of migrants in the deep layers and, the excretion of dissolved organic material (ammonium, dissolved organic nitrogen and dissolved organic carbon; see Steinberg *et al.*, 2000). Even if the excretion of dissolved organic matter has a relatively low proportion compared to primary production, the excretion flux varies between 2 and 19% of the primary production (Steinberg *et al.*, 2000).

The vertical migration of zooplankton and micronekton represents the most important movement of biomass in the ocean (Enright, 1977; Buskey and Swift, 1983; Atkinson *et al.*, 1992). Consequently, the zooplankton promote an important flux of matter and energy toward the deep layers of the ocean and its study has an important interest. In that context, this doctoral thesis presents the study of active carbon fluxes in the water column as a result of the vertical migrations of mesozooplankton in the Northeast Atlantic subtropical gyre and particularly in the Canary Current area.

In the actual context of global change, the ocean-atmosphere models predict deep changes of oceanic circulation, marine productivity as well as effectiveness of the ocean to absorb anthropogenic carbon. In order to predict the evolution of carbon dioxide concentrations in the atmosphere or to define credible strategies of stabilization (cf. Kyoto protocol agreements, 1997), it is necessary to study and understand the interactions between the marine biogeochemical cycles and the climate. The development of large scale marine biogeochemical models have experimented an important increase

during the last few years thanks to the advances of observations and studies of processes performed mainly by JGOFS and GLOBEC programs. Despite the advances carried out, the “Intergovernmental Panel for Climate Change” (IPCC) concluded in 2007 that “the present oceanic models are severely limited by the lack of equations characterizing the biological activities and specifying the temporary and spatial variations in these equations” (see reports, http://www.ipcc.ch/). This is particularly certain in the case of the oceanic respiration where the reduction of these uncertainties on the CO_2 budget of the open ocean would require international coordinated efforts on a large scale.

Due to the importance of vertical migrations on the transport of matter and energy, as well as the increasing importance of computerized models as prediction tools, a first step of this thesis has been the development of a one-dimension model to simulate the vertical migration of mesozooplankton and the associated active carbon fluxes in the Canary waters by using a compilation of published data. As second step was the obtention of more field data, covering different hydrographic conditions, regions and seasons of the year.

In the Canary Islands area (Figure 1.6), mesoscale structures have been identified south of the islands, e.g. island-induced eddies generated by the interaction of the islands with the Canary Current or the presence of filaments advected from the coastal African upwelling. These structures present high values of primary production (Arístegui *et al.*, 1994, 1997) and therefore promotes a transition zone between the African upwelling (eutrophic system) and the oligotrophic open ocean. Thus, to complete our knowledge on the active carbon fluxes in the Northeast Atlantic subtropical gyre and to determine the influence of mesoscalar structures on the active fluxes, several field studies were carried out in different areas of the Canary Current.

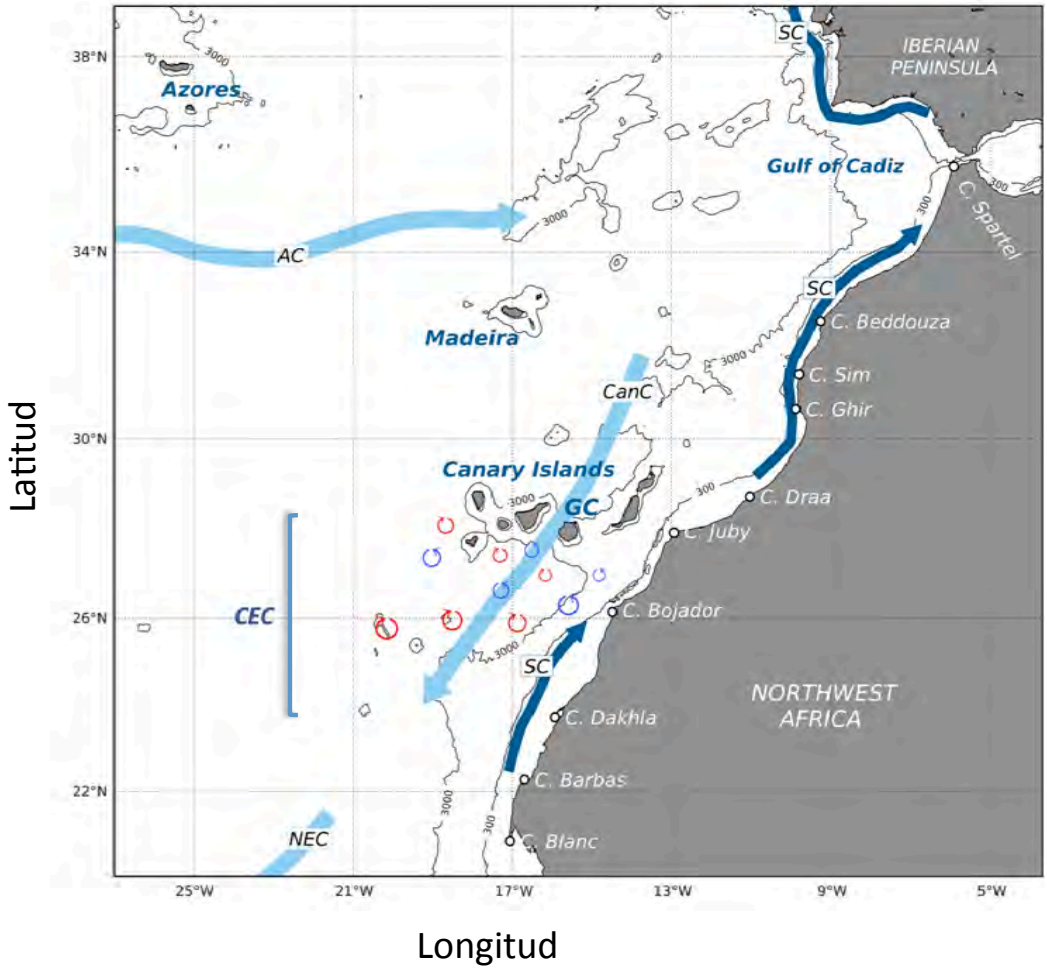

Figure 1.6. Schematic map of the Canary Basin showing the main currents (light blue: surface currents; dark blue: slope currents) and mesoscale eddies (blue: cyclonic; red: anticyclonic) south of the Canary Islands. AC: Azores Current; CanC: Canary Current; NEC: North Equatorial Current; Sc: Slope Current; CEC: Canary Eddy Corridor (from Arístegui *et al.*, 2009, redrawn by E. Masson).

The first field study was carried out at a station located North of Gran Canaria Island where the water column is almost not disturbed by the island effect. This area was chosen as a basis for the numerical model construction because it is a stable area, as it is detailed in the first chapter of Results section. Also, two other studies were carried out south of the Canary Archipelago in different seasonal periods. In each of these studies two transects located respectively at 21 and 26º North were sampled. Both transects started near the African coast and they extended toward the Atlantic open ocean. The sampling crossed several zones of different productivities. First, the coastal zone affected by the African upwelling and mesoscalar phenomena such as upwelling filaments. The second zone was located south

of the Archipelago and was influenced by eddies induced by the presence of the islands, affecting the water column stability. Some of these eddies were almost permanent structures while others were generated south of the islands and advected toward the open ocean by the Canary Current. The sampling finished in the open ocean where the water column was influenced by the Canary Eddy Corridor activity (Sangrá *et al.*, 2009).

Finally, the plankton outburst during the late winter bloom in subtropical waters was studied in relation to lunar illumination in the Canary Island waters. Epipelagic zooplankton biomass increases as the winter mixing progresses but peaks in every full moon and decreases thereafter due to predation by interzonal diel vertical migrants (DVMs). In order to estimate predation impact by DVMs on epipelagic zooplankton, and consequently in the active carbon flux, we performed a simple and conservative model using the criteria of previous works.

1.4 Objectives

Knowing the importance of vertical migrations on the transport of energy and matter, as well as the importance of mathematical models as prediction tools, the objective of this thesis has been to respond to the following questions:

1. Can we develop a mathematical model simulating the vertical migration and the associated active carbon flux?
2. Can we use this mathematical model to predict the movements of biomass and the active carbon flux in a specific zone of the Canary Islands?
3. Can we apply this numerical model to predict the active flux in the Canary Current system?

In order to answer the two first questions, we revised the works carried out previously on numerical models. The majority of them were developed trying to reproduce the migratory behavior using the influence of external factors. However, they did not include the migratory behavior impact on the

active carbon flux. Thus, a one-dimensional model has been developed to simulate the vertical migrations and the associate carbon flux.

The answer to the third question is negative. Indeed, the amount of data published on active fluxes and distribution of migrant biomass in Canary area, when this question was asked, was unsatisfactory. Therefore, a series of field studies were realized in order to increase our knowledge and understanding of this phenomenon in the zone. Besides the data acquisition to feed the model previously developed, the objectives of these works went to respond to the following questions:

4. Does the late winter bloom affect the migratory behavior and the linked active carbon flux?
5. Along the great variability found in the physical landscapes between North African upwelling to the open ocean is there a variation of the migrants vertical distribution and a difference in active carbon flux?
6. Does seasonality influence the active carbon flux?
7. What are the consequences of the lunar cycle on active carbon fluxes induced by diel vertical migrants?

II· METHODOLOGY

2.1 Model design

The one-dimensional numerical model was based on the work of Andersen and Nival (1991) and consists of a two-order partial equation that describes the temporal and spatial variation of the biomass. Four-meter-thick layers were considered down to 1000 m, which was set as the bottom of the water column. The irradiance was considered to be the forcing variable and temperature was also considered, in order to calculate metabolic rates. It was assumed that the vertical eddy diffusivity is negligible compared to the migration speed of the organisms.

The model was implemented with the metabolic rates computation using the equation of Ikeda (1985). The second characteristic of the model was the calculation of active carbon fluxes from the simulated metabolic rates.

2.2 Sampling

The biological sampling was carried out with a Longhurst Hardy Plankton Recorder (LHPR, Longhurst *et al.*, 1966). The LHPR was specially designed to study the vertical distribution patterns of planktonic organisms at high speed (~4 knots). The LHPR was based on the Hardy principle to collect plankton and it can be towed in a single V-shaped profile through the water column. The large aluminum frame is equipped with a conical net and a nose cone at the front. The frame channels water through the 200 μm conical net to a cod-end which contains two cylinders of gauze, which wind around a take-up spool every two minutes, sandwiching the samples of zooplankton between them and allowing semi-discrete sampling. Attached to the frame, one each side, there are two cylinders containing a rechargeable battery pack and the electronics for driving the cod-end, monitoring the sensors (Seabird CTD and a flowmeter) and communicating with the surface. To assist the sampler to dive, a 45 kg depressor weight was attached to the underside front and a drogue streams from the back of the frame to assist stability and maintain a horizontal position.

The fishing efficiency of the LHPR compared with other sampling methods has been determined in previous studies (e.g. Brander and Thompson, 1989; Halliday *et al.*, 2001; Richardson *et al.*, 2004; Stehle *et al.*,

2007) in which the calibration factors or the efficiency of the different sampling methods were determined. Those studies showed among others that LHPR device was the more appropriate net to sample diel migrant zooplankton. The samples collected with the LHPR were frozen in liquid nitrogen until their analysis in the laboratory.

2.3 Metabolic analyses

In the laboratory, samples were homogenized keeping the temperature below 4°C in dark conditions to avoid as much as possible degradation of chlorophyll, proteins, and loss of enzymatic activity. Subsamples were taken from the crude homogenates for (1) gut fluorescence (GF) as index of gut fullness, (2) ETS activity as a proxy for respiration, and (3) protein content analysis for biomass.

For GF analysis, aliquots (200 µL) of the homogenates were diluted in 10 mL of 90% acetone and stored at -20 °C during 24 h in darkness. Fluorescence was assayed before and after acidification (4% HCl) in a Turner Design fluorometer (10-005 R model), previously calibrated with pure chlorophyll *a* (Yentsch and Menzel, 1963). Pigment content was calculated from the equations given in Parsons *et al.* (1984).

All the GF data in this thesis include Chl *a* plus phaeopigments and no correction was made for pigment loss. GF values were corrected for the background fluorescence of the exoskeleton of the organisms captured from the deep scattering layer (DSL, Boden and Kampa, 1967; Hernández-León *et al.*, 2001a). We assumed that all the biomass had a background fluorescence of 0.1 µg of pigments per gram of wet weight (Willason and Cox, 1987) and a dry weight to wet weight ratio of 0.2 (Mauchline, 1969).

The electron transfer system (ETS) activity was assayed according to Packard (1971) modified by Gómez *et al.* (1996). ETS activity was recalculated to the *in situ* temperature using the Arrhenius equation and an activation energy of 15 Kcal·mol^{-1} (Packard *et al.*, 1975). Protein content was determined using the method of Lowry *et al.* (1951) modified for microanalysis by Rutter (1967), and using bovine serum albumine (BSA) as standard. Protein values were converted to dry weight using the relationship given by Hernández- León *et al.* (2001b) for the Canary Islands waters and to carbon

units assuming that carbon is 40% of dry weight (Dam and Peterson, 1993). Enzymatic activity and gut fluorescence were normalized to the amount of protein for each sample to obtain protein-specific values.

2.4 Carbon flux determination

The data obtained from the samples were categorized on 50 m intervals to obtain day and night vertical profiles of protein content, GF, and ETS activity. We subtracted paired day-night profiles to show only daily changes involving migrants as in Yebra *et al.* (2005). The negative values of the protein day-minus-night profile correspond to migrant biomass that reached the epipelagic layer at night including organisms living both above and under 800 m by day. This migrant biomass (mg protein·m^{-2}) was determined integrating the area of negative biomass values (mg protein·m^{-3}) as in Longhurst and Williams (1979) and Yebra *et al.* (2005):

$$\text{Migrant Biomass} = \int_{0\text{-}200} \text{Biomass}$$

Migrant biomass values were then converted to carbon units as shown before.

The gut pigment flux (mg pigments·m^{-2}·d^{-1}) was calculated performing a two-step operation. First, the day-minus-night positive GF data at depth were integrated and divided by the biomass at the same depth to obtain the specific gut content (µg pigment·mg $protein^{-1}$) at depth:

$$\text{Specific Gut content at depth} = \left[\int_{200\text{-}850} \text{GF}\right] \cdot \left[\int_{200\text{-}850} \text{Biomass}\right]^{-1}$$

The second step was to multiply this specific gut content at depth by the migrant biomass to obtain the gut pigment flux.

To determine the respiratory flux (µL O_2·m^{-2}·d^{-1}) positive values of the ETS day-minus-night profiles (µL O_2·m^{-3}·d^{-1}) were integrated and divided by the integrated biomass at the same depth:

$$\text{Specific ETS at depth} = \left[\int_{200\text{-}850} \text{ETS}\right] \cdot \left[\int_{200\text{-}850} \text{Biomass}\right]^{-1}$$

The specific ETS activity at depth (µLO_2·mg $protein^{-1}$·d^{-1}) obtained was then multiplied by the migrant biomass present in the epipelagic layer at night.

To assess metabolism of the migrant community, we determined also the potential ingestion (I, mgC·m^{-2}·d^{-1}) from the integrated day-minus-night positive respiration values (R) below 200 m depth. We assumed assimilation

to be 0.7 and a gross growth efficiency of 0.3 before applying the equation proposed by Ikeda and Motoda (1978):

$$I = 1 \cdot R/(0.7-0.3) = R \cdot 1/0.4 = 2.5 \cdot R$$

In order to determine the food source used by migrants to sustain their metabolism, we compared their potential ingestion with their pigmented gut content values. We calculated the omnivory index as [(ingestion - grazing) ingestion^{-1}] (Hernández-León *et al.*, 2002).

III· RESULTS

A MODEL OF ZOOPLANKTON DIEL VERTICAL MIGRATION OFF THE CANARY ISLAND: IMPLICATION FOR ACTIVE CARBON FLUX.

Putzeys, S. and S. Hernández-León (2005). Journal of Sea Research, 53, 213-222.

Abstract :

A mathematical model of the diel vertical migration of zooplankton off the Canary Islands is presented. It simulates the time and space variations of zooplankton biomass and allows calculations of metabolism over the diel cycle in the water column from 0 to 1000 m depth. The results are used to estimate the active carbon flux due to respiration by diel vertical migrants. This model depends mainly on the influence of absolute light intensity and of the rate of irradiance change. Swimming responses to the properties of the light field described the diel vertical migration of zooplankton. The simulated vertical distribution of animals in near-surface waters (75–112 m) during the night and in deeper layers during the day (428–436 m) was in good agreement with the *in situ* data used to initialise the model. The daytime respiration at depth obtained was compared with *in situ* estimations of respiration from ETS (electron transfer system) activity in a previous study and from published empirical equations relating temperature and metabolism of epiplanktonic zooplankton. We found that the latter procedure tends to overestimate active flux while the opposite was observed with ETS-derived assessments. Our results show that carbon consumption in the shallow layers estimated from metabolic rates and the subsequent production of large faecal pellets should be considered in the assessment of active carbon flux in the ocean.

Keywords

vertical migration, model, respiration, zooplankton, metabolism, Canary Islands.

Introduction

Diel vertical migration (DVM) of zooplankton is a common phenomenon in the sea and in freshwater. Many species of zooplankton (including copepods and euphausiids) perform daily vertical movements through the water column from the mesopelagic zone to the euphotic layer, thus following determined isolumes (Boden and Kampa, 1967). Numerous experiments in the field and in the laboratory have shown that the vertical migration can be initiated or influenced by endogenous factors (e.g. sex, age, biological rhythms) and/or exogenous (e.g. light, gravity, oxygen, temperature, predator and prey abundance). However, light is generally accepted to be the most significant external factor, although the importance of other factors cannot be neglected in the initiation of DVM.

Diel vertical migration could play a determining role in the downward flux of particulate and dissolved matter (Angel, 1985; Fowler and Knauer, 1986; Longhurst and Harrison, 1989). By feeding in superficial layers and defecating at depth, migrant organ- isms could accelerate the vertical flux of carbon. This transport of carbon to the mesopelagic zone is the so-called “gut flux” (Angel, 1985). Such a phenomenon will be important if (1) the migration rate of the organisms is fast or faster than the sinking rates of the faecal pellets, (2) the gut retention time is long enough to allow the animal to reach the maximum depth before defecation, and (3) if the amplitude of the migration, related to the migration speed, is great enough and faecal pellets are large. The diel vertical migration of plankton and micronekton could rein- force the flux of carbon by feeding at night near the surface and releasing faecal material at depth by day.

Another transport to the mesopelagic zone is the vertical flux of dissolved carbon caused by the night- time feeding in the shallower layers and the daytime respiration of the diel migrant biota at depth (Longhurst *et al.*, 1990). Some calculations (Longhurst and Harrison, 1988; Longhurst *et al.*, 1989, 1990) suggest that respiratory carbon from diel migrant biota below the euphotic zone during daytime represents a significant pathway of downward transport of carbon, relative to the gravitational vertical flux. In order to produce a downward respiratory carbon flux the diel migrant biota have to

fulfil two conditions: (1) the migration must cross the permanent barrier to physical vertical mixing (pycnocline), and (2) carbon must be ingested above this barrier for subsequent release of metabolised organic and inorganic carbon at deeper layers. This flux and the gut flux are two main components of the active flux, which jointly with mortality at depth (Zhang and Dam, 1997; Steinberg *et al.*, 2000) constitutes a significant portion of the so-called biological pump in the ocean compared to the passive or gravitational flux.

This paper presents a mathematical model of diel vertical migration of zooplankton, based on the model published by Andersen and Nival (1991), but allowing the calculation of ingestion and respiration in order to assess the carbon flux in the water column due to interzonal migrants. The model assumes that light is the only factor influencing zooplankton behaviour and considers parameter values that characterise euphausiids or large and fast-swimming zooplankton. The output is used to compare simulated data from the model and the results obtained from *in situ* measurements carried out in waters off the Canary Islands (Hernández-León *et al.*, 2001). Our results show that consumption in the shallower layers by diel migrants, assessed from metabolic rates, and the subsequent production of large faecal pellets should be considered in active carbon flux estimations.

Model design

This numerical model is a one-dimensional model based on the model of DVM of Andersen and Nival (1991) and consists of a two-order partial equation that describes the temporal and spatial variation of the biomass, with some modifications. Four-metre-thick layers are considered down to 1000 m, which is set as the bottom of the water column. The irradiance is considered to be the forcing variable and varies during the day. Temperature is also considered, in order to calculate metabolic rates. We assumed that the vertical eddy diffusivity is negligible compared to the migration speed of the organisms. So the equation describing the time- and depth-dependent changes in the biomass (B) is:

$$\frac{\partial B}{\partial t} = \frac{\partial (w \times B)}{\partial z}$$

where w is the migration speed (negative or positive depending on the downward or upward movement); B is the migrating biomass, and ∂_z, ∂_t the dimensions depending on depth and time. The model of Andersen and Nival (1991) considers physiological rates such as ingestion, excretion, mortality and moulting, summing these into an additional term (c) depending on biomass concentration.

Table 3.1.1 shows the variables and migration parameters used to initialise the model.

Table 3.1.1. Variables and parameters values of the model. ** (- without units)

Variables		Units
B	Zooplankton concentrations (fraction 1000-2000 µm)	$mgC \cdot m^{-3}$
I_z	Irradiance at the depth z	$W \cdot m^{-2}$
I_{L1}	Influence of absolute light intensity	- **
I_{L2}	Influence of rate of irradiance change	- **
w	Migration speed	$m \cdot h^{-1}$

Parameters of migration		Units	Values
I_s	Optimal Irradiance	$W \cdot m^{-2}$	10
I_e	Surface irradiance	$W \cdot m^{-2}$	0.10
a	Coefficient of the photo-inhibition curve	- **	0.012
I_v	Limit of the relative variation of irradiance	%	3
w_m	Initial speed of the migration	$m \cdot h^{-1}$	87.5

Influence of light on migration speed

According to the review of Forward (1988), light is generally agreed to be the most significant external factor influencing migration. Two hypotheses on the role of light exist: (1) the preferendum hypothesis (isolume hypothesis) and (2) the rate of change hypothesis, according to which the migration is

initialised with the rate of intensity change relative to initial intensity. The study of phototactic responses (McNaught and Hasler, 1964; Ringelberg, 1964) has shown that changes in relative light intensity may trigger diel vertical migration. As a consequence, processes acting on migration speed affect the displacement of the deep maximum biomass concentration. In this model, speed of migration is a synthesis of two processes that both depend on the pattern of light intensity during the day (Table 3.1.1): the influence of absolute light intensity (I_{L1}) and the influence of the rate of irradiance change (I_{L2}). This effect of light on migration speed is expressed according to Andersen and Nival (1991). In contrast, the influence of phytoplankton concentration on the migration speed was not considered in the present work because of the transparency of these waters.

Model implementation

We considered a vertical grid of n layers (i=1 to i=n) of width Δz=4 m. We could approximate the equation cited above by the finite differential equation:

$$\frac{B_{t+1} - B_t}{\Delta t} = \frac{-d_1 \times w_{i-1} \times B_{i-1}^t - |w_i| \times B_i^t + d_2 \times w_{i+1} \times B_{i+1}^t}{\Delta z}$$

In which B is the zooplanktonic biomass (Table 3.1.1), for different layers (i) of the water column and for different times (*t*) and w the migration speed of organisms defined as follows:

$w = w_m.I_{L1}.I_{L2}$

and d_1 and d_2, two coefficients defined according to Andersen and Nival (1991):

if $w_{i-1} < 0$ then $d_1=1$

if $w_{i-1} \geq 0$ then $d_1=0$

if $w_{i+1} < 0$ then $d_2=1$

if $w_{i+1} \leq 0$ then $d_2=0$

An explicit schema was used, with Δt=90 s and Δz=4 m, to conserve stability of the model for this schema ($\Delta t \leq \Delta z / w$).

Forcing function

The forcing function of the model of Andersen and Nival (1991) was done in a different way. In our model, the irradiance variable is entirely simulated. The surface light is calculated using the model for sun heights given by Basterretxea and Arístegui (1999).

The intensity and the variation of the solar radiation at the surface and subsurface (4 m depth) to 1000 m depth were calculated as a function of time of day, day of year, and according to geographical position. The maximum solar radiation in the external part of the atmosphere was calculated from the equation of Basterretxea and Arístegui (1999), which uses the solar constant of Igbal (1983). The solar declination was calculated from the latitude using the equation of Spencer (1971). Only part of the solar radiation (I_t^m, W m^{-2}) can go through the ocean surface because of the effect of the atmosphere (I^m_{surf}, W m^{-2}). Cloud effects and other losses due to transmission through the atmosphere can be calculated by the equation of Paltridge and Platt (1976), assuming that the atmosphere is of a Rayleigh type (Paltridge and Platt, 1976). Using this equation, we can calculate the albedo for a clear sky day. Only part of the solar radiation could cross the air-water interface because of losses for reflectance. We assumed that this energy is:

$$I^m_{surf} = I^m_t \times \left(R - 1\right)$$

where R is the reflectance dependency and calculated as follow:

$$R = \frac{1}{2} \times \frac{\sin^2\left(\theta_a - \theta_w\right)}{\sin^2\left(\theta_a + \theta_w\right)} + \frac{1}{2} \times \frac{\tan^2\left(\theta_a - \theta_w\right)}{\tan^2\left(\theta_a + \theta_w\right)}$$

with θ_a is the incident angle of the light in the air, and θ_w is the incident angle of the light in the water.

The reflectance dependency (R) as a percentage was taken from the Fresnel relation. The fact that light reflectance is a function of the zenith angle and of the wind speed (Gordon, 1969) was not considered in the model. The portion of light that could go through the ocean surface changes its direction due to the refraction. This angle could be estimated by the Snell relation:

θ_a x sin θ_a = θ_w x sin θ_w

where n_w and n_a are refraction indices of water and air, respectively. The ratio value of n_w/n_a is 1.341 (Kirk, 1983), which could be used for salt water or freshwater at ambient temperatures and for waves length photosynthetically usable. The angle θ_a is calculated from the equation of the solar elevation angle, β:

$\sin \beta = \cos \theta_a$ and $\sin \beta = \sin \phi \times \sin \delta - \cos \phi \times \cos \delta \times \cos \tau$

then $\cos \theta_a = \sin \phi \times \sin \delta - \cos \phi \times \cos \delta \times \cos \tau$

where τ is the daytime in radians.

We also calculated I_z (Table 3.1.1), the intensity of light from the subsurface to the bottom using the classic Beer-Lambert function, with an extinction coefficient calculated as:

$$K(z) = 0.0384 + 0.0088 \times C(z) + 0.054 \times C(z)^{2/3}$$

where C(z) is the chlorophyll biomass at depth (z).

Observed phytoplankton profiles were converted to carbon units, averaged and shifted to Gaussian function with:

$$C(z) = C_O + \frac{h}{\sigma\sqrt{2\pi}} \times e^{-\left[\frac{(z - z_m)^2}{2\sigma^2}\right]}$$

where C(z) is the chlorophyll biomass (mgC m^{-3}) as a function of depth, z; C_0 is the background concentration of chlorophyll biomass (0.075 mgC m^{-3}) on which a Gaussian curve whose peak is centred at depth z_m; σ the standard deviation around the peak (50 m); $C_O + \frac{h}{\sigma\sqrt{2\pi}}$, chlorophyll concentration at the maximum (65.79 mgC m^{-3}); z_m, depth of the maximum concentration of chlorophyll-a (100 m). The values used for this function are presented in parenthesis.

Metabolic rates

Respiration rates were directly calculated from biomass data using the equation of Ikeda (1985):

$\ln Y = a_0 + a_1 \times \ln X_1 + a_2 \times \ln X_2$

in which Y is the quantity of oxygen used (μlO_2 ind^{-1} h^{-1}); a_0, a_1 and a_2 are coefficients defined in Table 3.1.2; X_1 is the individual biomass (µgC), and X_2 is the temperature at the depth corresponding with biomass data.

This equation determines metabolic rates of epipelagic zooplankton as a function of individual weight and water temperature. The oxygen consumption obtained was converted into carbon units using a respiratory quotient of 0.97 (Omori and Ikeda, 1984) to obtain the carbon consumption. The ingestion rate was calculated from metabolic rates considering that assimilation was 70% and half of the assimilated food was used for growth and the other half respired.

Table 3.1.3. Coefficients of Ikeda's equation (Ikeda, 1985). ** ($p<0.01$, $R^2=95.5$)

Symbol	Value	Test t for a=0
a_0	0.5254	23.91**
a_1	0.8354	130.01**
a_2	0.0601	39.87**

Initialization

The simulations were initialised with profiles of average biomass obtained during a cruise south of the island of Gran Canary in August 1993 (Hernández-León et al., 2001). During this cruise, a series of 16 oblique hauls were carried out during night and day periods using a Longhurst-Hardy Plankton Recorder (LHPR, Longhurst and Williams, 1976). Depth intervals sampled from 0 to 800–900 m were used to produce synthetic profiles of zooplanktonic biomass distribution during night and day. The original profiles of biomass in mg of protein per m^3 were trans- formed to carbon units using the relationship given by Hernández-León *et al.* (2001) to convert proteins to dry weight (1.445+4.283 proteins; r=0.90; n=306; p<0.001) and assuming that carbon is 40% of dry weight (Båmstedt, 1986; Dam and Peterson, 1993).

In order to calculate the fraction of biomass which was involved in diel vertical migrations, we subtracted day values of biomass from night values. A secondary increase in biomass was observed between 700 and 800 m depth

due to migrating organisms from deeper layers and not from surface layers. Therefore, the biomass increase obtained from 600 m to 900 m was ignored (see Hernández-León *et al.*, 2001, for details). Temperature profiles recorded during the cruise were averaged to obtain one synthetic temperature profile, which was used to calculate the metabolic rates.

Results

Irradiance variation of the model and migration speed.

The evolution of irradiance in superficial layers (0–35 m) during the day (Figure 3.1.1) showed that the irradiance was higher than 1000 W m^{-2} in the 0–5 m layer, and decreased quickly from 5 to 30 m depth. The influence of absolute light intensity (I_{L1}) decreased from surface to the bottom (Figure 3.1.2 top). During daytime, the influence of rate of irradiance change (I_{L2}) was negative between 05h30 and 08h30 and positive between 15h30 and 18h30 (Figure 3.1.2 bottom) representing sunrise (negative values) and sunset (positive values). In consequence, we obtained negative values of velocity (downward movement) due to the negative influence of the rate of irradiance change (Figure 3.1.3). The influence of the rate of irradiance change controlled the velocity sign and induced the downward movement at sunrise and the upward movement at sunset. Values of speed decreased with depth, being strongly negative at sunrise and strongly positive at sunset. Maximum migration speeds for upward and downward movement were 110 m h^{-1}.

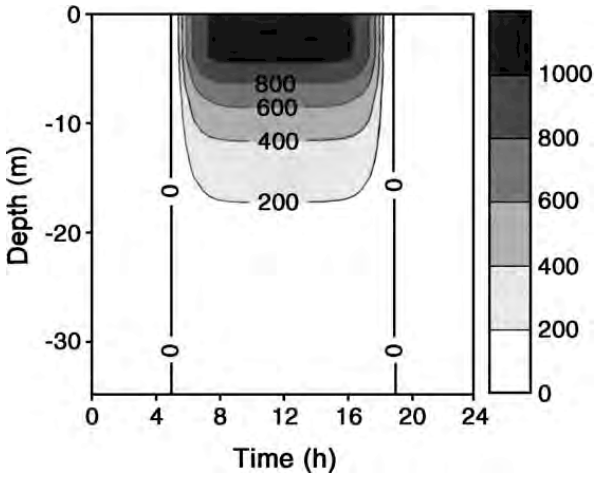

Figure 3.1.1. Irradiance (W·m^{-2}) as a function of depth (m) during the simulated day in the 0 to 35 m layer.

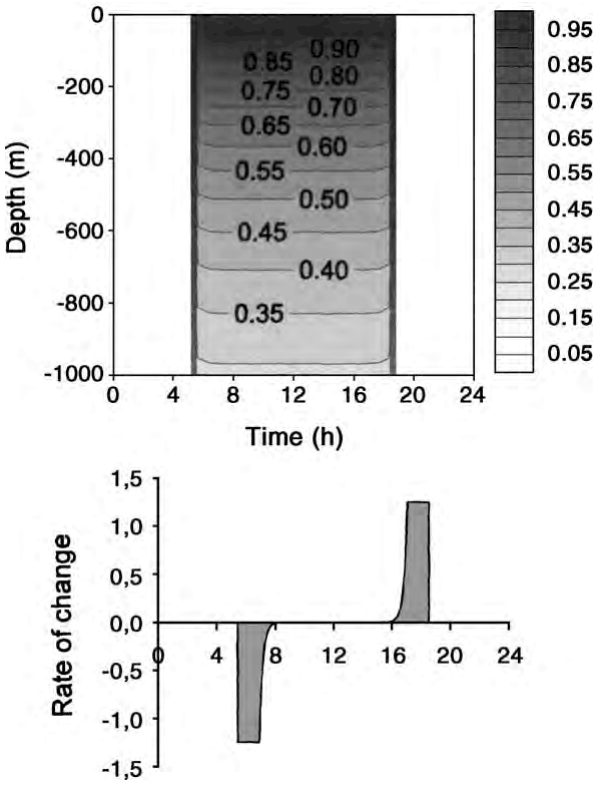

Figure 3.1.2. (top) Influence of absolute light intensity (I_{L1}) during the simulated day as a function of depth (m). (bottom) Influence of rate of irradiance change (I_{L2}) during the simulated day as a function of time (h).

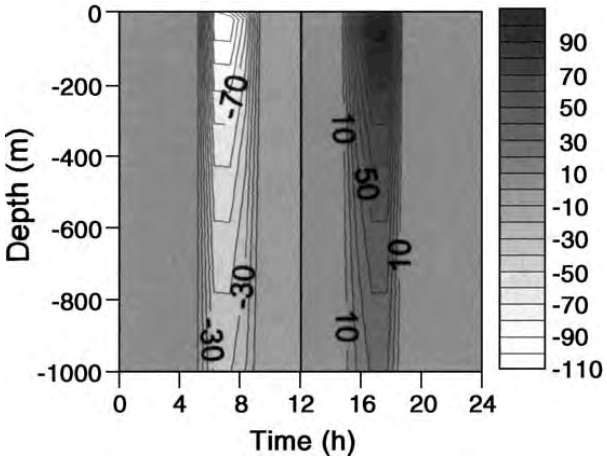

Figure 3.1.3. Speed of zooplankton migration ($m \cdot h^{-1}$) as a function of depth (m) along the day (simulation).

Migrating biomass evolution.

The biomass maxima in our simulation (Figure 3.1.4) appeared at 75 m and 112 m depth during the night in the superficial layers, for the first and second dark period respectively. This result was very similar to the one

observed in the initial data (Table 3.1.3). During daytime, the biomass peak appeared in deeper layers at 428 m and 436 m depth for the first and the second day period, respectively. Biomass peaks were located in the same range of depth as the initial data for day and night periods (Table 3.1.3). The day minus night profile of biomass was similar to the variation in the initial data set (Figure 3.1.5). Biomass integrated in the upper layers at night showed higher values in our simulation than the initial data (Table 3.1.3). During the day, the integrated biomass at depth showed lower values in the simulation than the initial data (Table 3.1.3).

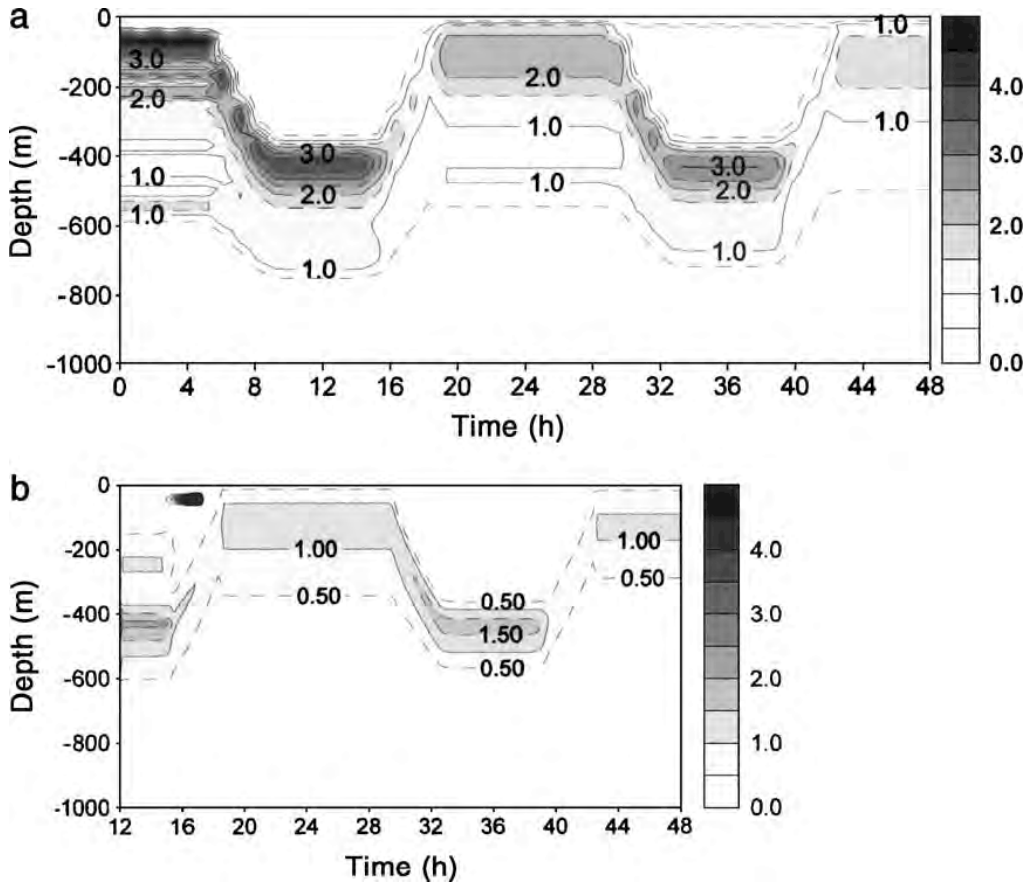

Figure 3.1.4. (a) Simulated evolution of migrating biomass (mgC·m^{-3}) as a function of time and depth (m) initialised with a night profile. (b) Simulation of migrating biomass (mgC·m^{-3}) as a function of time and depth (m) initialised with a day profile.

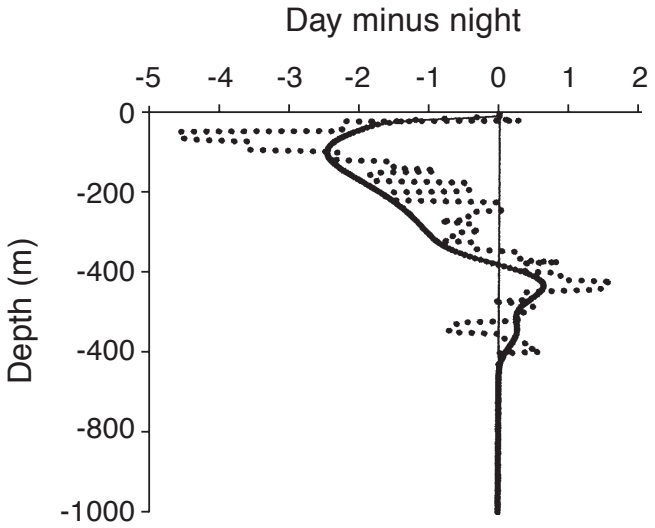

Figure 3.1.5. Simulated and initial (dashed line) values of day minus night biomass ($mgC \cdot m^{-3}$) as a function of depth (m).

Table 3.1.2. Comparison between the initial data set and the model simulations. ** (Ikeda's equation)

	Initial profile	Simulations
Integrated biomass in 28-352 m layer ($mgC \cdot m^{-2}$)	491	575
Integrated biomass in 356-1000 m layer ($mgC \cdot m^{-2}$)	128	76
Depth of day maximal biomass (m)	432-436	428-436
Depth of night maximal biomass (m)	72-104	75-112
Nighttime consumption ($mgC \cdot m^{-2} \cdot d^{-1}$)	19.4	42.1
		37.2**
Daytime respiration at depth ($mgC \cdot m^{-2} \cdot d^{-1}$)	2.68	3.96
		6.96**

Carbon consumption and respiration data simulated and in situ.

The comparison between the *in situ* respiratory data (Figure 3.1.6a) assessed from the ETS activity (Hernández-León *et al.*, 2001), the results of the equation of Ikeda (1985) (Figure 3.1.6b) and the model (Figure 3.1.6c) showed some differences such as the presence of a maximum shallower than the one obtained with the results of Ikeda's equation and the model. However, respiratory flux values obtained from ETS results were of the same order as

those found with the model simulation but about 50% lower than the one assessed using the equation of Ikeda. During the night, the carbon consumption values obtained from the model were slightly higher than the calculation using the equation of Ikeda (Table 3.1.3).

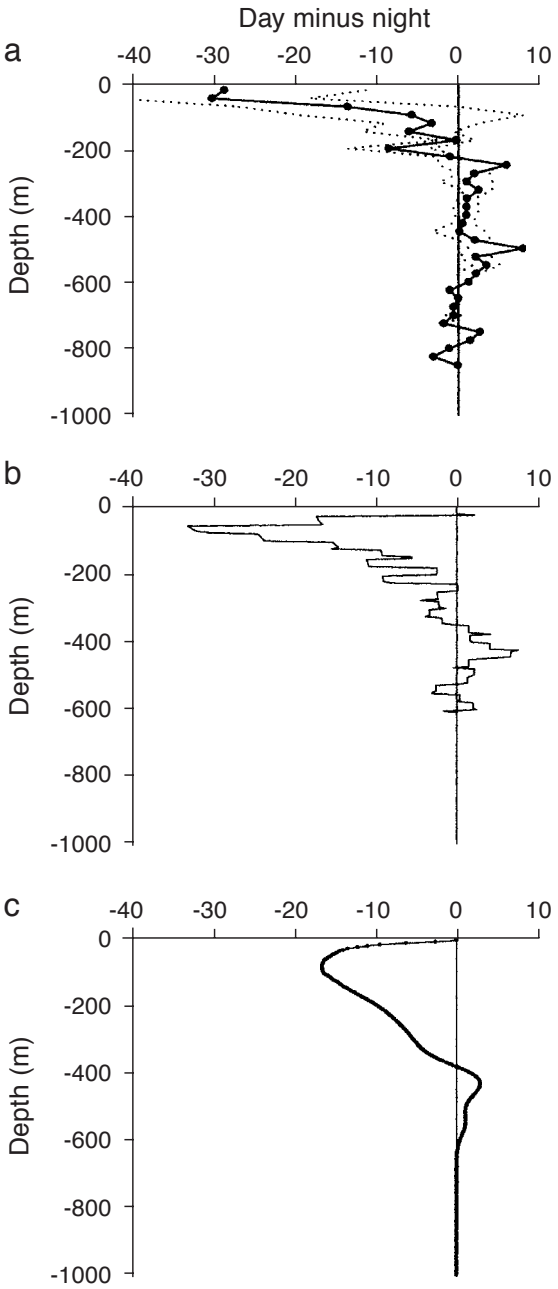

Figure 3.1.6. (a) Average values and standard deviation (dashed lines) of day minus night values of ETS activity ($\mu lO_2 \cdot m^{-3} \cdot d^{-1}$) in both small and large size fractions (from Hernández-León *et al.*, 2001). (b) Day minus night profile of respiration ($\mu gC \cdot m^{-3} \cdot d^{-1}$) as a function of depth (m), calculated from Ikeda's equation. (c) Day minus night profile of carbon quantity used for respiration ($\mu gC \cdot m^{-3} \cdot d^{-1}$) as a function of depth (m), calculated from the model.

Discussion

The vertical movements of large zooplankton have been modelled assuming that sunlight is the only exogenous or endogenous factor used by animals to regulate their vertical movements. As observed by Andersen and Nival (1991), the preferendum hypothesis (isolume hypothesis) and the rate of change hypothesis (Figure 3.1.2) have shown to be capable of regulating zooplankton movements such that animals are located deeper during the day than during the night (Figure 3.1.4). The rate of change hypothesis controls the direction of movements (up or down), whereas the preferendum hypothesis controls the intensity of the migration speed. As a result, zooplankton did not move vertically at night due to the null migration speed (Figure 3.1.3). The migration is initiated when the stimulus is strong (at sunrise) or when the stimulus is slight (at sunset). During the night, zooplankton organisms in our model behave like passive particles. The ascent and descent migration takes 3-4 h, which is similar to the modelling results of Andersen and Nival (1991) and *in situ* observations of between 3 h (Williams and Fragopoulu, 1985) and 3h45 (Boysen and Buchholz, 1984). Our estimates of migration speed agree with the *in situ* data reported in the literature, which are in the range of 31-91 $m \cdot h^{-1}$ (Enright, 1977), 42-122 $m\ h^{-1}$ (Roe *et al.*, 1984), 40-151 $m\ h^{-1}$ (Plueddemann and Pinkel, 1989) and 67-186 $m\ h^{-1}$ (Wiebe *et al.*, 1992). Migration speeds obtained were similar during the ascent and descent movements, whereas Widder and Frank (2001) found that migration speed differs at sunset and at sunrise; the speed will be slower on the ascent at sunset and faster on the descent at sunrise than would be predicted using just surface irradiance measurements and a constant diffuse attenuation coefficient. Plueddemann and Pinkel (1989) found that during the upward migration at sunset, the deeper layer migrated faster than the intermediate layer and the intermediate layer migrated faster than the shallow layer. Therefore, caution must be taken when comparing observations in nature with distributions generated by this model. Sunlight is not the only factor influencing vertical migration; other factors such as moonlight should be considered (Blaxter, 1973; Roger, 1974; Tarling *et al.*, 1999; Pinot and Jansá,

2001). Therefore, the model should be used to account for these sources of variation.

The use of the equation of Ikeda results in higher values than the values of daytime respiration at depth using the *in situ* results of Hernández-León *et al.* (2001) and of our model results. The large difference between the *in situ* values and those obtained by the equation of Ikeda could be related to the respiration/ETS ratio (0.5) used *in situ*, which has been considered conservative in calibration exercises. The use of a respiration/ETS ratio of 1.0 (Hernández-León and Gómez, 1996) does not introduce a larger value than the equation of Ikeda. However, the use of empirical relationships obtained for epipelagic animals can also produce some overestimation. Therefore, we caution against the use of these two approaches: the errors and uncertainties involved in such estimates are considerable.

The respiratory flux of carbon into the ocean, together with the sinking flux of particulate carbon (gravity flux), must contribute to the draw-down of atmospheric CO_2 across the sea surface (Volk and Hoffert, 1985). Longhurst and Harrisson (1988, 1989), Longhurst et al. (1989, 1990), Dam *et al.* (1995), Emerson et al. (1997), Le Borgne and Rodier (1997), Zhang and Dam (1997), Steinberg *et al.* (2000), Al-Mutairi and Landry (2001) and Hernández-León et al. (2001) have established that a significant downward export flux is caused by diel vertical migration of zooplankton due to respiration and excretion at depth. Defecation can take place above or below the thermocline due to the variable gut passage time of migrant zooplankton (Dagg *et al.*, 1989; Morales et al., 1993; Atkinson *et al.*, 1996). Some calculations (Hays et al., 2001) showed that the amount of carbon lost when the gut content is defecated is relatively small compared to the respiratory carbon losses during the day below the thermocline. However, night-time consumption by migrants in our simulation was in the range of 37-42 mgC $m^{-2}\cdot d^{-1}$ (Table 3.1.3), which gives a defecation rate in the range of 11.2-12.6 mgC $m^{-2}\cdot d^{-1}$, assuming an assimilation efficiency of 70%. Moreover, consumption calculated from the day minus night profile of ETS activity and converted into respiration using a conservative respiration/ETS ratio of 0.5 gave a value of 19.4 mgC $m^{-2}\cdot d^{-1}$ (Table 3.1.3).

In contrast, export production calculated from primary production using the equation of Lohrenz *et al.* (1992) showed values ranging from 9.5 to 12.0 mgC $m^{-2}\cdot d^{-1}$ at 150 m depth. Faecal pellet production is probably continuous during the night, but there is evidence that the gut residence time in strong diel migrants can be higher than in non-migrating organisms (Flint *et al.*, 1991; Morales *et al.*, 1993; Atkinson *et al.*, 1996). Because diel migrants are larger and during migration move into water of lower temperature and lower food concentration, a gut passage time of an hour could be assumed. This supports the view that some diel migrants can transport some of the food that they ingest in the shallower layers to the mesopelagic zone during their downward movement. Assuming that half of the rate obtained is egested and/or sinks below the pycnocline, the export flux due to the faecal matter should account for about 24-66% of the gravitational flux.

Our calculations also support the effect of the interzonal fauna on epizooplankton during the moon cycle observed by Hernández-León (1998) and Hernández-León *et al.* (2001, 2002). A clear decrease of mesozooplankton in the upper 200 m layer was observed from full to new moon periods, as in the cycle described by Gliwicz (1986) for lakes. The predatory pressure of diel migrants during the dark phase of the moon promotes a decrease of the small zooplankton in the upper layers while during the full moon migrants remain below 100 m depth at night (Blaxter, 1973; Tarling *et al.*, 1999; Pinot and Jansá, 2001), allowing the growth of mesozooplankton. Recent calculations based on the biomass disappearance during the moon cycle show values of active flux due to predation of 63% of the gravitational flux (Hernández-León *et al.*, 2002). Therefore, *our in situ* data, the model results and the results using the equation of Ikeda (1985) support the view that the feeding impact as well as the metabolic flux of diel migrants should be seriously considered in export flux studies because it can be equivalent to the gravitational flux in subtropical waters.

Acknowledgements

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INFLUENCE OF THE LATE WINTER BLOOM ON MIGRANT ZOOPLANKTON METABOLISM AND ITS IMPLICATIONS ON EXPORT FLUXES.

Putzeys, S., Yebra L., Almeida C., Bécognée P. and S. Hernández-León (2011). Journal of Marine Systems, 88, 553-562.

Abstract:

Studies on carbon active fluxes due to diel migrants are scarce and critical for carbon flux models and biogeochemical estimates. We studied the temporal variability and vertical distribution of biomass, indices of feeding and respiration of the zooplanktonic community north off the Canary Islands during the end of the late winter bloom, in order to assess vertical carbon fluxes in this area. Biomass distribution during the day presented two dense layers of organisms at 0-200 m and around 500 m, whereas at night, most of the biomass concentrated in the epipelagic layer. The gut pigment flux (0.05 - 0.18 $mgC \cdot m^{-2} \cdot d^{-1}$) represented 0.22 % of the estimated passive export flux (POC flux) while potential ingestion represented 3.91 % of the POC (1.24 - 3.40 $mgC \cdot m^{-2} \cdot d^{-1}$). The active respiratory flux (0.50 - 1.36 $mgC \cdot m^{-2} \cdot d^{-1}$) was only 1.57 % of the POC flux. The total carbon flux mediated by diel migrants (respiration plus potential ingestion) ranged between 3.37 - 9.22 % of the POC flux; which is three-fold higher than calculating ingestion fluxes from gut pigments. Our results suggest that the fluxes by diel migrants play a small role in the downward flux of carbon in the open ocean during the post-bloom period.

Keywords:

Canary Islands, carbon flux, metabolism, respiratory flux, vertical migration, zooplankton, late winter bloom.

Introduction

Understanding the mechanisms involved in the production cycle of the subtropical waters is needed to elucidate the fate of organic matter produced in these large areas of the ocean. A process involved is the annually observed productive pulse named late winter bloom (Menzel and Ryther, 1961). In subtropical waters this bloom is due to erosion of the thermocline driven by surface cooling that enhances vertical diffusion of nutrients from below the mixed layer. Its influence in relation to the particle formation, transformation and flux is obvious. The late winter bloom in the Canary Island waters is fairly well known from the standpoint of plankton biomass and production (De León and Braun, 1973; Arístegui *et al.*, 2001; Hernández-León, 2004). In general, primary production and chlorophyll *a* increase from January to March and decrease during April (Arístegui *et al.*, 2001). Zooplankton biomass closely follows phytoplankton, developing through February, reaches a maximum in March and decreases in April. The evolution of zooplankton biomass and metabolic activity during this annual event is well described (Hernández-León *et al.*, 2004). However, our knowledge of the influence of productive pulses on the active carbon flux mediated by diel vertical migration is scarce.

Vertical migration is a common feature in zooplankton communities and also one of the most important movements of biomass in the ocean (Enright, 1977; Buskey and Swift, 1983; Atkinson *et al.*, 1992). A review by Hutchinson (1967) examines some hypothesis to explain the adaptive significance of vertical migration. The influence of sunlight, modified by other physical and biological factors, and the attempt to avoid visual orientating predators (Zaret and Suffern, 1976) are the most common explanations for this particular behaviour. Other authors (Gliwicz, 1986; Frost, 1988; Bollens and Frost, 1991; Pinot and Jansá, 2001) support these conclusions. Diel-migrant zooplankton usually migrates to the surface to feed at night and returns to deeper layers at dawn (Lampert, 1989). By feeding in shallower layers and defecating, respiring, excreting and dying at depth, migrant organisms play a determining role in the vertical downward flux of particulate and dissolved matter in the water column (Longhurst and Harrison, 1988; Longhurst *et al.*, 1990). This active flux is a complex mechanism composed by a sum of

different components. The flux of particulate carbon due to the production of fecal pellets in the mesopelagic zone is the so-called “gut flux” (Hu, 1978; Angel, 1985). A more subtle transport to the mesopelagic zone is the vertical flux of dissolved carbon caused by the night time feeding at the shallower layers and the daytime respiration of the diel migrant biota at depth (Longhurst and Harrison, 1988; 1989; Longhurst *et al.*, 1990, among others). Several studies (Longhurst and Harrison, 1988; Longhurst *et al.*, 1989, 1990; Dam *et al.*, 1995; Zhang and Dam, 1997; Yebra *et al.*, 2005; Steinberg *et al.*, 2008) show that respiratory carbon from diel migrant biota below the epipelagic zone during daytime represents a significant pathway of downward transport of carbon compared to the gravitational vertical flux. The active flux also includes the fluxes due to mortality at depth (Dam *et al.*, 1995), dissolved organic excretion (Steinberg *et al.*, 2000) and predatory activity (Hernández-León, 1998; Hernández-León *et al.*, 2001a, 2002, 2004). Nevertheless, the respiratory flux jointly with the gut flux are two main components of the biological pump in the ocean when compared to the passive or gravitational flux (Zhang and Dam, 1997; Steinberg *et al.*, 2000).

The gut pigment flux can be calculated with the gut fluorescence method (Hernández-León *et al.*, 2001b) while respiration of migrants can be assessed using an average value of respiration at depth (under 200 m depth) or, alternatively, measuring the electron transfer system activity (ETS, Packard, 1971) to obtain detailed profiles of *in situ* potential respiration at depth. The use of ETS activity to approach metabolic rates is not straightforward. However, it provides us with an *in situ* instantaneous cellular respiration rate much more accurate than simple estimations based on body size, abundance and temperature (Putzeys and Hernández-León, 2005). Therefore, determining the *in situ* potential respiration and the pigments contained in the gut of migrants we obtain an overview of the migrant community metabolic level during the study period.

Diet is the starting point of metabolism and it is clear that a diet shift could have an influence on the active carbon fluxes. Estimates of the carbon transported from surface to deep waters by diel vertical migration are rare and critical for carbon flux models and biogeochemical estimates. There are also

few studies on the temporal development of the late winter bloom in oceanic waters of the subtropical gyre. None of them deal with the possible impact of a diet change on the biological pump efficiency. We determined the vertical distribution of mesozooplankton (200-1000 µm) biomass (as protein content), indices of gut fullness (gut fluorescence) and respiration (ETS activity) in order to calculate the contribution to carbon export flux by diel vertical migrants at the end of the late winter bloom north off the Canary Islands.

Materials and methods

Sampling took place from 12th to 23th March 2000 at a station located 100 km to the North of Gran Canaria Island (28.8ºN, 15.4ºW), on the eastern flank of the subtropical North Atlantic gyre (Figure 3.2.1).

This area is not influenced by the high mesoscale activity observed leeward of the islands (Barton *et al.*, 1998). Vertical profiles of temperature, conductivity and fluorescence were obtained using a Neil Brown Mark III CTD. Fluorescence data were converted to chlorophyll using *in situ* chlorophyll values as reference. Samples for chlorophyll *a* were taken at 5 m depth with a 5 litres Niskin bottle, and pigments were measured following standard procedures (Yentsch and Menzel, 1963; Strickland and Parsons, 1972). A series of 8 oblique hauls were carried out from the R.V. “Garcia del Cid” using a Longhurst-Hardy Plankton Recorder (LHPR) equipped with a flowmeter and 200 µm mesh net (Longhurst and Williams, 1976). The use of 200 µm mesh net was justified by previous studies performed in the area determining the 100-200 µm fraction to be only 7% of the total zooplanktonic biomass (Hernández-León *et al.*, 2001b). More details of the fishing method used are given by Hernández-León *et al.* (2001a). Hauls were performed to fit with day and night times. Samples were obtained from 813 to 0 m depth with a number of samples per haul ranging between 17 to 26. Each sample corresponded to a different layer, each one with a vertical extent of 20-40 m. For each sample we calculated the mean depth of the layer sampled.

On board, samples were rinsed and quickly frozen in liquid nitrogen (-196 ºC) for biomass and metabolic rates determination. Very large organisms (mainly decapods and mesopelagic fish) appeared occasionally and were

removed because those organisms are thought to avoid the inlet of the LHPR net (0.4 m diameter), and we did not correct for daytime avoidance of nets.

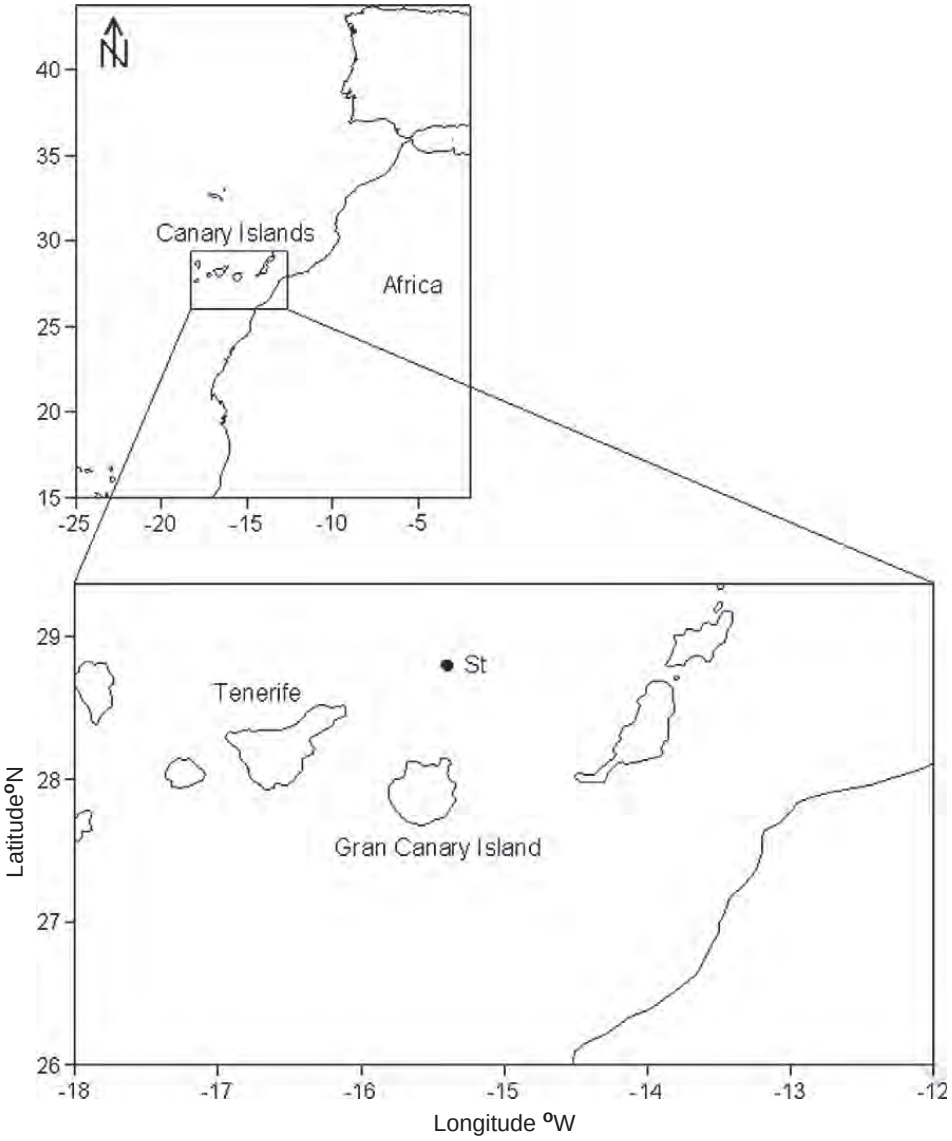

Figure 3.2.1. Sampling location.

In the laboratory, frozen samples were homogenized keeping the temperature below 4ºC in dark conditions to avoid as much as possible degradation of chlorophyll and proteins, and loss of enzymatic activity. Subsamples were taken for (1) gut fluorescence (GF), as index of gut fullness, (2) ETS activity, as a proxy for respiration and (3) protein content analysis, as biomass.

For GF analysis, aliquots (200 µL) of the homogenates were diluted in 10 mL of 90% acetone and stored at -20 ºC during 24 hours in darkness. Fluorescence was assayed before and after acidification (4% HCl) in a Turner Design fluorometer (10-005 R model), previously calibrated with pure chlorophyll *a* (Yentsch and Menzel, 1963). Pigment content was calculated from the equations given in Hernández-León *et al.* (2001b).

All the GF data in this work include Chl *a* plus phaeopigments and no correction was made for pigment loss. GF values were corrected for the background fluorescence of the exoskeleton of the organisms captured from the well-described deep scattering layer (DSL, Boden and Kampa, 1967; Hernández-León *et al.*, 2001a). We assumed that all the biomass had a background fluorescence of 0.1 µg of pigments per gram of wet weight (Willason and Cox, 1987) and a dry weight to wet weight ratio of 0.2 (Mauchline, 1969).

Electron transfer system (ETS) activity was assayed according to Packard (1971) modified by Gómez *et al.* (1996). ETS activity was recalculated to the *in situ* temperature using the Arrhenius equation and an activation energy of 15 Kcal·mol^{-1} (Packard *et al.*, 1975). Protein content was determined using the method of Lowry *et al.* (1951) modified for microanalysis by Rutter (1967), and using bovine serum albumine (BSA) as standard. Protein values were converted to dry weight using the relationship given by Hernández-León *et al.* (2001b) for the Canary Islands waters and to carbon units assuming that carbon is 40% of dry weight (Dam and Peterson, 1993). Enzymatic activity and gut fluorescence were normalized to the amount of protein for each sample to obtain protein-specific values.

Data from all stations were categorized on 50 m intervals to obtain day and night vertical profiles of protein content, GF and ETS activity. Pearson correlation matrices were performed on categorized profiles in order to determine whether consecutive day (or night) biomass profiles were different. The biomass profiles on consecutive days were not significantly similar (all $p<0.05$). The same was observed for the night biomass profiles (all $p<0.05$). Therefore, the different sampling days were treated independently. We subtracted each night profile from the corresponding day profile to show only daily changes involving migrants as in Yebra *et al.* (2005). The negative

values of the protein day-minus-night profile correspond to migrant biomass that reached the epipelagic layer at night including organisms living both above and under 800 m by day. This migrant biomass (mg protein·m^{-2}) was determined integrating the area of negative biomass values (mg protein·m^{-3}) as in Longhurst and Williams (1979) and Yebra *et al.* (2005):

$$\text{Migrant Biomass} = \int_{0\text{-}200} \text{Biomass} \qquad \text{(eq. 1)}$$

Migrant biomass values were then converted to carbon units as indicated before.

The gut pigment flux (mg pigments·m^{-2}·d^{-1}) was calculated performing a two-steps operation. First, the day-minus-night positive GF data at depth were integrated and divided by the biomass at the same depth to obtain the specific gut content (µg pigment·mg $protein^{-1}$·m^{-2}) at depth:

$$\text{Specific Gut content at depth} = \left[\int_{200\text{-}850} \text{GF}\right] \cdot \left[\int_{200\text{-}850} \text{Biomass}\right]^{-1} \qquad \text{(eq. 2)}$$

The second step was to multiply this specific gut content at depth by the migrant biomass to obtain the gut pigment flux.

To determine the respiratory flux (µL O_2·m^{-2}·h^{-1}) positive values of the ETS day-minus-night profiles (µL O_2·m^{-3}·h^{-1}) were integrated and divided by the integrated biomass at the same depth:

$$\text{Specific ETS at depth} = \left[\int_{200\text{-}850} \text{ETS}\right] \cdot \left[\int_{200\text{-}850} \text{Biomass}\right]^{-1} \qquad \text{(eq. 3)}$$

The specific ETS activity at depth (µL O_2·mg $protein^{-1}$·h^{-1}) obtained was then multiplied by the migrant biomass present in the epipelagic layer at night.

To assess metabolism of the migrant community, we determined potential ingestion (I, mgC·m^{-2}·d^{-1}) from the integrated day-minus-night positive respiration values (R) below 200m depth. We assumed assimilation to be 0.7 and a gross growth efficiency of 0.3 before applying the equation proposed by Ikeda and Motoda (1978):

$$I = 1 \cdot R/(0.7\text{-}0.3) = R \cdot 1/0.4 = 2.5 \cdot R \qquad \text{(eq. 4)}$$

In order to determine the food source used by migrants to sustain their metabolism, we compared their potential ingestion with their pigmented gut content values. We calculated the omnivory index as [(ingestion - grazing)·$ingestion^{-1}$] (Hernández-León *et al.*, 2002).

Results

Hydrography

During the sampling period, hydrographical data showed surface temperatures (Figure 3.2.2a) below 19ºC and a pycnocline (Figure 3.2.2b) at 100 m depth, denoting the typical conditions of the late winter bloom.

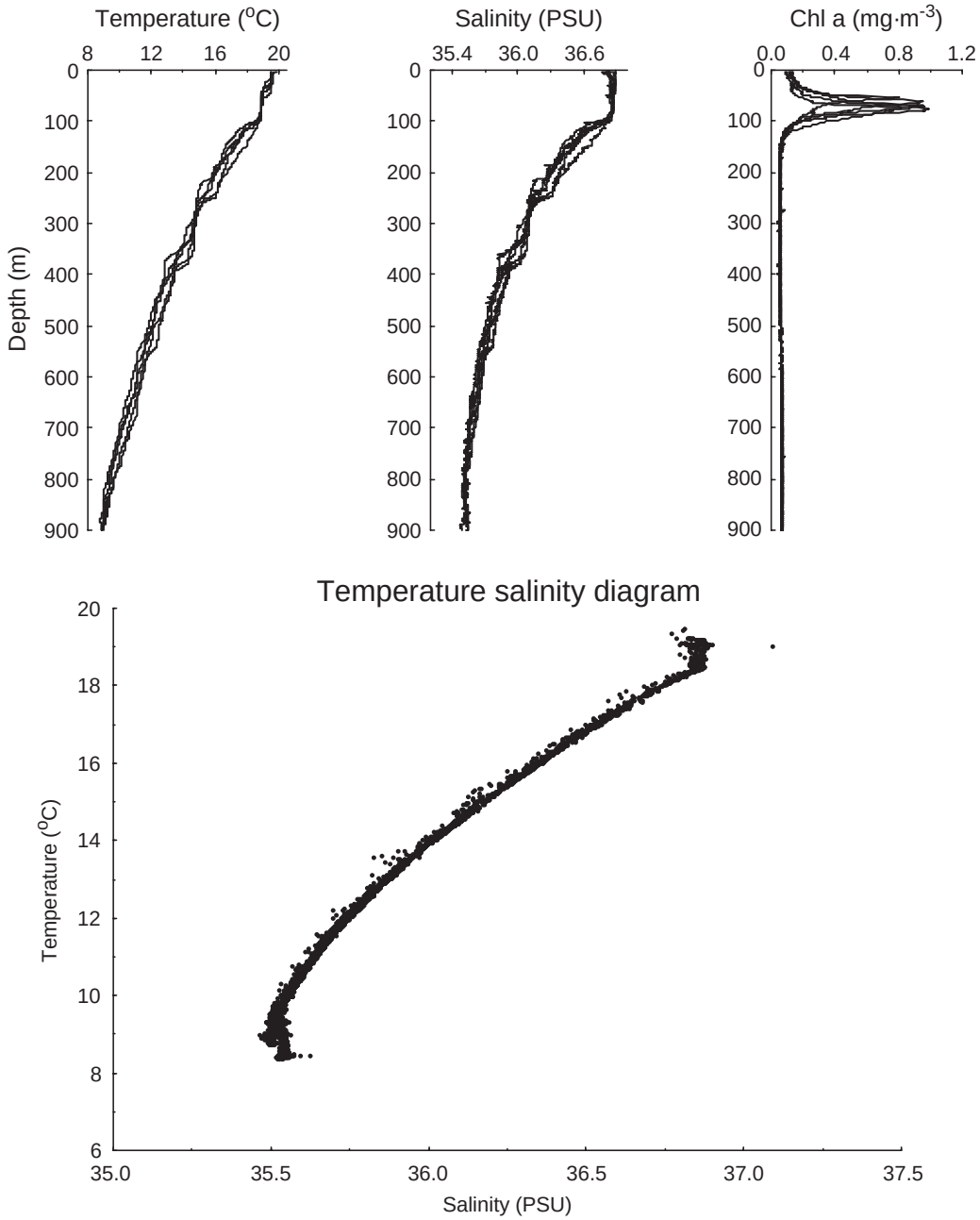

Figure 3.2.2. CTD profiles of temperature (ºC), salinity (PSU), chlorophyll *a* (mg·m^{-3}) and TS diagram of the performed hauls.

Chlorophyll *a* distribution (Figure 3.2.2c) in the water column presented a maximum at around 75 m depth. The TS diagram (Figure 3.2.2d) during the

cruise showed that the different hauls were carried out within the same water mass.

Biomass

Biomass vertical distribution differed between sampling days (Figure 3.2.3a, $p<0.05$) and the same was seen on the night profiles ($p<0.05$). We observed that during the day, biomass was concentrated above 300 m but also peaked between 450-650 m depth, forming the DSL. At night, biomass between 450-650 m depth weakened, except some single layers (on the 12th and 19th of March), and most of the biomass was concentrated above 300 m except on the 19th of March. The spatial patchiness of the zooplankton was reflected in the day-minus-night profiles (Figure 3.2.3b).

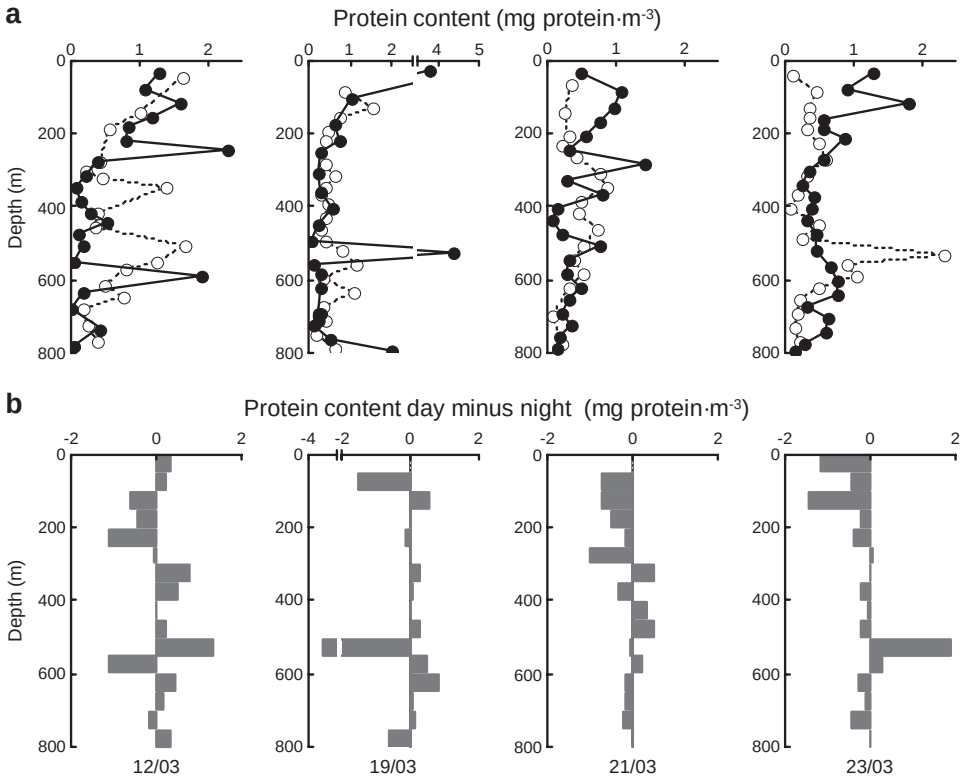

Figure 3.2.3. Biomass profiles and day minus night variations. a) Protein content (mg protein·m^{-3}) of the different hauls performed. White dots for day time and black dots for night time. Day-minus-night profiles of biomass in the water column (mg protein·m^{-3}).

Integrated epipelagic biomass (0-200m) during daytime decreased along the cruise, with values ranging from 468.69 on the 12th of March to 86.45 mgCm^{-2} on the 21st (Table 3.2.1), with a slight increase on the 23rd

(129.37.mgC·m^{-2}). The same tendency was observed on the integrated total water column biomass during day time, with values ranging from 1198.81 to 586.75 mgC·m^{-2} (Table 3.2.1). During day time epipelagic biomass (0-200m) represented a sixth to a third of the total zooplankton biomass (0-800m). Migrant biomass increased towards the end of the bloom and ranged between 108.01 and 341.48 mgC·m^{-2} (Table 3.2.1).

Table 3.2.1. Zooplankton biomass (mg C·m^{-2}), omnivory index and active fluxes (mg C·m^{-2}·d^{-1}).

date		12/03/00	19/03/00	21/03/00	23/03/00	Mean ± SD
Epipelagic biomass during day time (0-200 m)		468.69	313.52	86.45	129.37	249.50 ± 176.22
Total biomass during day time (0-800 m)		1198.81	967.41	586.75	793.31	886.57 ± 259.89
Migrant biomass		108.01	161.33	206.91	341.48	204.43 ± 99.90
Gut flux		0.18	0.15	0.06	0.05	0.11 ± 0.06
Respiratory flux		0.62	0.75	0.50	1.36	0.81 ± 0.38
Potential ingestion		1.55	1.88	1.24	3.40	2.02 ± 0.96
Omnivory index	Epipelagic	0.97	0.95	0.93	0.95	0.95 ± 0.02
	Migrants	0.88	0.92	0.95	0.98	0.93 ± 0.04
Total carbon flux[1] (R. flux + G. flux)		0.80	0.91	0.56	1.41	0.92 ± 0.36
Total carbon flux[2] (R flux + P. ing. flux)		2.18	2.64	1.74	4.76	2.83 ± 1.34
% of POC[1]		1.55	1.76	1.08	2.74	1.78 ± 0.70
% of POC[2]		4.22	5.11	3.37	9.22	5.48 ± 2.59

R. flux: Respiratory flux; G. flux: Gut flux; P. ing. flux: potential ingestion flux; [1]: sum of R. flux and G. flux; [2]: sum of R. flux and P. ing. Flux

Gut fluorescence

Community gut fluorescence (ng pigments·m^{-3}) was highly variable (Figure 3.2.4a). The day GF values in the epipelagic zone were two to four-fold higher on the 12th, 19th and 23rd of March (12.34, 13.06 and 5.9 µg pigment·m^{-2} respectively) than the 21st of March 2000 (2.85 µg pigment·m^{-2}). During the night, GF in the epipelagic zone was lower than during the day time on the 12th and 19th, which was reflected in the day-minus-night profiles (Figure 3.2.4b). Inversely, on the last two sampling days (21st and 23rd) the

epipelagic GF values were higher than during the day. The night time profiles (Figure 3.2.4a) also presented few single peaks of GF which did not always correspond to the DSL depth.

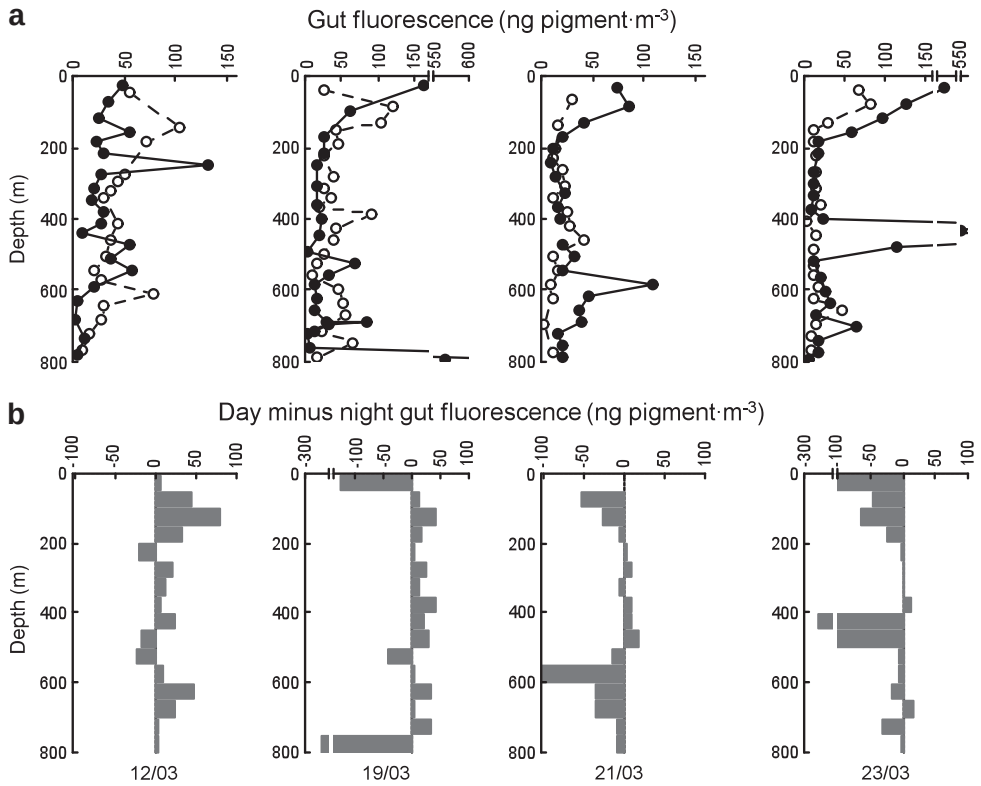

Figure 3.2.4. Gut fluorescence and day-minus-night variations. a) Gut fluorescence profiles (ng pigments·m^{-3}) of the different hauls performed. White dots for day time and black dots for night time. b) Day-minus-night profiles of gut fluorescence (ng pigments·m^{-3}).

The gut fluxes ranged between 1.78 (on the 23rd) and 10.40 µg pigments·m^{-2} (on the 12th). Using a carbon/pigment ratio of 30 (Vidal 1980), an assimilation efficiency of 0.7 (Conover, 1966) and assuming that pigments were defecated during the vertical downward or during the residence time at depth, we estimated daily gut fluxes between 0.05 and 0.18 mg C·m^{-2}·d^{-1} (Table 3.2.1).

3.4 Electron transfer system activity

The day ETS activity profiles (Figure 3.2.5a) showed high values above 200 m and between 450-700 m depth coinciding with the DSL. Also, the epipelagic ETS activity during the day time, was 2 to 5 fold-higher on the 12th

and 19th of March (3.87 and 2.40 ml $O_2 \cdot m^{-2} \cdot h^{-1}$ respectively) than on the last sampling days (0.77 and 1.02 ml $O_2 \cdot m^{-2} \cdot h^{-1}$ on the 21th and the 23rd, respectively). The ETS activity at night presented a maximum above 300 m depth except for some thin layers. The day-minus-night ETS activity profiles (Figure 3.2.5b) reflected the presence of deep water migrants that reached the DSL on the 12th and 19th (Figure 3.2.3b).

The respiratory fluxes varied between 0.39 and 1.35 $\mu lO_2 \cdot m^{-2} \cdot d^{-1}$. Assuming a conservative respiration/ETS ratio of 0.5 (Hernández-León and Gómez, 1996) and a respiratory quotient of 0.97 (Omori and Ikeda, 1984), we estimated the respiratory flux mediated by the diel migrants, during the 12h of residence time at depth observed, to be between 0.50 and 1.36 mg $C \cdot m^{-2} \cdot d^{-1}$ (Table 3.2.1).

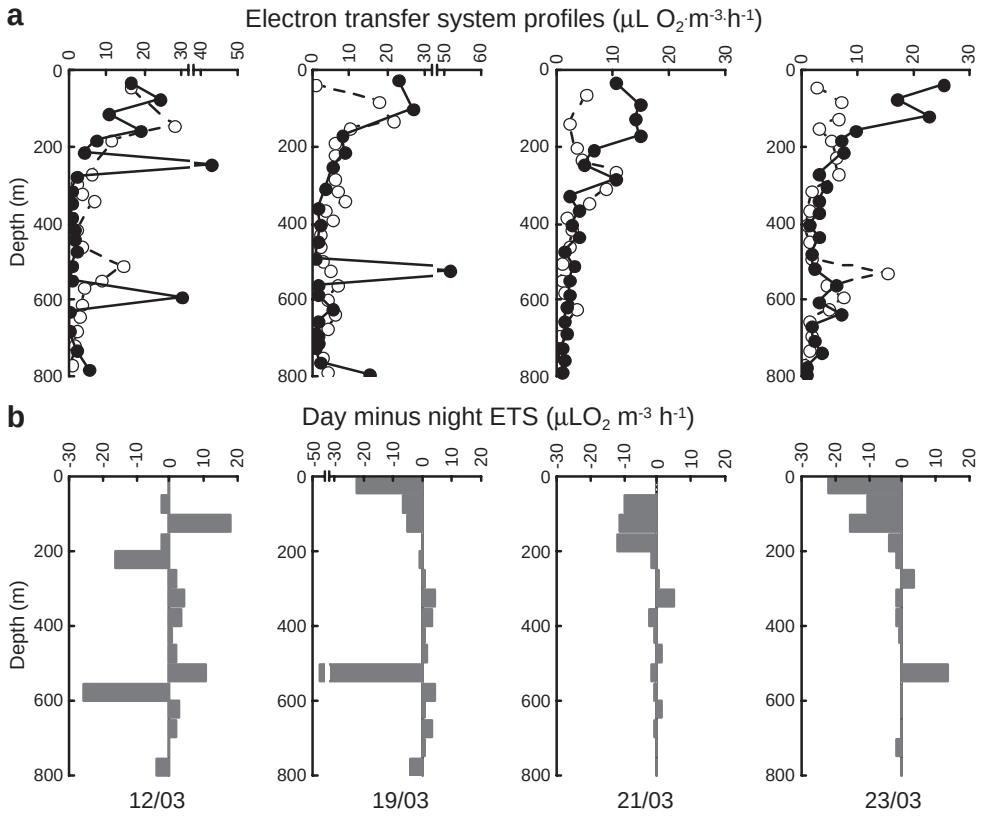

Figure 3.2.5. Electron transfer system and day-minus-night variations. a) ETS profiles of the different hauls performed ($\mu lO_2 \cdot m^{-3} \cdot h^{-1}$). White dots for daytime and black dots for night time. b) Day-minus-night profiles of ETS activity ($\mu lO_2 \cdot m^{-3} \cdot h^{-1}$).

Metabolic activity

Using the respiratory fluxes we calculated the potential ingestion requirements of the migrant community, which ranged between 1.24 and 3.40 mgC·m^{-2}·d^{-1} (Table 3.2.1). In Figure 3.2.6 we show the evolution of zooplankton biomass during the post bloom period. Both the integrated epipelagic biomass (0-200 m) collected with the LHPR and the epipelagic biomass (0-100m) assessed by Hernández-León *et al.* (2004) with a WP2 net decreased overtime (as well as the Chl *a*) while the migrant biomass increased. This was reflected as an imbalance between the gut flux and the carbon required to sustain the metabolism. This discrepancy increased significantly on the last sampling day (23rd of March), when Chl *a* and epipelagic zooplankton biomass reached minimum values but migrant biomass and its potential ingestion increased notably. The omnivory index assessed for the migrant community during the sampling period increased slightly from 0.88 to 0.98 (Table 3.2.1), while the values remained constant (0.95 ± 0.2) for the epipelagic community.

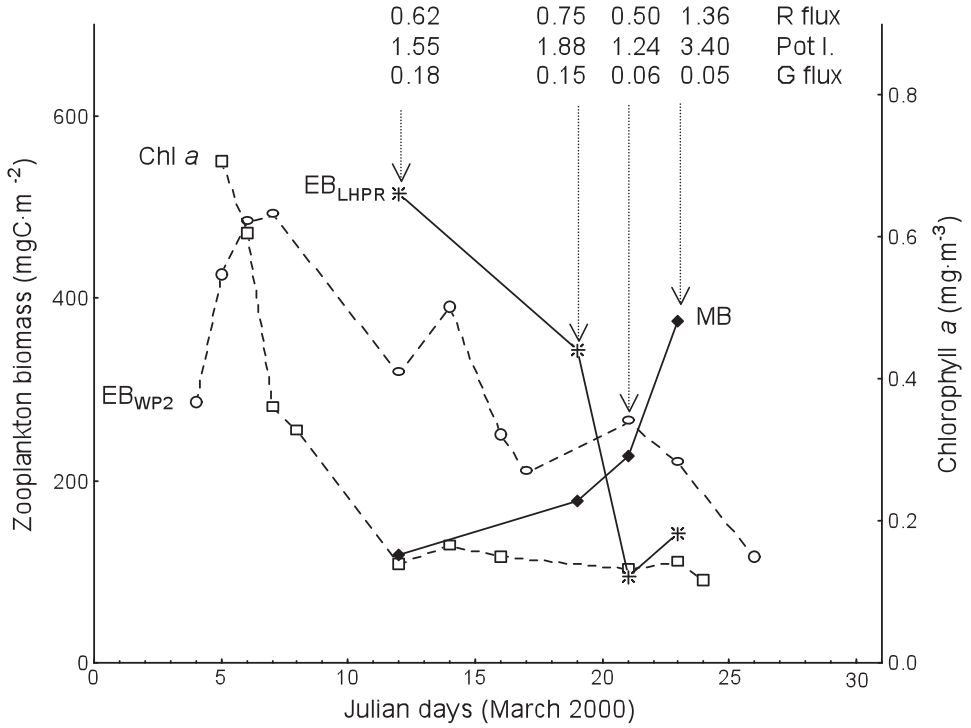

Figure 3.2.6. Evolution of biomass (mg C·m^{-2}) and active fluxes (mg C·m^{-2}·d^{-1}). EB$_{LHPR}$: epipelagic biomass (0-200 m), EB$_{WP2}$: epipelagic biomass (0-100 m, Hernández-León *et al.*, 2004), MB: migrant biomass, Chlorophyll *a* (mg·m^{-3}, Hernández-León *et al.*, 2004), R flux: respiratory flux, Pot. I.: potential ingestion, G flux: gut flux.

Discussion

Hydrological conditions indicate that the late winter bloom influenced our sampling. A sharp outburst of chlorophyll *a* in the study area occurred during February-March 2000 (Hernández-León *et al.*, 2004). This bloom coincided with the vertical mixing at the end of winter and also with a dust storm formed in the Sahara desert a week before the start of our sampling. The dust cloud reached the Canaries and approached the Azores Islands (see http://visibleearth.nasa.gov/cgi-bin/viewrecord?22352). The dust cloud coincided with the increase in phytoplankton biomass, and was followed by an increase in small zooplankton (100–500 µm). The average primary production measured during our cruise was 1088.4 mg $C \cdot m^{-2} \cdot d^{-1}$ (Hernández-León *et al.* 2004). This value is close to previously reported values for Canary Island waters during the late winter bloom (De León and Braun, 1973; Arístegui *et al.*, 2001). Also, the migrant biomass that we observed varied within the range of previous studies in Canary zone and in other subtropical areas around the globe (see Table 3.2.2 and references therein), but the integrated epipelagic zooplankton biomass decreased four-folds in eleven days, coinciding with the end of the bloom. It is suggested that the zooplanktonic biomass during the late winter bloom in subtropical waters is driven by the interplay between resource and consumer controls (Hernández-León *et al.*, 2004). The combined effect of the bloom sustained by the dust storm allowed the growth of an important epipelagic biomass. At the end of the bloom, the omnivory index observed in both epipelagic and migrant zooplankton was very high, indicating a shift in diet of mesozooplankton from phytoplankton to microzooplankton and/or small zooplankton. This shift and the dramatic reduction of the gut pigment content that we observed in the migrant community would explain the lower values of epipelagic zooplankton biomass found at the end of the bloom.

Gut pigment fluxes calculated are within the range of previously observed records in the Canary Islands (Table 3.2.2).

Table 3.2.2: Zooplankton active flux estimated in different oceanic regions. Revised from Ducklow et al. (2001).

Location	Time of year	Migrant biomass (mg C·m^{-2})	Respiratory flux (mg C·m^{-2}·d^{-1})	Gut flux (mg C·m^{-2}·d^{-1})	Mortality flux (mg C·m^{-2}·d^{-1})	% of POC flux	References
Pacific Ocean							
Eastern Equator	March - April	96.0 ± 25.2	4.2 ± 1.2	-	2.9 ± 0.8	18.4[1]	Zhang and Dam, 1997
Eastern Equator	October	154.8 ± 32.4	7.3 ± 1.4	-	5.4 ± 1.1	25.4[1]	Zhang and Dam, 1997
Central Equator (HNLC)	October	52.9	6	-	-	4[1]	Le Borgne and Rodier, 1997
Western Equator	October	46.9	3	-	-	6[1]	Le Borgne and Rodier, 1997
Western Equator	February	367 (144-447)	22.7 (7.3-19.1)	-	4.8 (2.6-4.4)	24 (13-35)[1]	Hidaka et al., 2001
ALOHA	Year-round	162 (108-216)	3.6 (2.6-4.8)	-	-	15 (12-18)[1]	Al-Mutairi and Landry, 2001
ALOHA	June - July	157.9	3.7	-	-	18[1]	Steinberg et al., 2008
Equator divergence		2.8-21.8	0.9-1.2	-	-	<1-2[1]	Roman et al., 2002
Oligotrophic area		30.2 - 33.8	1.3-1.7	-	-	4[1]	Roman et al., 2002
Atlantic Ocean					-		
NFLUX	September	29.0	1.9	-	-	3[1]	Longhurst et al., 1989, 1990
Oligotrophic (BATS)	March/April	192 (84–540.0)	14.5 (6.2-40.8)	-	-	34 (18-70)[1]	Dam et al., 1995
Oligotrophic (BATS)	year-round	50.0 (0-123.0)	2.0 (0-9.9)	-	-	8 (0-39)[2]	Steinberg et al., 2000
Oligotrophic (BATS)	year-round	83.0 (0.7-468.0)	-	0.8 (0.007-4.5)	-	4 (0.03-21)[3]	Schnetzer and Steinberg, 2002
North (coastal)	Oct-November	360.0 ± 70.0	30.3 ± 1.9	-	-	-	Isla and Anadón, 2004
North (poleward current)	Oct-November	270.0 ± 210.0	10.4 ± 6.3	-	-	-	Isla and Anadón, 2004
North (Oceanic)	Oct-November	30.0 ± 10.0	2.2 ± 0.3	-	-	-	Isla and Anadón, 2004
Canary Islands	August	247.8-124.8	4.3-1.9	0.3-2.4	-	20-45[4]	Hernández-León et al., 2001a
Canary Islands	June	580.0-1280.0	1.8-8.3	0.1-0.4	-	15-53[4]	Yebra et al., 2005
Canary Islands	March	204.4 (108.0-341.5)	0.8 (0.5-1.4)	0.1 (0.05-0.2)[5] 1.2-3.4[6]	-	1.1-2.7[4] 3.4-9.2[7]	Present work

[1]%POC flux represents only respiratory flux; [2]active flux includes DOC; [3]active flux represents only gut flux; [4]respiratory flux plus gut flux; [5]gut flux assessed with GF; [6]gut flux assessed from potential ingestion; [7]respiratory flux plus potential ingestion flux.

However, as in previous studies performed in this area, we only assessed the gut flux due to pigment ingestion. As the gut fluorescence method underestimates the amount of ingested food, the gut fluxes obtained should be taken as a baseline of total ingested carbon flux. For instance, in the Canary Island waters the non-pigmented organisms could constitute 35-80% of the diet of zooplankton (Hernández-León *et al.*, 2001c, 2002, 2004), which is in agreement with the results of diverse authors working in other oligotrophic areas (Dam *et al.*, 1995; Gaudy *et al.*, 2003). A predominantly carnivorous diet would explain the small pigmented gut flux observed at the end of the bloom. The high omnivory index agrees with the taxonomical composition of the mesopelagic vertical migrants described in the Canary current: copepods, decapods, euphausiids and fish (Baker, 1970; Pugh, 1974; Rudyakov, 1979; Roe, 1984). Also different authors noticed the ability of zooplankton to feed on marine snow composed of sinking algae, fecal pellets and aggregates (Alldredge *et al.*, 1998), which could provide a rich source of carbon to zooplankton. Moreover, in the study zone, lateral advection of particles stemming from areas closer to the African upwelling margin and from associated filaments can interact with sinking particles by aggregation (Hill and Nowell, 1990; Neuer *et al.*, 1997, 2002). This lateral advection could transport marine snow to the study area which would be available for the zooplanktonic community.

The respiratory flux of carbon into the deep ocean, together with the sinking flux of particulate carbon (gravitational flux), contributes to the draw-down of atmospheric CO_2 fixed by photosynthesis (Volk and Hoffert, 1985). Several authors established that a significant downward export flux is caused by diel vertical migration of zooplankton due to respiration and excretion at depth (Yebra *et al.*, 2005 and references therein). The respiratory fluxes that we estimated north off the Canary Islands ranged from 0.6 to1.32 mg $C \cdot m^{-2} \cdot d^{-1}$ (Table 3.2.2). The higher values observed were similar to the respiratory fluxes observed by Roman *et al.* (2002) in the equatorial Pacific divergence. However, our estimations are below the lower range of data obtained in the Atlantic oligotrophic, including the Canary Island waters (Table 3.2.2). Nevertheless, the previous studies in the Canaries were performed in the southern part of the archipelago where mesoscale activity has a huge

influence on water masses, biomass and carbon fluxes. For example, mesoscale structures such as anticyclonic eddies can increase the vertical transport of carbon due to diel vertical migrants (Yebra *et al.*, 2005). As our sampling area was located outside the influence of the high mesoscale turbulence promoted by the archipelago, the total carbon fluxes estimated from respiration and gut content at depth due to diel migrant activity were very low (0.6 and 1.44 mg $C \cdot m^{-2} \cdot d^{-1}$). As observed by other authors (Table 3.2.2) the export fluxes associated with migrating zooplankton play a quite variable role in the biological pump. The migratory fluxes could range from 0 to 70% of the particulate organic carbon (POC) flux in the oligotrophic Atlantic. The POC flux that we calculated from the equation given by Lohrenz *et al.* (1992) was 51.6 mg $C \cdot m^{-2} \cdot d^{-1}$. Thus, the total active flux (respiratory and gut fluxes) represented between 1.08-2.74% of the POC flux, which is below the values found leeward of the archipelago in summer (15-53%, Table 3.2.2). This difference was probably due to the lower biomass of diel migrants found in our study but also to the timing, at the end of the late winter bloom. Also, some studies have investigated the annual contribution of migrants to carbon fluxes focusing on the global output values of carbon flux (Steinberg *et al.* 2000, Al-Mutairi *et al.* 2001). In our case, we followed migrants metabolism through a late winter bloom event in order to determine its impact on the active carbon flux. We observed that from the metabolic point of view, the migrant community used both pigmented and non-pigmented food sources to increase their biomass. However, there was a diet shift, probably when the pigmented food diminished. This diet shift was also described for the epipelagic zooplankton in Hernández-León (2004). In these cases, the gut fluorescence method is useless to determine the true contribution of migrants to carbon flux. Since ETS activity provides us with a baseline of potential respiration at depth, we consider that the potential ingestion derived from this type of data could be used to approach the gut flux. The gut flux due to migrants potential ingestion (derived from respiration) ranged between 1.2 and 3.36 mg $C \cdot m^{-2} \cdot d^{-1}$. Adding the R flux and the G flux calculated from potential ingestion, the contribution of migrants to the carbon flux mediated by diel migrants increases from 2.74% to 9.22% of the POC flux at the end of the bloom (Table 3.2.1).

However, the active flux performed by the zooplanktonic migrants north off the Canary Islands was still low compared to other oligotrophic values (see Table 3.2.2). Only few estimations accounted for more than 25% of POC flux, and those were mostly related to estimations carried out in areas characterized for the presence of mesoscale structures. However, Hidaka *et al.* (2001) compared the active flux due to both mesozooplankton and micronekton showing that the later organisms transported 56-60% of the total active flux. Hernández-León *et al.* (2010) also assessed total active flux and showed this value to be similar to the gravitational flux. Therefore, micronekton should play a much more important role in active flux than zooplankton. Unfortunately, sampling micronekton is a gap in biological oceanography due to the need to work with large nets and acoustics, and the time required on board to deploy such nets.

This study of diel migrant mediated active carbon fluxes in an area not influenced by the high mesoscale activity generated by the Canary Islands allowed a comparison point for further studies in this area. The carbon fluxes determined were 1 to 5-fold lower than in the southern part of the archipelago showing once again the great importance of mesoscale structures on vertical export linked to diel vertical migrants. The mesoscale variability, seasonality and probably the diet of the migrant community could play an important role in the transport and fate of the organic matter annually produced in the subtropical ocean. Furthermore, the productive pulse due to the late winter bloom in combination with dust storm events is likely to enhance the gut flux and should be further investigated since estimates of the total active flux in the ocean, as well as our knowledge of this transport, is still quite poor.

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ACTIVE CARBON FLUX BY DIEL MIGRANT ZOOPLANKTON IN EUTROPHIC AND OLIGOTROPHIC WATERS OF THE CANARY CURRENT.

Putzeys S., Yebra L., Almeida C., Bécognée P., Marrero Diaz A., Arístegui J. and S. Hernández-León. (Unpublished).

Abstract:

The Canary Current is characterized by a strong disruption of its flow by the Canary archipelago, forming a downstream region of high mesoscale activity. This Canaries-African coastal transition zone connects the NW African upwelling system with the oligotrophic open ocean waters of the Eastern North Atlantic subtropical gyre. Further south, the Cape Vert Frontal zone is a highly productive area influenced by a quasi-permanent upwelling and a thermohaline front. To assess the role of zooplankton in the vertical export of carbon in those areas, we studied zooplankton biomass distribution and metabolism from the coast to the open ocean in an oligotrophic zone (26ºN) and in a meso- or eutrophic one (21ºN). Zooplankton biomass followed the same pattern in both transects, presenting two dense layers of organisms. The upper layer was located above 200 m and the second one below 400 m depth coincident with the deep scattering layer. However, the average migrant biomass (0-200 m) was 2.6-fold higher at 21ºN (71.4 ± 51.4 mmolC·m^{-2}) than at 26ºN (27.1 ± 12.4 mmolC·m^{-2}). This was reflected in the downward export of respiratory carbon (0-900 m depth), which was 10-fold higher in the southern than in the northern transect (0.54 ± 0.42 and 0.05 ± 0.05 mmolC·m^{-2}·d^{-1}, respectively). Moreover, the estimated pigmented gut flux was 31-fold higher in the south than in the north (1.89 ± 3.43 and 0.06 ± 0.11 mmolC·m^{-2}·d^{-1}). The contribution of zooplankton metabolism to the particulate organic carbon flux was 3.4% in the oligotrophic transect, contrasting with the 66.0% observed in the eutrophic transect.

Keywords: Diel vertical migration, ETS activity, Gut Fluorescence, active Carbon flux, Respiratory flux, Gut pigment flux, Potential ingestion.

Introduction

The Eastern boundary upwelling systems (EBUS) constitute the largest contribution to the world ocean productivity, sustaining up to 17% of the global fish catch and playing a biological and socio-economical key role. The Canary Current marine ecosystem is one of the four major EBUS. The high production of EBUS supports large downward export of organic carbon and also a significant fraction of the organic carbon is exported laterally into the open ocean (Arístegui *et al.*, 2004). In particular, the NW African upwelling transports upwelled water masses (Barton *et al.*, 1998), organic matter (Arístegui *et al.*, 1997; Hernández-Guerra *et al.*, 1993), mesozooplankton (Hernández-León *et al.*, 2002) and neritic larvae (Rodriguez *et al.*, 1999) to the open ocean by means of both Ekman transport and offshore extensions of the coastal jet. The so-called “upwelling filaments” create a longitudinal export gradient from the coastal highly eutrophic areas to the oligotrophic open ocean. Futhermore, the numerous filaments associated with the presence of capes and their variable productivity along the NW African coast add a latitudinal gradient of productivity to this area. In terms of organic matter export, the most significant filaments in the NW African coast are the Cape Jubi (28ºN), the Cape Bojador (26ºN) and the giant filament of Cape Blanc (21ºN) (Gabric *et al.*, 1993, Neuer *et al.*, 2002, Sangrà *et al.*, 2009).

Diel vertical migration is the most important movement of zooplanktonic biomass in the ocean and also plays a determining role in the downward flux of particulate and dissolved matter (e.g. Longhurst and Harrison, 1988). Individuals normally migrate to the surface to feed at dusk and return to deeper water layers at dawn (Lampert, 1989). Vertical migration produces a constant flux of matter and energy to deep layers of the ocean. The flux of particulate carbon due to the production of fecal pellets in the mesopelagic zone is the “gut flux” (Hu, 1978; Angel, 1985; Fowler and Knauer, 1986). The vertical flux of dissolved carbon caused by the night time feeding at the shallower layers and the daytime respiration of the diel migrant biota at depth is another source of active carbon transport to the mesopelagic zone (Longhurst and Harrison, 1988; Longhurst *et al.*, 1989, 1990). In addition, the respiratory carbon from diel migrant biota below the epipelagic zone during

daytime represents a significant but quite variable pathway of downward transport of carbon compared to the gravitational vertical flux (i.e. Longhurst and Harrison, 1988; Longhurst *et al.*, 1989, 1990; Dam *et al.*, 1995; Zhang and Dam, 1997). The carbon active flux also includes the fluxes due to mortality at depth (Dam *et al.*, 1995), dissolved organic excretion (Steinberg *et al.*, 2000) and predatory activity (Hernández-León, 1998; Hernández-León *et al.*, 2001a, 2002, 2004). Nevertheless, the respiratory flux jointly with the gut flux are two main components of the biological pump in the ocean compared to the passive or gravitational flux (Smetacek, 1980; Noji *et al.*, 1991; Gonzales and Smetacek, 1994; Zhang and Dam, 1997; Steinberg *et al.*, 2000; Wilson *et al.*, 2009).

Hydrographic conditions and their variability affect zooplankton community structure, physiology and also the carbon fluxes mediated by diel vertical migrants (Isla and Anadón, 2004; Yebra *et al.*, 2005, 2009; Putzeys *et al.*, 2011, Shatova *et al.*, 2012). These authors showed, among others, the impacts of mesoscale variability, seasonality and diet of the migrant community on the active carbon flux. None of the previously cited studies deal with the impact of a diet change on the biological pump efficiency, in eutrophic and oligotrophic areas at both meso and macroscale. In order to i) improve our knowledge of the active carbon fluxes in the NW African upwelling area, and ii) determine the influence of both latitudinal and longitudinal productivity gradients on the biogeochemical cycle of carbon, here we determined the vertical distribution of mesozooplankton (200–1000 mm) biomass, the gut and respiratory fluxes in order to estimate the contribution to carbon export flux by diel vertical migrants in the area.

Material and methods

Sampling took place during COCA 1 cruise on board RV Hespérides from 10th September to 3rd October 2002. Two transects were sampled, the North transect (**N**) from North of Cape Bojador to 1200 km offshore at latitude 26ºN, and the South transect (**S**) from Cape Blanc to 900 km offshore at 21ºN (Figure 3.3.1).

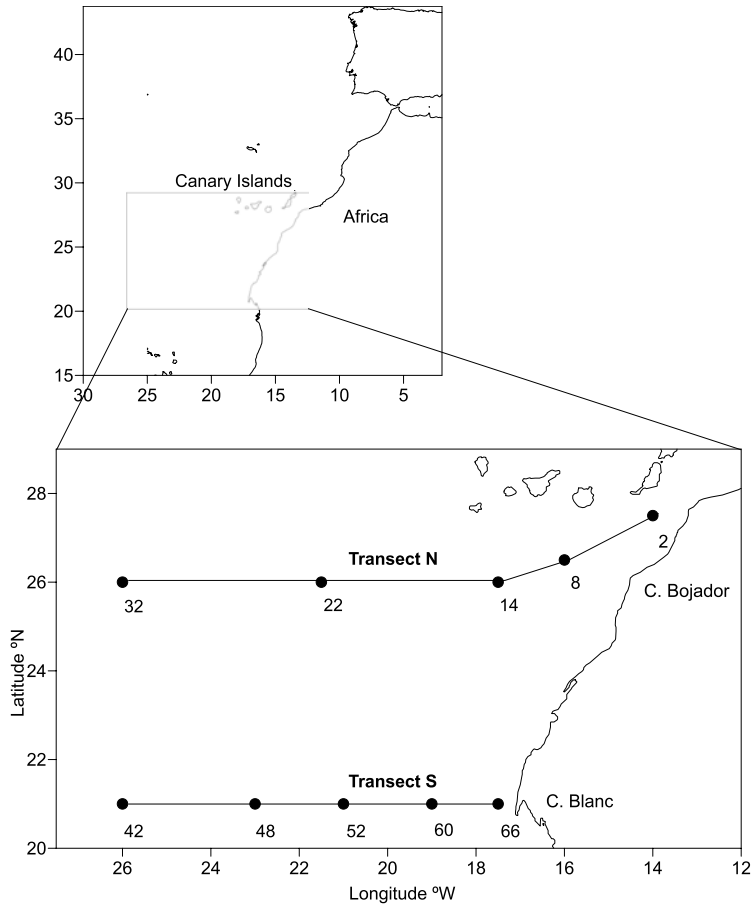

Figure 3.3.1. Study area. **N**: North transect at 26ºN. **S**: South transect at 21ºN.

Vertical profiles of temperature and conductivity from 0 to 1000 m depth and profiles of fluorescence from 0 to 400 m depth were obtained using a CTD (Idronaut MK-317 from stations 2 to 14 and Mar III-IOC from station 16 onwards) mounted on a General Oceanics rosette sampler. Due to a malfunction of the fluorescence sensor during the North transect, fluorescence data for stations 2, 8 and 14 were missing.

Sinking particles were collected from 200 m depth during the cruise. We used a free-drifting multi-trap array holding 8 cylinders, similar to the model described by Knauer *et al.* (1979). NaCl (~45 g L^{-1}; analytical reagent-grade) was added to increase the salinity inside the traps and no poisons were used to retard bacterial decomposition. Upon recovery (24 h after deployment), the swimmers, if present, were removed and the samples were filtered onto pre-combusted (450 ºC, 12 h) 25 mm Whatman GF/F filters. The filters were wrapped in pre-combusted aluminum foil and frozen at -20 ºC until

processing. In the lab, filters were analyzed for POC using a CHN method.

Mesozooplankton samples were collected with a Longhurst-Hardy Plankton Recorder equipped with a flowmeter and a 200 µm mesh net (Longhurst and Williams, 1976). A series of 20 oblique hauls were carried out at midday and at night from 0 to 900 m depth with a mean of 43 samples per haul. Each sample corresponded to a different sampled layer with a vertical extent of 20 to 40 m. For each of them we determined the mean depth of the layer sampled.

On board, samples were rinsed and quickly frozen in liquid nitrogen (-196 ºC) for later biomass and metabolic rate assessments. Due to the sampling method (cod-end of the LHPR net), feeding during sampling was considered insignificant and no correction factors have been applied. Very large organisms (mainly decapods and mesopelagic fish) appeared occasionally and were removed because those organisms are thought to avoid the inlet of the LHPR net (0.4 m diameter) and we did not correct for daytime avoidance of nets.

In the laboratory frozen samples were homogenized keeping the temperature below 4ºC in dark conditions to avoid as much as possible degradation of chlorophyll, enzymatic activity or proteins. Subsamples were taken to analyse (1) gut fluorescence (GF) as index of pigmented ingestion, (2) ETS activity as proxy for respiration and (3) protein content as biomass.

For GF analysis an aliquot (200 ml) of the homogenates was diluted in 10 ml of 90% acetone and stored at -20ºC during 24 hours in darkness. Fluorescence was assayed before and after acidification (4% HCl) in a Turner Design fluorometer (10-005R model), previously calibrated with pure chlorophyll *a* (Yentsch and Menzel, 1963). Pigments were calculated using the equations given by Parsons *et al.* (1984). All the GF data in this work include Chl *a* plus phaeopigments and no correction was made for pigment loss. GF values were corrected for the background fluorescence of the exoskeleton of the organisms captured from the deep scattering layer (DSL, Boden and Kampa, 1967; Hernández-León *et al.*, 2001a). We assumed that all the biomass had a background fluorescence of 0.1 µg of pigments per gram of wet weight (Willason and Cox, 1987) and a dry weight to wet weight

ratio of 0.2 (Mauchline, 1969).

ETS activity was assayed according to Packard (1971) modified by Gómez *et al.* (1996). ETS activity was recalculated to in situ temperature using the Arrhenius equation and an activation energy of 15 Kcal·mol^{-1} (Packard *et al.*, 1975).

Protein content was determined using the method of Lowry (1951) modified for microanalysis by Rutter (1967), and using bovine serum albumine (BSA) as standard. Protein values were converted to dry weight using the equation given by Hernández-Leon *et al.* (2001) for the Canary Island waters and to carbon units assuming that carbon is 40% of dry weight (Dam and Peterson, 1993).

All data were categorized on 50 m intervals to obtain day and night vertical profiles of protein content, GF and ETS activity at each station. The night profiles were then subtracted from the midday profiles to show only daily changes involving migrants as in Yebra *et al.* (2005). The negative values of the day-minus-night protein profiles correspond to migrant biomass that reached the epipelagic layer at night including organisms living both above and under 900 m by day. The migrant biomass (mg protein·m^{-2}) was calculated integrating biomass negative areas (0-200 m) as in Longhurst and Williams (1979) and Yebra *et al.* (2005):

$$\text{Migrant Biomass} = \int_{0\text{-}200} \text{Biomass}$$

Migrant biomass values were converted to carbon units as shown above.

To calculate the gut pigment flux a two step operation was performed. First, the day-minus-night positive GF data at depth were integrated and divided by the biomass at the same depth to obtain the specific gut content (mg pigment·mg protein^{-1}·m^{-2}) at depth:

$$\text{Specific gut content at depth} = \left[\int_{200\text{-}900} \text{GF}\right] \cdot \left[\int_{200\text{-}900} \text{Biomass}\right]^{-1}$$

Then we multiplied the specific gut content by the migrant biomass to obtain the gut pigment flux (mg pigment·m^{-2}·d^{-1}).

To determine the respiratory flux (µl O_2·m^{-2}·h^{-1}) positive values of the ETS day-minus-night profiles (µl O_2·m^{-3}·h^{-1}) at depth were integrated and divided by the integrated biomass at the same depth:

$$\text{Specific ETS at depth} = \left[\int_{200\text{-}900} \text{ETS}\right] \cdot \left[\int_{200\text{-}900} \text{Biomass}\right]^{-1}$$

The specific ETS activity at depth ($\mu lO_2 \cdot mg\ protein^{-1} \cdot h^{-1}$) obtained was then multiplied by the migrant biomass present in the epipelagic layer at night. Assuming a conservative respiration/ETS ratio of 0.5 (Hernández-León and Gómez 1996), 12h of maximum residence time at depth and a respiratory quotient of 0.97 (Omori and Ikeda 1984), we estimated the respiratory flux mediated by the diel vertical migrants in $mmolC \cdot m^{-2} \cdot d^{-1}$ (Table 3.3.1).

To assess the metabolism of the migrant community, we determined their potential ingestion (I, mg $C \cdot m^{-2} \cdot d^{-1}$) from the integrated day-minus-night positive respiration values (R) below 200m depth. We assumed assimilation to be 70% of ingestion and a gross growth efficiency of 30% and we applied the equation proposed by Ikeda and Motoda (1978):

$$I = 100 \cdot R/(0.7\text{-}0.3) = 2.5 \cdot R$$

The potential ingestion account for the total amount of carbon required by the metabolism of the migrant community. A potential gut flux was determined assuming an assimilation efficiency of 70% (Conover, 1966; Head and Harris, 1996) on the potential ingestion values. Also, in order to determine the food source used by migrants to sustain their metabolism, we calculated the omnivory index as [(ingestion-grazing)·ingestion^{-1}] (see Hernández-León *et al.*, 2002).

Results

Hydrographic conditions

The northern transect (**N**) was performed from station 2 to 32 and was located South of the Canary archipelago (Figure 3.3.1). The Canary Current passing through the Canary Islands generates eddies to the south of the archipelago and creates also an eddy region known as the Canary Eddy Corridor (CEC; Arístegui *et al.*, 1994; Sangrà *et al.*, 2007; Sangrà *et al.*, 2009). The CEC constitutes a direct zonal pathway that conveys horizontally water masses and biogeochemicals properties offshore from the Canary/NW African upwelling system towards the oligotrophic open ocean. The stations

close to Africa were affected by the coastal upwelling of Cape Bojador and by the coastal Canaries-African transition zone, CTZ (Barton *et al.*, 1998; Barton *et al.* 2004; Pelegrí *et al.*, 2005; Rodríguez *et al.*, 2006, Van Camp *et al.*, 1991). Station 2 on transect **N** (Figure 3.3.2a) was influenced by the coastal upwelling off Cape Bojador and the strong vertical temperature gradient in the first 50 m depth (St 2) suggested the presence of an upwelling filament.

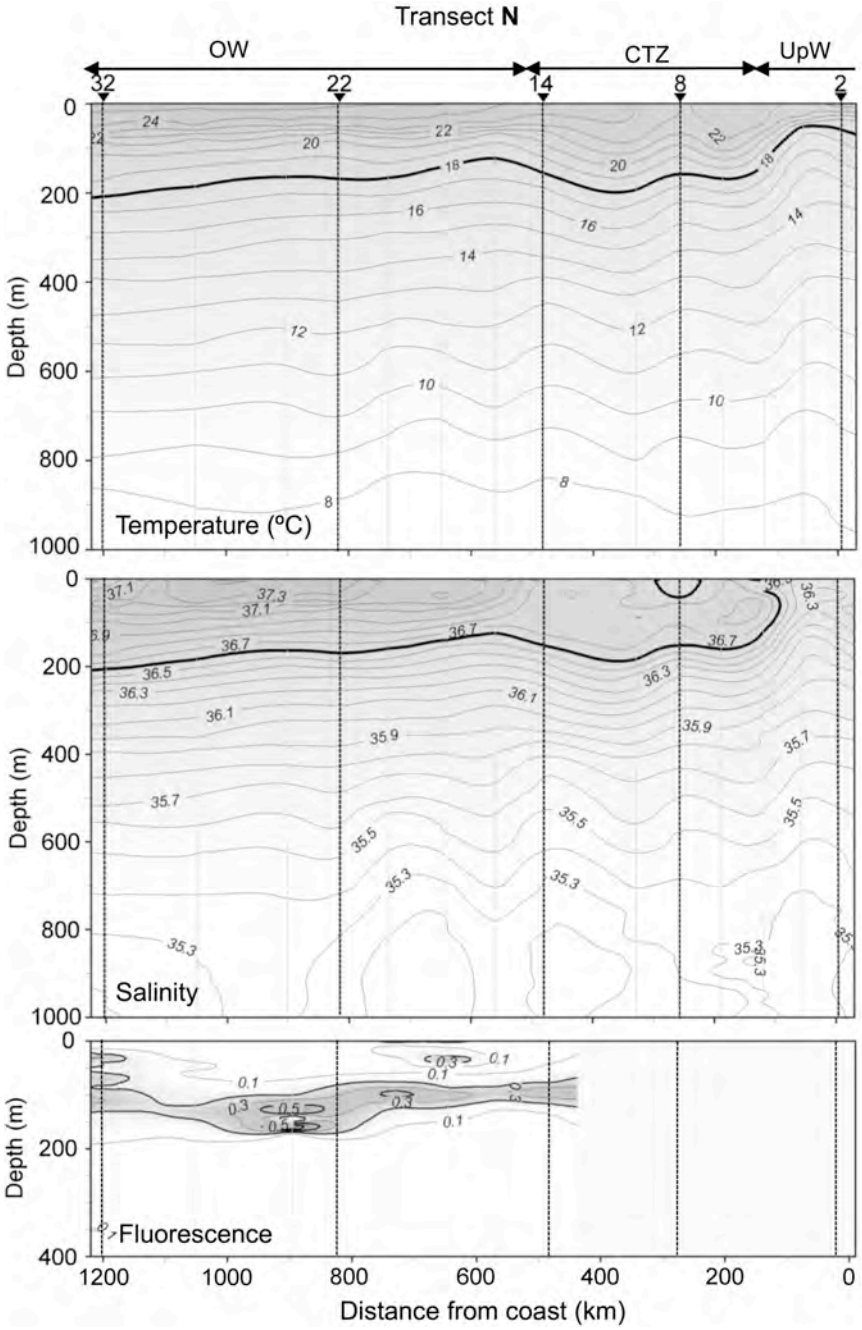

Figure 3.3.2a. Temperature (ºC), salinity and fluorescence profiles along transect **N** from open ocean (West) to coast (East). Dashed grey lines indicate hydrographical stations and the dashed black lines indicate hydrographical plus biological stations. OW: Oligotrophic waters, CTZ: Coastal Transition Zone, UpW: Upwelled waters.

Between stations 2 and 8 we observed the influence of the upwelling with the ascent of the 18ºC isotherm more than 100 m and the presence of 36.6 isohaline in the surface. Station 8 was located within the CTZ. Between stations 8 and 14 we observed the presence of an anticyclonic eddy. Due to a malfunction of the fluorescence sensor no chlorophyll distribution data are available for the stations influenced by the upwelling. West of the station 14 we found oligotrophic waters typical of the oceanic zones. Stations 22 and 32 were located in the typical of oceanic waters of the Canary basin.

The southern transect (**S,** Figure 3.3.2b) was done from station 66 until station 42 and was located close to the quasi- permanent upwelling area of Cape Blanc (Hagen, 2001; Pelegrí *et al.*, 2006), influencing the more coastal stations. Transect **S** coincided with the latitude where the Canary Current recirculates towards the West (Strammma, 1984). This allows the presence of South Atlantic Central Water (SACW) and originates the Cape Vert Frontal Zone (CVFZ). Its latitud coincided with the CVFZ, where a thermohaline front between the North Atlantic Central Water (NACW) and the South Atlantic Central Water (SACW) is the CVFZ, generating a high spatial and temporal variability (Pelegrí *et al.*, 2006; Pérez-Rodríguez *et al.*, 2001; Zenk, 1991).

On transect **S** we used the criterion of Zenk *et al.* (1991) to locate the CVFZ. According to this principle the front was located where the 36 isohaline reached 150 m depth. On the salinity section the 36 isohaline was represented with a doted line. We found that the frontal zone was close to the coast between stations 60 and 66. Therefore, station 60 presented SACW, which was suffering an upwelling process, ascending the 18ºC water until 50 m depth and inducing a vertical ascent of the isohalines. Superficial and sub-superficial maxima of fluorescence were observed extending from the coast to station 60. This station was located at the edge of a cyclonic eddy close to the thermohaline front. The influence of meanders was also observed from station 52 to 42. They promoted the ascent of the chlorophyll maximum up to the surface at station 48.

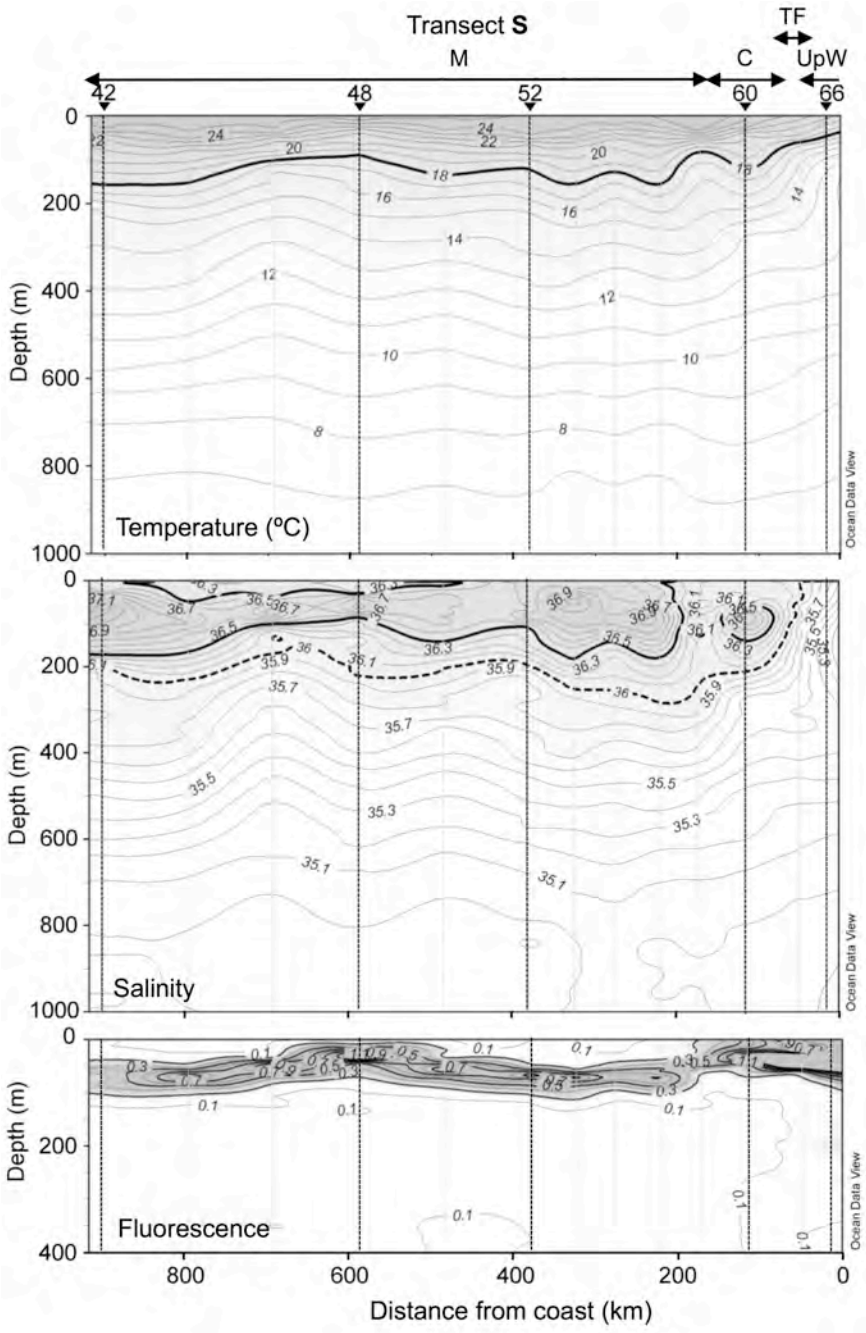

Figure 3.3.2b. Temperature (ºC), salinity and fluorescence profiles along transect **S** from open ocean (West) to coast (East). Dashed grey lines indicate hydrographical stations and the dashed black lines indicate hydrographical plus biological stations. OW: Oligotrophic waters, UpW: Upwelled waters, M: Meanders, TF: Thermohaline Front, C: Cyclonic eddy.

Biomass

A common layered biomass distribution (mg protein·m^{-3}) was observed on vertical profiles of both **N** and **S** transects (Figure 3.3.3a, c). By day, biomass was concentrated above 200 m depth. Biomass peaked also

between 350 and 750 m depth forming the deep scattering layer (DSL). The distribution range of the DSL varied slightly between profiles. However, the DSL appeared to be located deeper in **N** than in **S** transect (450-750 m and 350-550 m, respectively). The coastal stations (2 and 66) together with station 48 (in transect **S**) showed the highest biomasses compared to the other sampled stations. During nighttime, biomass in the upper 250 m increased at all sites.

Biomass in the DSL also increased at the coastal stations 2, 8 and 66. This variability was reflected in the day-minus-night biomass profiles (Figure 3.3.3 b, d). The epipelagic day biomass (0-200 m) in transect **N** ranged between 16.30 to 38.32 mmolC·m^{-2} (25.59 ± 8.01 mmolC·m^{-2}), while in transect **S**, was almost 2-fold higher (50.12 ± 18.31 mmolC·m^{-2}) ranging from 31.31 to 70.6 mmolC·m^{-2}. Also, migrant biomass was 2.6-fold higher in **S** (71.44 ± 51.44 mmolC·m^{-2}) than in **N** transect (27.12 ± 12.39 mmolC·m^{-2}). In addition, migrant biomass tended to decrease from the coastal upwelling areas toward the open ocean (Table 3.3.1). In transect **N**, the migrant biomass at St 2 was 40.52 mmolC·m^{-2}, decreasing to 29.85 ± 9.28 mmolC·m^{-2} in the CTZ (stations 8, 14) and to 17.69 ± 12.47 mmolC·m^{-2} in the oligotrophic open ocean waters (Stations 22 and 32). Within **S** transect, Stations 66 and 48 showed the highest migrant biomass (121.59 mmolC·m^{-2} and 133.44 mmolC·m^{-2} respectively). The other stations of transect **S** averaged a migrant biomass of 34.06 ± 4.06 mmolC·m^{-2}.

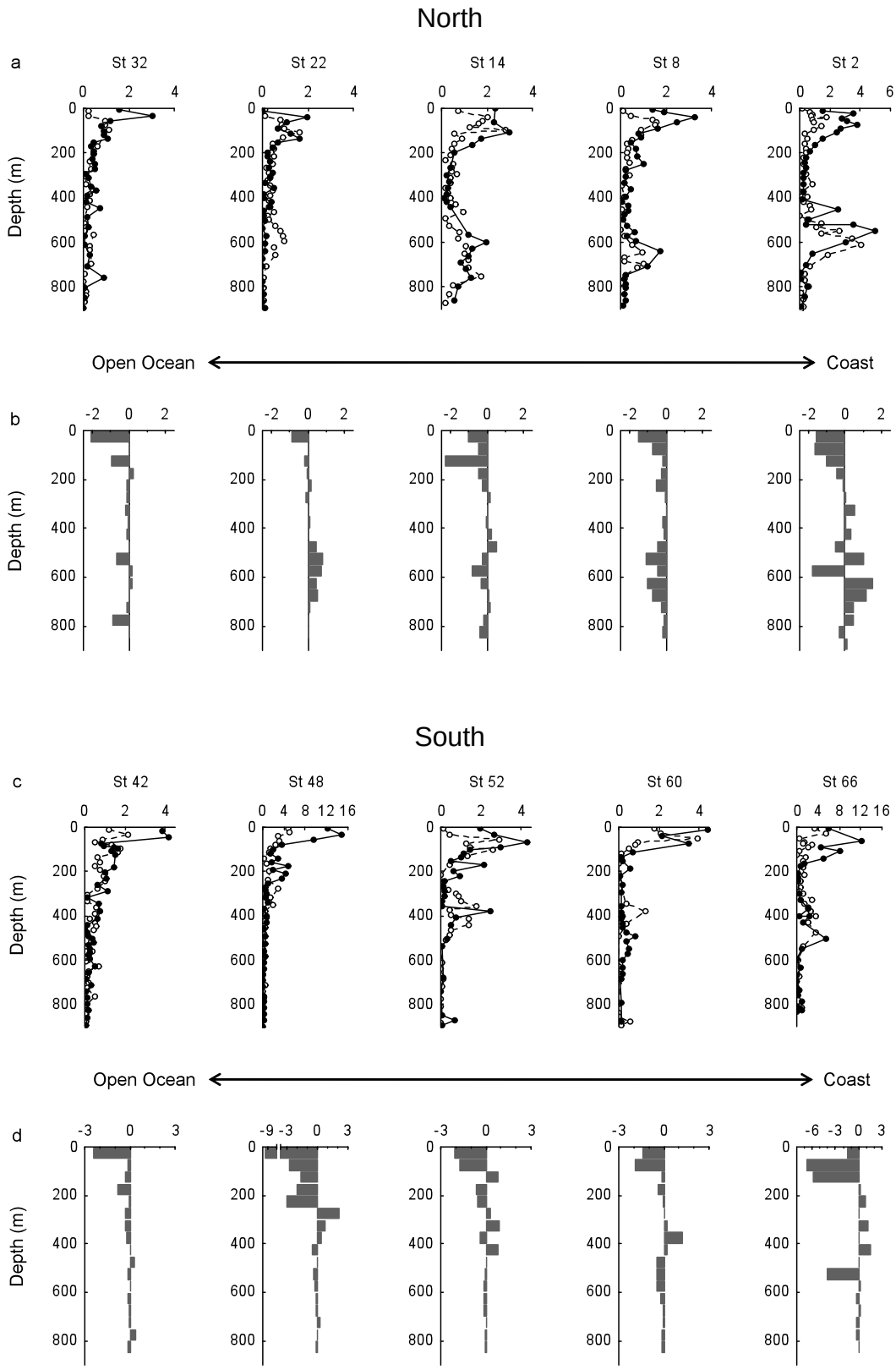

Figure 3.3.3. Biomass vertical profiles (mg protein·m^{-3}) in transects **N** and **S** (a, c; open circles: day, closed circles: night). Day-minus-night variations profiles in transects **N** and **S** (b, d).

Table 3.3.1. Biomasses and fluxes assessed from coast to open ocean. Biomass in mmolC·m^{-2}, [1] Pigmented gut flux plus respiratory flux (mmolC·m^{-2}·d^{-1}), [2] Potential ingestion flux (mmolC·m^{-2}·d^{-1}). * Negative value due to the high value of the gut pigment content considered as zero when calculating the mean±SD.

Stations	Migrant biomass	Epipelagic day biomass	Omnivory index	Pigmented Gut flux	Respiratory flux	Potential ingestion flux	Total carbon flux [1]	Total carbon flux [2]
2	40.52	23.87	0.74	0.065	0.10	0.25	0.16	0.25
8	23.28	26.12	0.86	0.002	0.005	0.014	0.007	0.014
14	36.41	38.32	0.44	0.003	0.002	0.005	0.005	0.005
22	8.87	23.33	0.99	0.001	0.05	0.13	0.05	0.13
32	26.50	16.30	-0.08 *	0.253	0.09	0.24	0.35	0.24
66	121.59	69.00	-1.58 *	8.01	1.24	3.10	9.25	3.10
60	32.89	31.31	0.84	0.20	0.47	1.18	0.67	1.18
52	38.57	39.90	0.65	0.42	0.48	1.19	0.90	1.19
48	133.44	70.60	0.34	0.72	0.44	1.09	1.16	1.09
42	30.71	39.77	0.51	0.11	0.09	0.23	0.20	0.23
North mean (SD)	27.12 (12.39)	25.59 (8.01)	0.76 (0.24)	0.06 (0.11)	0.05 (0.05)	0.13 (0.12)	0.12 (0.14)	0.13 (0.12)
South mean (SD)	71.44 (51.44)	50.12 (18.31)	0.59 (0.21)	1.89 (3.43)	0.54 (0.42)	1.36 (1.06)	2.43 (3.83)	1.36 (1.06)

Gut pigment content

Community gut pigment content (µg pigments·m^{-3}) was very different in transects **N** and **S** (Figure 3.3.4 a, c). The coastal stations (2 and 66) showed the highest GF values within each transect, although the GF at station 66 was 5.2 fold-higher than at station 2. On average, the oceanic stations in transect **S** presented 4-fold more gut pigment content than in transect **N**.

In transect **N** (Figure 3.3.4a), the maximum values were registered in the epipelagic zone for stations 2 and 8 while the others stations presented higher values below 600 m depth. Contrarily, in transect **S** (Figure 3.3.4c), GF at the coastal station 66 presented higher values in the mesopelagic zone (200 - 600 m) while the oceanic stations presented maxima above 250 m depth.

The day-minus-night profiles (Figure 3.3.4 b, d) showed marked differences between day and night periods and between **N** and **S** transects. The St 42 (west limit of transect **S**) showed almost no trend variations from day to night (Figure 3.3.4 d).

The estimated pigmented gut flux was 29-fold higher in the South than in the North (1.89 ± 3.43 and 0.06 ± 0.11 mmolC·m^{-2}·d^{-1} respectively, Table 3.3.1).

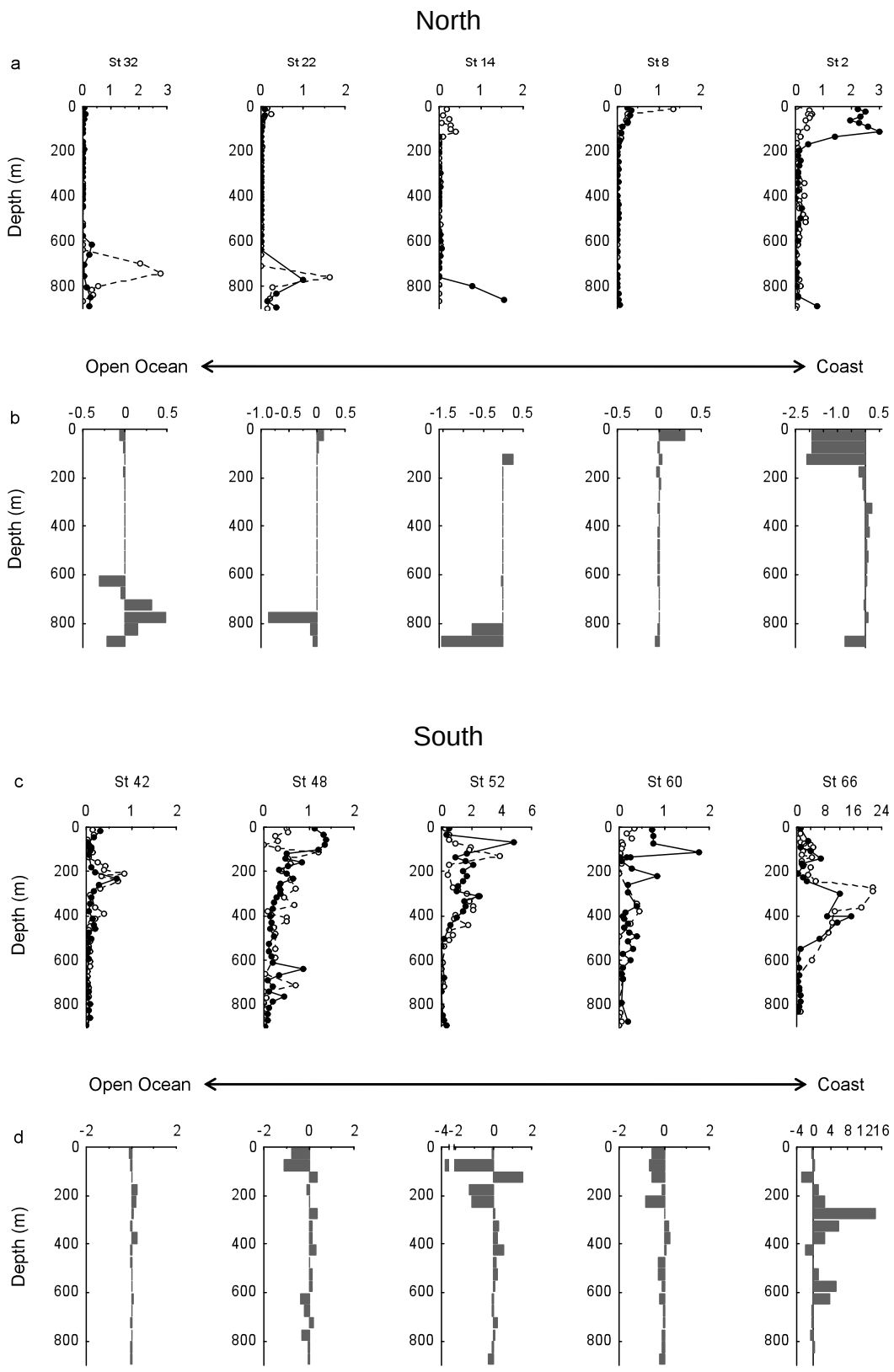

Figure 3.3.4. Gut fluorescence vertical profiles (µg pigments·m^{-3}) in transects **N** and **S** (a, c; open circles: day, closed circles: night). Day-minus-night variations profiles in transects **N** and **S** (b, d).

Electron transfer system activity (ETS)

The highiest values of ETS activity were found above 200 m depth at all stations (Figure 3.3.5 a, c). Some night samples from station 42 were lost during the ETS assay. However, the missing data did not affect the respiratory flux results because only 2 points were missing for the integration.

In transect **N** (Figure 3.3.5 a), similar values were registered by night in the epipelagic layer at all stations except in stations 8 and 14, which showed the lowest ETS values. In the mesopelagic layer, the ETS activity was rather constant except in the DSL at stations 2 and 14 (Figure 3.3.5 b). In transect **S** the ETS activity was variable from station to station and values ranged from 100 to 790 $\mu lO_2 \cdot m^{-3} \cdot h^{-1}$.

As observed for biomass and GF, ETS activity was high at the coastal stations (2, 66). Also, the ETS activity at station 66 was 5-fold higher than at station 2 (678.70 and 135.31 $\mu lO_2 \cdot m^{-3} \cdot h^{-1}$, respectively). The ETS activity at the DSL was low compared to the high biomass values in this zone.

Respiratory fluxes obtained at transect **N** ranged from 0.002 to 0.1 $mmolC \cdot m^{-2} \cdot d^{-1}$, whereas at transect **S**, varied from 0.09 to 1.24 $mmolC \cdot m^{-2} \cdot d^{-1}$. On average the respiratory flux in transect **S** was 10-times higher than at transect **N** (Table 3.3.1).

Using those respiratory fluxes we calculated the carbon potential ingestion requirements of the migrant community. In transect **N**, the potential ingestion was 10-times lower within the CTZ (stations 8, 14; 0.01 ± 0.01 $mmolC \cdot m^{-2} \cdot d^{-1}$) than in the other stations (0.19 ± 0.15 $mmolC \cdot m^{-2} \cdot d^{-1}$). In **S**, the potential ingestion diminished from 3.10 to 0.23 $mmolC \cdot m^{-2} \cdot d^{-1}$ along the coast-ocean gradient. The omnivory index of the migrant community was 1.3-fold higher in **N** (0.76 ± 0.24) than in **S** transect (0.59 ± 0.21). The omnivory index calculated at St 32 and 66 was negative (-0.08 and -1.58 respectively) due to the high pigmented gut flux compared to the potential ingestion required, and it was considered as a zero when calculating the average omnivory index value for the transects (Table 3.3.1).

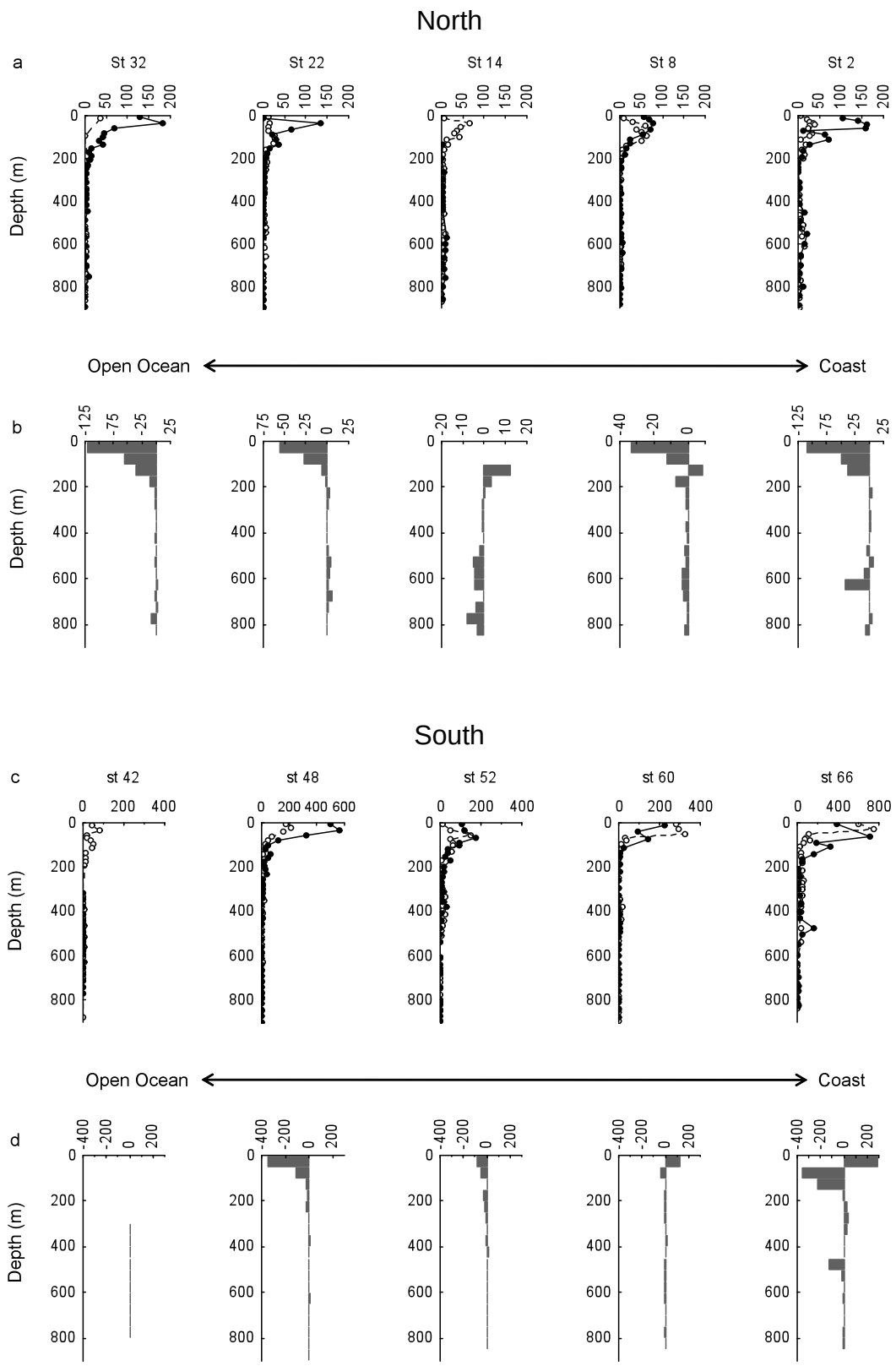

Figure 3.3.5. ETS activity vertical profiles ($\mu lO_2 \cdot m^{-3} \cdot h^{-1}$) in transects **N** and **S** (a, c; open circles: day, closed circles: night). Day-minus-night variations profiles in transects **N** and **S** (b, d).

Discussion

The Northern transect (**N**, 26ºN, Figure 3.3.1) extended offshore from the boundary of the African coastal upwelling toward the oligotrophic Atlantic subtropical gyre and the coastal station was affected by the presence of a filament associated with Cape Bojador (26ºN). Filaments were a recurrent oceanographic feature in the area (Barton *et al.*, 2004). Further west, the **N** transect crossed the CTZ (stations 8 and 14), an area of strong and well-described mesoscalar oceanographic activity (Mittelstaeds, 1991; Hernández-Guerra *et al.*, 1993; Arístegui *et al.*, 1994, 1997; Barton *et al.*, 1998). The eddy field generated in the south of the Canary Islands Archipelago was connected to the upwelling area with filaments.

In this area the signal of a recurrent anticyclonic eddy was observed. The CTZ is the starting point of a permanent structure called the "Canary eddy corridor" (CEC), a zonal long-lived (>3 months) mesoscale eddy corridor (Sangrá *et al.*, 2009). This corridor is a direct pathway that conveys water masses and may be seen as a recurrent offshore pump of organic matter and carbon to the oligotrophic ocean. Futhermore, the eddy field generated by Canary Archipelago is well known to affect the distribution, abundance and metabolism of the zooplanktonic community (Hernández-León *et al.*, 2002; Yebra *et al.*, 2005; Landeira *et al.*, 2009, 2010; Bécognée *et al.*, 2009). Indeed, the CEC is not only a zonal conduit carrying properties from the upwelling region but also is considered a highly productive area since the PP of the CEC can be as high as the upwelling region (10.9×10^{10} *vs* 11.6×10^{10} $gC \cdot d^{-1}$, see Sangrá *et al.*, 2009). The **N** section ended in the oligotrophic waters of the North Atlantic subtropical gyre but still presented a rather high chlorophyll signal as far as 1200 km from the coastal upwelling. The **S** transect (21ºN, Figure 3.3.1) extended from the Cape Blanc coastal upwelling waters to the open ocean across the Cabo Verde Frontal Zone (Stramma, 1984; Zenk, 1991). The hydrography in **S** is more complex than in **N** transect due to the influence of upwelled waters, a cyclonic eddy, a thermohaline front and various meanders. The hydrodynamic fronts and meanders are known to affect zooplanktonic communities and specially the migrant zooplankton communities and the corresponding active carbon export flux (Isla and

Anadón, 2004). Then stations affected by theses structures could present an increase of migrant biomass and a possibly enhanced active carbon flux compared to the stations not affected.

The typical two layered distribution pattern observed in **N** transect was already described in Canary Islands area by Hernández-León *et al.* (2001a). This biomass layered pattern was also observed in **S** transect. The observed increases in epipelagic biomass by night due to vertical migration are well documented in the Canary area and they are not merely due to a possible increase of effectiveness of net hauls by night (Hernández-León *et al.*, 2001a; Yebra *et al.*, 2005). During nighttime organisms of the DSL migrated to upper layers and the majority of the biomass concentrated in the uppermost 300 m. Moreover, biomass in the DSL by day was of the same range or higher than in the upper 200 m. The biomass peak observed below 700 m depth during the night is also consistent with previous measurements (Plueddemann and Pinkel, 1989; Hernández-León *et al.*, 2001a).

Despite the similar vertical distribution, the epipelagic day biomass assessed in **S** transect was two-fold higher than in **N** sampling area. This was due to the higher fluorescence signal in the south compared to the north transect (0.9 *vs* 0.5). In both areas the phytoplanktonic and zooplanktonic communities were transported toward the oligotrophic ocean by filaments and meanders. However in **S** the meanders promoted the ascent of the chlorophyll maximum, reaching the superficial waters (e.g. station 48), and promoting an increase of the epipelagic biomass. The **N** transect was also under the influence of oligotrophic waters coming from the Canary Current. The epipelagic biomass abundance could be a limiting factor for the migrant community as a bottom-up control in terms of low/high prey abundance in both **N** and **S** transects.

Migrant biomass in **N** showed in a similar range than previous studies in the Canary Island area (see Table 3.3.2 and references therein). In the CTZ, the anticyclonic eddy presented low values of both migrant and epipelagic biomass at the eddy edge (St 8) and high values at the eddy core (St 14) compared to oligotrophic waters, as previously observed by Yebra *et al.* (2005) in an anticyclonic eddy shed by Gran Canaria Island.

Table 3.3.2. Zooplankton active flux estimated in different oceanic regions.

Location	Time of year	Migrant biomass (mg C·m^{-2})	Respiratory flux (mg C·m^{-2}·d^{-1})	Gut flux (mg C·m^{-2}·d^{-1})	% of POC flux	References
Oligotrophic area						
HOT		30.2 - 33.8	1.3-1.7	-	4[a]	Roman *et al.* (2002)
Equator divergence		2.8 - 21.8	0.9-1.2	-	<1-2[a]	Roman *et al.* (2002)
BATS	March/April	192 (84–540)	14.5 (6.2-40.8)	-	34 (18-70)[a]	Dam *et al.* (1995)
BATS	year-round	50 (0-123)	2.0 (0-9.9)	-	8 (0-39)[b]	Steinberg *et al.* (2000)
BATS	year-round	83 (0.7-468)	-	0.8 (0.007-4.5)	4 (0.03-21)[c]	Schnetzer and Steinberg (2002)
Western Equator	October	46.9	3	-	6	Le Borgne and Rodier (1997)
North (Oceanic)	Oct-Nov	30 ± 10	2.2 ± 0.3	-	-	Isla and Anadón (2004)
Eastern Equator	March - April	96 ± 25.2	4.2 ± 1.2	-	18[a]	Zhang and Dam (1997)
Eastern Equator	October	154.8 ± 32.4	7.3 ± 1.4	-	25[a]	Zhang and Dam (1997)
ALOHA	Year-round	162 (108-216)	3.6 (2.6 - 19.1)	-	15 (12-18)[a]	Al-Mutairi and Landry (2001)
ALOHA	June - July	157.9	3.7	-	18[a]	Steinberg *et al.* (2008)
Eu- Meso-trophic area						
Central Equator (HNLC)	October	52.9	6	-	4[a]	Le Borgne and Rodier (1997)
North (coastal)	Oct-Nov	360 ± 70	30.3 ± 1.9	-	-	Isla and Anadón (2004)
North (poleward current)	Oct-Nov	270 ± 210	10.4 ± 6.3	-	-	Isla and Anadón (2004)
Western Equator	October	46.9	3	-	6[a]	Le Borgne and Rodier (1997)
Western Equator	February	367 (144-447)	22.7 (7.3-19.1)	4.8 (2.6-4.4)	24 (13-35)[a]	Hidaka *et al.* (2001)
Canary Current						
Canary Islands	June	580-1280	1.8 - 8.3	0.1 - 0-4[e]	15-53[d]	Yebra *et al.* (2005)
Canary Islands	August	247 - 125	4.2 - 1.9	0.3 - 2.4[e]	20-45[d]	Hernández-León *et al.* (2001a)
Canary Islands	March	204 (108-341)	0.8 (0.5-1.4)	0.1 (0.05-0.18)[e]	1.8 (1.1-2.7)[d]	Chapter 3.2
26ºN	Sept-Oct	325 (106-486)	0.6 (0.02-1.2)	0.7 (0.01-3.1)[e]	3.3 (0.1-9.0)[f]	Present work
21ºN	Sept-Oct	857 (368-1601)	6.5 (1.1-14.9)	22.7 (1.3-96.1)[e]	66.0 (32.4-149.5)[f]	Present work

[a] %POC flux represents only respiratory flux. [b]Active flux includes DOC. [c]Active flux represents only gut flux. [d]Respiratory flux plus gut flux. [e]Gut flux assessed with GF. [f]Potential ingestion flux assessed from respiration.

These authors showed that anticyclonic eddies enhanced vertical migration due to the accumulation of zooplankton inside the eddy. In the **S** transect, the average migrant biomass (0-200 m) was 2.6-fold higher at 21ºN (71.4 ± 51.4 mmolC·m^{-2}) than at 26ºN (27.1 ± 12.4 mmolC·m^{-2}). This is pointing out the strong impact of mesoscale structures in **S** than in **N** on migrant zooplankton communities as observed by other authors (Isla and Anadón; 2004; Yebra *et al.*, 2005).

Respiratory fluxes in the **N** transect were in the lower range of values obtained for oligotrophic waters (see table 3.3.2). In **S** transect, the respiratory fluxes obtained were in the lower range of values obtained for meso-eutrofic waters (see Table 3.3.2). The downward export of respiratory carbon (0-900 m depth) was 10-fold higher in **S** than in **N** transect (0.54 ± 0.42 and 0.05 ± 0.05 mmolC·m^{-2}·d^{-1}, respectively).

The gut flux estimated in this study is directly based on pigment gut content. The estimated pigmented gut flux was 29-fold higher in the southern transect than in the north (1.89 ± 3.43 and 0.06 ± 0.11 mmolC·m^{-2}·d^{-1}). Using data of exported flux (POC) measured during the cruise, we estimated the contribution of active flux to the total exported POC flux (Table 3.3.3). Estimates of net downward transport based on the gut fluorescence method are underestimates in oligotrophic areas as the gut pigment content does not represent the total amount of carbon transported in the gut to the mesopelagic zone. By opposite, the estimates of net downward transport based on the gut fluorescence showed to be overestimates in highly productive areas compared to the potential ingestion flux. The total gut flux of omnivores and carnivores was not measured by the fluorescence method but it is quite important, especially in the large sized migrants. For instance, in the Canary waters the non-pigmented organisms could constitute 35-80% of the diet of zooplankton (Hernández-León *et al.*, 2001c, 2002, 2004; Putzeys *et al.*, 2011), which is in agreement with other oligotrophic areas (Dam *et al.*, 1995; Gaudy *et al.*, 2003). Also, laboratory experiments have shown that migrants such as euphausiids vary their diet and fed on diatoms or mesozooplankton depending on the abundance of the food type (Stuart and Huggett, 1992). The omnivory index suggests that in **N** transect migrants were mainly

omnivorous/carnivorous, whereas in transect **S** migrants were mostly herbivorous grazers. The correction factor applied for the background fluorescence of the exoskeleton of the organisms captured in the eutrophic transect could be higher than the factor used in this study and could justify the higher differences observed in the percentage of active flux to the POC flux. The variability of total gut pigment flux observed along both transects could be due to a diet adaptation to the different food sources which depends on hydrodynamics, epipelagic abundance and composition. From our omnivory calculations a more reliable estimation of the carbon export flux could be determined using the potential ingestion flux. In this way we assessed the gut flux independently from the food source used by the migrants and the background pigment fluorescence of the exoskeleton avoiding the drawbacks associated with the fluorimetric method.

Table 3.3.3. Summary of the POC flux measured at 200m depth ($mmolC \cdot m^{-2} \cdot d^{-1}$) and contribution percentage of the active carbon flux to the POC flux. ([1]) Sum of respiratory flux and pigmented gut flux *versus* POC; ([2]) Potential ingestion flux *versus* POC.

Stations	POC flux (200m)	Contribution to POC [1] (%)	Contribution to POC [2] (%)
2	16.6	0.99	1.50
8	4.9	0.15	0.28
14	3.7	0.14	0.14
22	2.4	2.21	5.42
32	2.6	13.35	9.05
66	5.6	165.26	55.44
60	2.6	25.66	45.42
52	0.8	111.84	149.32
48	2.3	50.26	47.50
42	0.7	28.75	32.39

The diel vertical migrants were responsible for a net and variable transport of carbon to the mesopelagic zone. However, the total contribution of zooplankton metabolism to the particulate organic carbon flux were very variable and ranged from 3.28 ± 3.87% in the oligotrophic transect to 66.01 ±

47.30% in **S** transect. Additionally, the active carbon flux contributions ranged between 0.14 to 149.32% of the POC flux. Despite of an increase in migrant biomass inside the anticyclonic eddy (in **N**) the active carbon flux was slightly higher than outside the eddy as observed by Yebra *et al.* (2005). In **S** transect the extreme values of contribution to export carbon flux were found under the upwelling, thermohaline front and the meander influence. Isla and Anadón (2004) also observed differences in carbon fluxes due to DVMs between coastal and oceanic areas, concluding that fronts and meanders explained the differences. These hydrological structures could locally enhance primary production and concentrate epipelagic biomass allowing a larger amount of prey availability for the migrant community. Comparing the export fluxes of the two transects, values assessed were 20 fold-lower in the north than in the south. This could be explained by the lower hydrographic complexity, lower epipelagic biomass and phytoplanktonic abundance in the north transect compared to the southern area.

In summary, the active carbon fluxes observed show a high contrast between the oligotrophic and meso-eutrophic transects. The whole sampling area presents a complex hydrodynamic diversity, which have a deep impact in terms of abundance, metabolic activity and composition on the epipelagic ecosystem. The food abundance influenced the migrant community and the active carbon exported fluxes. The total contribution of zooplankton metabolism to the particulate organic carbon flux was 3.28 % in the oligotrophic transect, contrasting with the 66.01 % observed in the eutrophic transect. The diel vertical migrants could actively export as much as the passive gravity flux. The intensity of the upwelling as well as the associated mesoscalar stuctures such as the oceanic fronts could increase the productivity of a specific area and consequently increase by 20 the amount of carbon drained to deep waters by migrant zooplankton.

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SEASONALITY EFFECT ON ACTIVE CARBON FLUX BY DIEL MIGRANT ZOOPLANKTON IN EUTROPHIC AND OLIGOTROPHIC WATERS OF THE CANARY CURRENT.

Putzeys, S., Yebra, L., Almeida, C., Bécognée, P., Marrero Diaz, A., Arístegui, J. and S. Hernández-León. (Unpublished).

Abstract :

The Canary current is a region of high mesoscale activity due to the strong disruption of its flow by the Canary Archipelago. This high mesoscale influenced area, called coastal transition zone (CTZ), connects the highly productive area of the NW African upwelling system with the oligotrophic open ocean waters of the eastern subtropical North Atlantic gyre. Zooplanktonic biomass, indices of grazing and metabolism were studied from 0 to 850 m depth along two sections at 26 (oligotrophic) and 21ºN (meso-eutrophic) to assess the vertical export of carbon in this area during spring. Biomass presented a typical layered pattern in both transects. However the average migrant biomass (0-200 m) was 5.9-fold higher at 21ºN (153.39 ± 152.60 $mmolC \cdot m^{-2}$) than at 26ºN (26.19 ± 11.01 $mmolC \cdot m^{-2}$). The downward export of respiratory carbon (0-850 m depth) was 10-fold higher in the southern than in the northern transect (1.87 ± 1.81 and 0.19 ± 0.08 $mmolC \cdot m^{-2} \cdot d^{-1}$, respectively). Also, the estimated pigmented gut flux was 50-fold higher in the south than in the north (0.79 ± 0.94 and 0.02 ± 0.01 $mmolC \cdot m^{-2} \cdot d^{-1}$). The higher total contribution of zooplankton metabolism to the particulate organic carbon flux was 64.3% in the oligotrophic transect, contrasting with the average 119% observed in the meso-eutrophic transect. The results were compared to a cruise performed in the same area during fall period in order to determine seasonality effect. The fluxes as well as the migrant biomasses were higher in spring compared to fall period. The contribution of migrant zooplankton to POC flux was 1.8 to 14-fold higher in spring than during fall.

Keywords: Diel vertical migration, ETS activity, Gut Fluorescence, Carbon flux, Respiratory flux, Gut flux, seasonality.

Introduction

The Canary Current (CC) marine ecosystem is one of the four major eastern boundary upwelling systems (EBUS). The NW African upwelling system can transport upwelled water masses to the open ocean because of both Ekman transport and offshore extensions of the coastal jet (Barton *et al.*, 1998). The latter, also called filaments, can transport mesozooplankton (Hernández-León *et al.*, 2002), neritic larvae (Rodriguez *et al.*, 1999; Bécognée *et al.*, 2009) and organic matter. The filaments distributed along the coast are associated with the presence of capes. The most significant filaments in terms of organic matter export are Cape Jubi (28ºN), Cape Bojador (26ºN) and the giant filament of Cape Blanc (21ºN) (Neuer *et al.*, 2002, Sangrà *et al.*, 2009). The latitudinal distribution of those capes together with the in-shore/offshore productivity differences creates both latitude and longitude productivity gradients along the entire CC area.

The export of carbon from the surface to the deep ocean as a part of the biological pump has a direct implication on the removal of carbon-dioxide (CO_2) from the atmosphere. As the diel vertical migration is the most important movement of zooplanktonic biomass in the ocean, it plays a determining role in the downward flux of particulate and dissolved matter (e.g. Longhurst and Harrison, 1988). However, the mesoscale hydrographic variability can affect the zooplankton communities and the carbon export fluxes mediated by diel vertical migrants (Isla and Anadón, 2004; Yebra *et al.*, 2005; Putzeys *et al.*, 2011; Shatova *et al.*, 2012). Normally, individuals migrate to the surface to feed at night and return to deeper layers at dawn (Lampert, 1989). This daily movement produces a constant flux of matter and energy to deep layers of the ocean. The flux of particulate carbon due to the production of fecal pellets in the mesopelagic zone is called “gut flux” (Hu, 1978; Angel, 1985; Fowler and Knauer, 1986). Another transport to the mesopelagic zone is the vertical flux of dissolved carbon caused by the nighttime feeding at the shallower layers and the daytime respiration of the diel migrant biota at depth (Longhurst and Harrison, 1988; Longhurst *et al.*, 1989, 1990). Different estimations (i.e. Longhurst and Harrison, 1988; Longhurst *et al.*, 1989, 1990; Dam *et al.*, 1995; Zhang and Dam, 1997)

suggest that respiratory carbon from diel migrant biota below the euphotic zone during daytime represents a significant pathway of downward transport of carbon, relative to the gravitational vertical flux. The respiratory flux plus the gut flux are two main components of the active flux, which jointly with mortality at depth (Zhang and Dam, 1997; Steinberg *et al.*, 2000) constitute a significant percentage of the biological pump in the ocean compared to the passive or gravitational flux.

Here, we determined the vertical distribution of mesozooplankton (>200 µm) biomass, the gut and respiratory fluxes in order to i) estimate the contribution to the carbon export flux by diel vertical migrants in the CC area during a spring cruise, and ii) we determine the impact of seasonality on the biogeochemical cycle of carbon by comparing our results with a previous study covering the same area during the previous fall.

Material and methods

Sampling took place during COCA 2 cruise on board RV Hespérides from the 21th of May to the 7th of June 2003. Two transects were sampled from the African coast toward the open ocean. A northern transect (**TN**) from North of Cape Bojador to 1200 km offshore at latitude 26ºN and a southern transect (**TS**) from Cape Blanc to 900 km offshore at 21ºN (Figure 3.4.1). Vertical profiles of temperature and conductivity from 0 to 1000 m depth and profiles of fluorescence from 0 to 400 m depth were obtained using a CTD (MAR III-IOC) mounted on a General Oceanics rosette sampler.

Sinking particles were collected from 200 m depth during the cruise. We used a free-drifting multi-trap array holding 8 cylinders, similar to the model described by Knauer *et al.* (1979). NaCl (~45 g L^{-1}; analytical reagent-grade) was added to increase the salinity inside the traps and no poisons were used to retard bacterial decomposition. Upon recovery (24 h after deployment), the swimmers, if present, were removed and the samples were filtered onto pre-combusted (450 ºC, 12 h) 25 mm Whatman GF/F filters. The filters were wrapped in pre-combusted aluminum foil and frozen at -20 ºC until processing the POC in the laboratory using a CHN method.

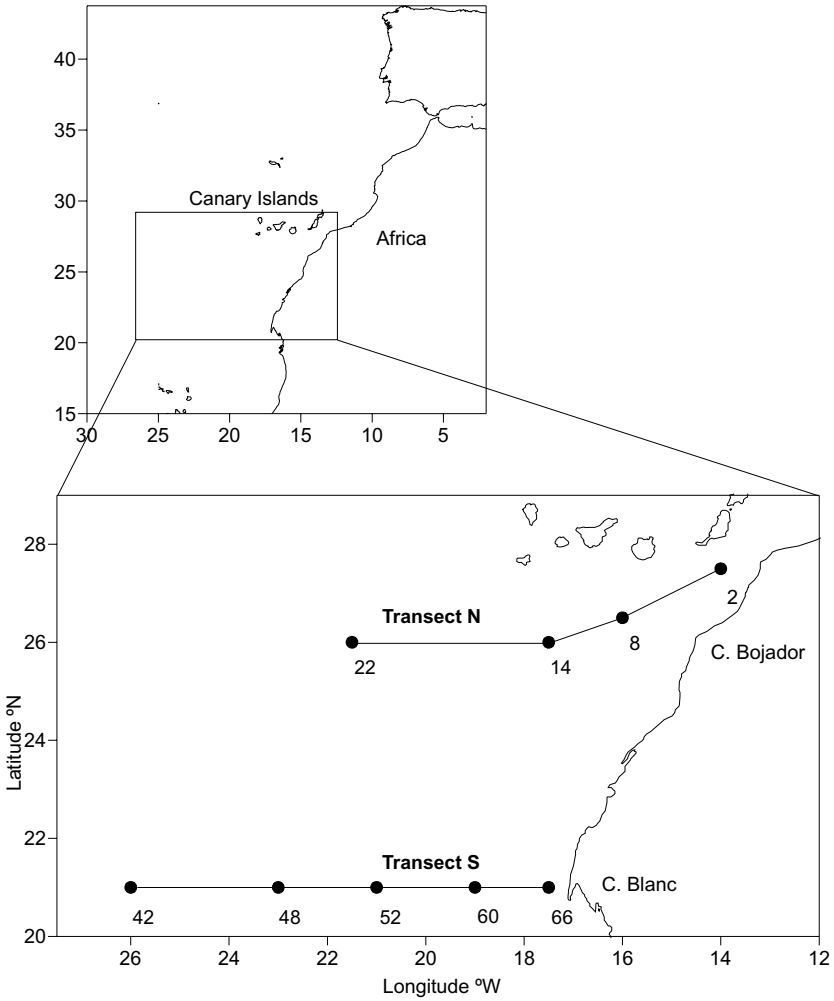

Figure 3.4.1. Study area. **N**: North transect at 26º N. **S:** South transect at 21ºN.

Mesozooplankton samples were collected with a Longhurst-Hardy Plankton Recorder equipped with a flowmeter and a 200 µm mesh net (Longhurst and Williams, 1976). A serie of 18 oblique hauls were carried out at midday and at night from 0 to 850 m depth with a mean of 43 samples per hauls. Each sample corresponded to a different sampled layer with a vertical extent of 20 to 40 m. For each sample we assessed the mean temperature and depth of the sampled layer. On board, samples were rinsed and quickly frozen in liquid nitrogen (-196 ºC) for biomass and metabolic rate analysis.

In the laboratory frozen samples were homogenized keeping the temperature below 4ºC in dark conditions to avoid as much as possible degradation of chlorophyll, loss of enzymes activity or proteins degradation. Fractions of the homogenate of each sample were taken for gut fluorescence (GF, as index of gut pigment content), ETS activity (as a proxy for respiration) and protein analysis (as biomass).

GF was assayed as in Parsons *et al.* (1984) using a carbon/pigment ratio of 30 (Vidal, 1980). GF values were corrected for the background fluorescence of the exoskeleton of the organisms captured from the DSL. We assumed that all the biomass had a background fluorescence of 0.1 µg of pigments per gram of wet weight (ww) of individual (Willason and Cox, 1987) and a dw/ww ratio of 0.2 (Mauchline, 1969). All the GF data in this work include Chl *a* plus phaeopigments.

Electron transfer system (ETS) activity was assayed according to Packard (1971) modified by Gómez *et al.* (1996). Details of the procedure are also given in Hernández-León and Gómez (1996). ETS activity was recalculated to *in situ* temperature using the Arrhenius equation and activation energy of 15 Kcal·mol^{-1} (Packard *et al.*, 1975).

Protein content was determined using the method of Lowry (1951) modified for microanalysis by Rutter (1967), and using bovine serum albumine (BSA) as standard. Proteins values were converted to dry weight using the relationship given by Hernández-Leon *et al.* (2001) for Canary Island waters and to carbon units assuming that carbon is 40% of dry weight (Båmstedt, 1986; Dam and Peterson, 1993).

In order to determine the vertical fluxes the data were categorized on 50 m depth intervals to create day and night vertical profiles of protein content, GF and ETS activity. The night profiles were then subtracted from the day profiles to only show daily changes involving diel vertical migrants (DVMs) as in Yebra *et al.* (2004) and Putzeys *et al.* (2011). The migrant biomass was determined by integrating negative values from the day-minus-night biomass profiles (mg prot·m^{-3}) as follow:

$$\text{Migrant Biomass} = \int_{0\text{-}200} \text{Biomass}$$

The migrant biomass calculated in this way corresponds to the organisms that reached the epipelagic layer at night including organisms living both above and under 850 m depth by day.

The gut pigment flux (mg pigments·m^{-2}·d^{-1}) was assessed performing a two-steps operation. First, the day-minus-night GF positive data at depth (200-850 m) were integrated and divided by the integrated biomass at the same depth in order to determine a specific gut content at depth:

$$\text{Specific Gut content at depth} = \left[\int_{200\text{-}850} \text{GF}\right] \cdot \left[\int_{200\text{-}850} \text{Biomass}\right]^{-1}$$

The second step was to multiply this value of specific gut content at depth by the migrant biomass to obtain the pigment flux due to DVMs.

To assess the respiratory flux (μL $O_2 \cdot m^{-2} \cdot h^{-1}$) positive values of the ETS day-minus-night profiles (μL $O_2 \cdot m^{-3} \cdot h^{-1}$) were integrated and divided by the integrated biomass within the 200-850 m depth range:

$$\text{Specific ETS at depth} = \left[\int_{200\text{-}850} \text{ETS}\right] \cdot \left[\int_{200\text{-}850} \text{Biomass}\right]^{-1}$$

The specific ETS activity at depth (μL $O_2 \cdot$mg protein$^{-1} \cdot h^{-1}$) obtained was then multiplied by the migrant biomass present in the epipelagic layer at night. Assuming a conservative respiration/ETS ratio of 0.5 (Hernández-León and Gómez, 1996) and a respiratory quotient of 0.97 (Omori and Ikeda, 1984), we estimated the respiratory flux mediated by the diel migrants, during the 12h of residence time at depth.

To assess the metabolism of the migrant community, we determined their potential ingestion (I, mg $C \cdot m^{-2} \cdot d^{-1}$) from the integrated day-minus-night positive respiration values (R) below 200m depth. We assumed assimilation to be 70% of ingestion (Conover, 1966; Head and Harris, 1996) and a gross growth efficiency of 30% and we applied the equation proposed by Ikeda and Motoda (1978):

$$I = 100 \cdot R/(0.7\text{-}0.3) = 2.5 \cdot R$$

The potential ingestion account for the total amount of carbon required by the metabolism of the migrant community. Also, in order to determine the food source used by migrants to sustain their metabolism, we calculated the omnivory index as [(ingestion-grazing)·ingestion^{-1}] (see Hernández-León *et al.*, 2002).

Results

Hydrography

Nine biological sampling stations were distributed along two transects, 4 stations in the **TN** (2, 8, 14 and 22) and 5 stations in **TS** (66, 60, 52, 48, 42; Figure 3.4.1). On **TN** transect (26ºN, Figure 3.4.2 a) the stations 2 and 8 were influenced respectively by upwelled waters and by the presence of a filament.

The station 8 was also at the edge of a cyclonic gyre as well as the station 14, being both stations located in the Canary Transition Zone (CTZ). The other stations of **TN** were located in oligotrophic waters (0.05 µg Chl *a* L^{-1}; Table 3.4.1).

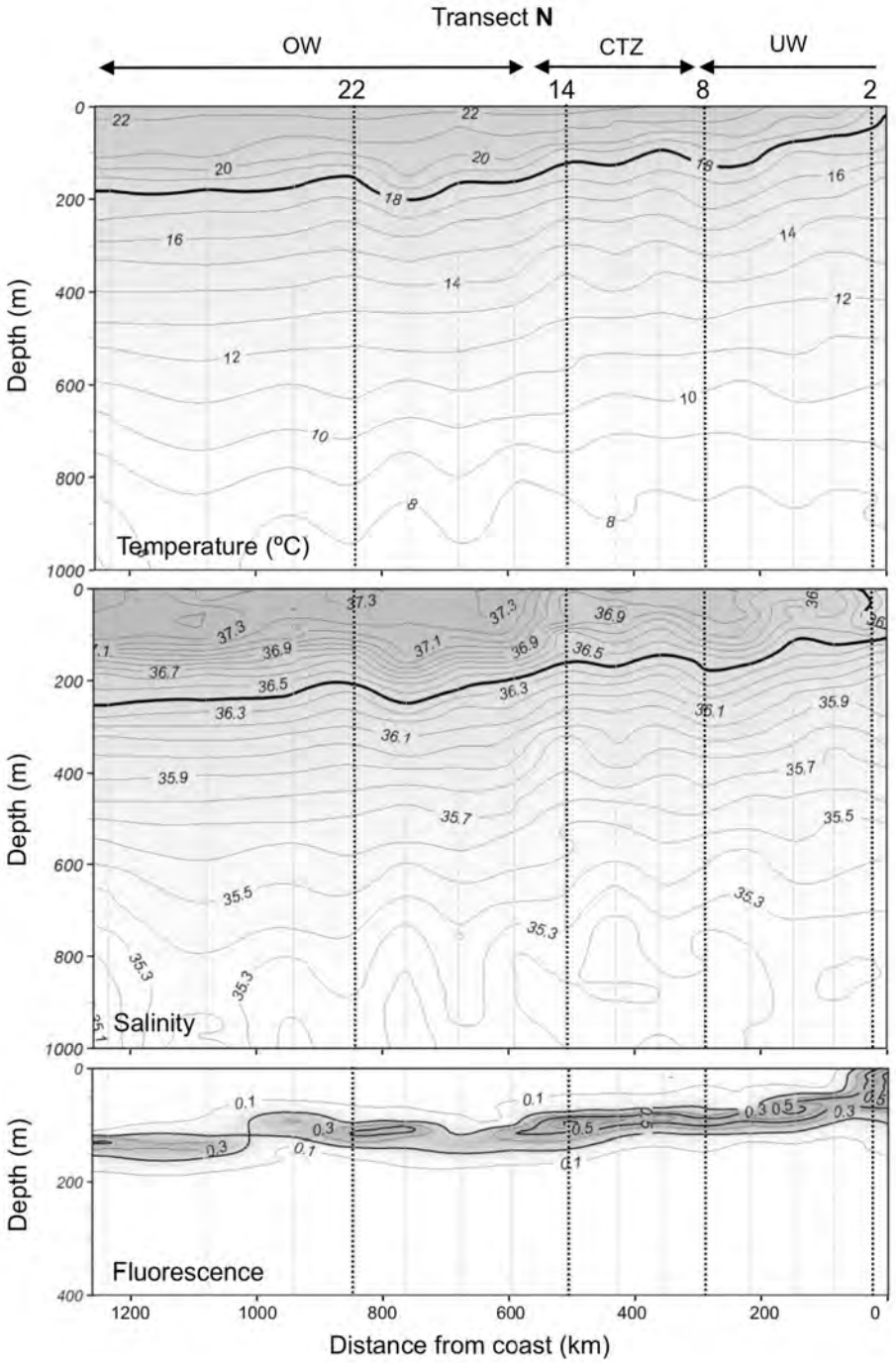

Figure 3.4.2a. Temperature (ºC), salinity and fluorescence profiles along **N** transect from open ocean (West) to coast (East). Grey lines: Hydrographical stations, black lines: hydrographical plus biological stations. UW upwelling, CTZ Canary Transition Zone, OW Oligotrophic waters.

The **S** transect (21ºN, Figure 3.4.2 b) was located close to the quasi-permament upwelling area of Cape Blanc (Hagen, 2001; Pelegrí *et al.*, 2006).

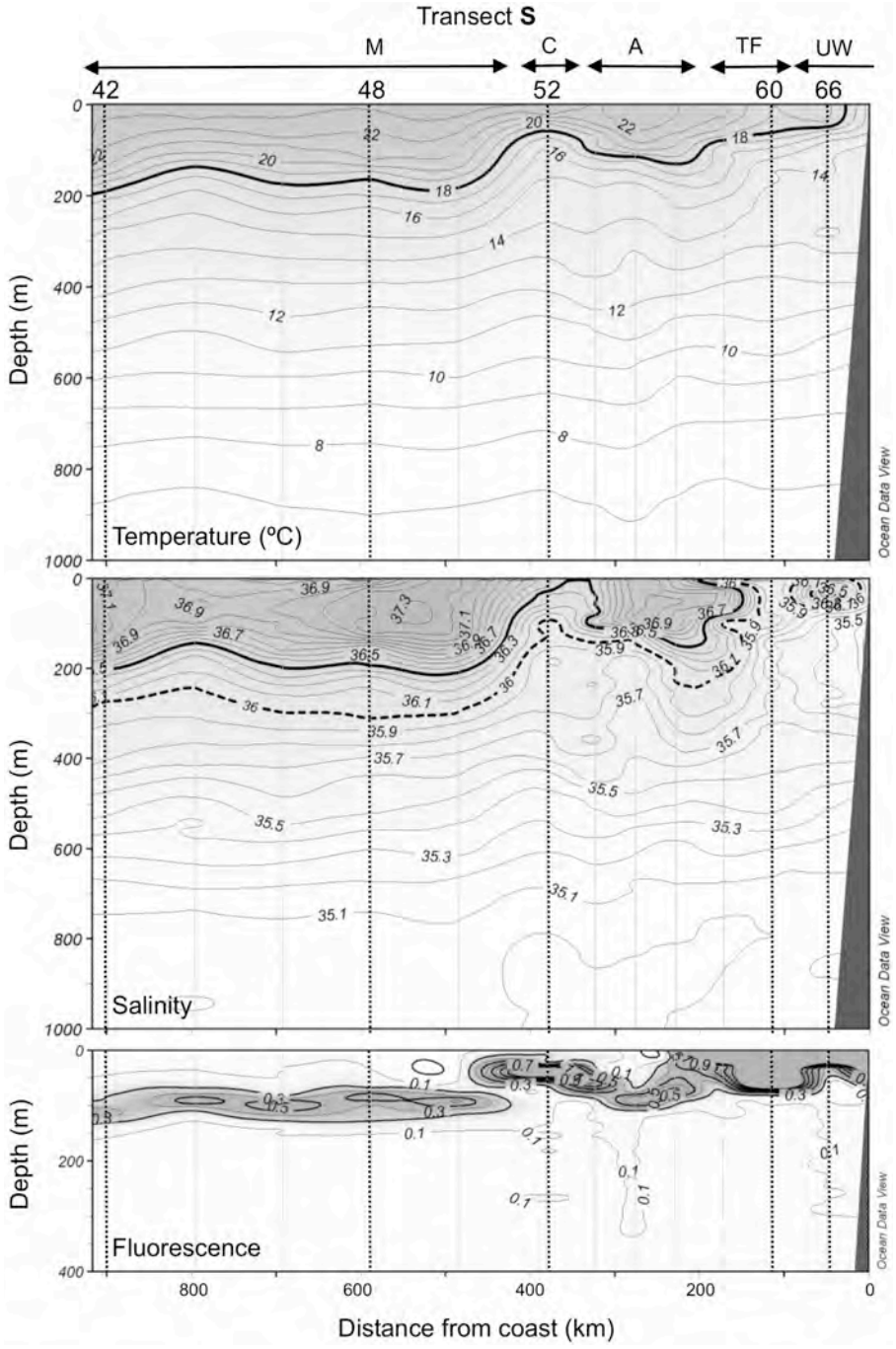

Figure 3.4.2b. Temperature (ºC), salinity and fluorescence profiles along **S** transect from open ocean (west) to coast (east). Grey lines: Hydrographical stations, black lines: hydrographical plus biological stations. UW upwelling, TF Thermohaline Front, A Anticyclonic eddy, C cyclonic eddy, M Meanders.

The latter influenced the coastal stations (66 and 60; 3.0 µg Chl *a* L^{-1}; Table 3.4.1). Also, the station 60 was close to a thermohaline front, the Cape Vert

Frontal Zone, which increases slightly the phytoplankton biomass (3.1 µg Chl *a* L^{-1}; Table 3.4.1). However the primary production was higher at the coastal station 66 than at station 60 (225 and 112 µgC $L^{-1}\cdot d^{-1}$ respectively; Gutiérrez-Rodríguez *et al.*, 2011). The station 52 was located in a cyclonic eddy, which raised the chlorophyll maximum from 100 m depth to 50 m depth. The other stations in this transect are located in oligotrophic waters (0.09 µg Chl *a* L^{-1}; Table 3.4.1).

Biomass

We observed a common layered biomass distribution (mg protein·m^{-3}) on both **TN** and **TS** vertical profiles (Figure 3.4.3a, c). By day biomass was concentrated above 200 m depth. Biomass peaked also generally between 400 and 750 m depth coinciding with the deep scattering layer (DSL), although the distribution range of the DSL varied slightly between stations. Despite the similar pattern, the DSL appeared to be located deeper in **TN** than in **TS** (400-750 m and 250-500 m, respectively). The highest biomass was found at the coastal stations (2 in **TN**, 60-66 in **S**) and at station 52 (in **TS**). During nighttime, biomass in the upper 250 m increased at all stations except at station 2 (in **TN**). This variability was reflected in the day-minus-night biomass profiles (Figure 3.4.3 b, d). The epipelagic biomass (0-200 m) by day in **TN** ranged between 23.96 to 134.99 mmolC·m^{-2} (69.51 ± 47.04 mmolC·m^{-2}, Table 3.4.1), while in **TS**, was almost 1.6-fold higher (109.56 ± 109.28 mmolC·m^{-2}) ranging from 45.8 to 257.65 mmolC·m^{-2}. Also, migrant biomass was 5.8-fold higher in **TS** (153.39 ± 152.60 mmolC·m^{-2}) than in **TN** (26.19 ± 11.01 mmolC·m^{-2}). In **TN** at station 2, the day-minus-night profile presented positive values and it was not possible to calculate the migrant biomass. Migrant biomass at stations 60 and 52 was 6.8-fold higher than at the other stations in **TS** (373.29 mmolC·m^{-2} and 254.53 mmolC·m^{-2} respectively, Table 3.4.1), which in average presented a migrant biomass of 46.37 ± 10.15 mmolC·m^{-2}.

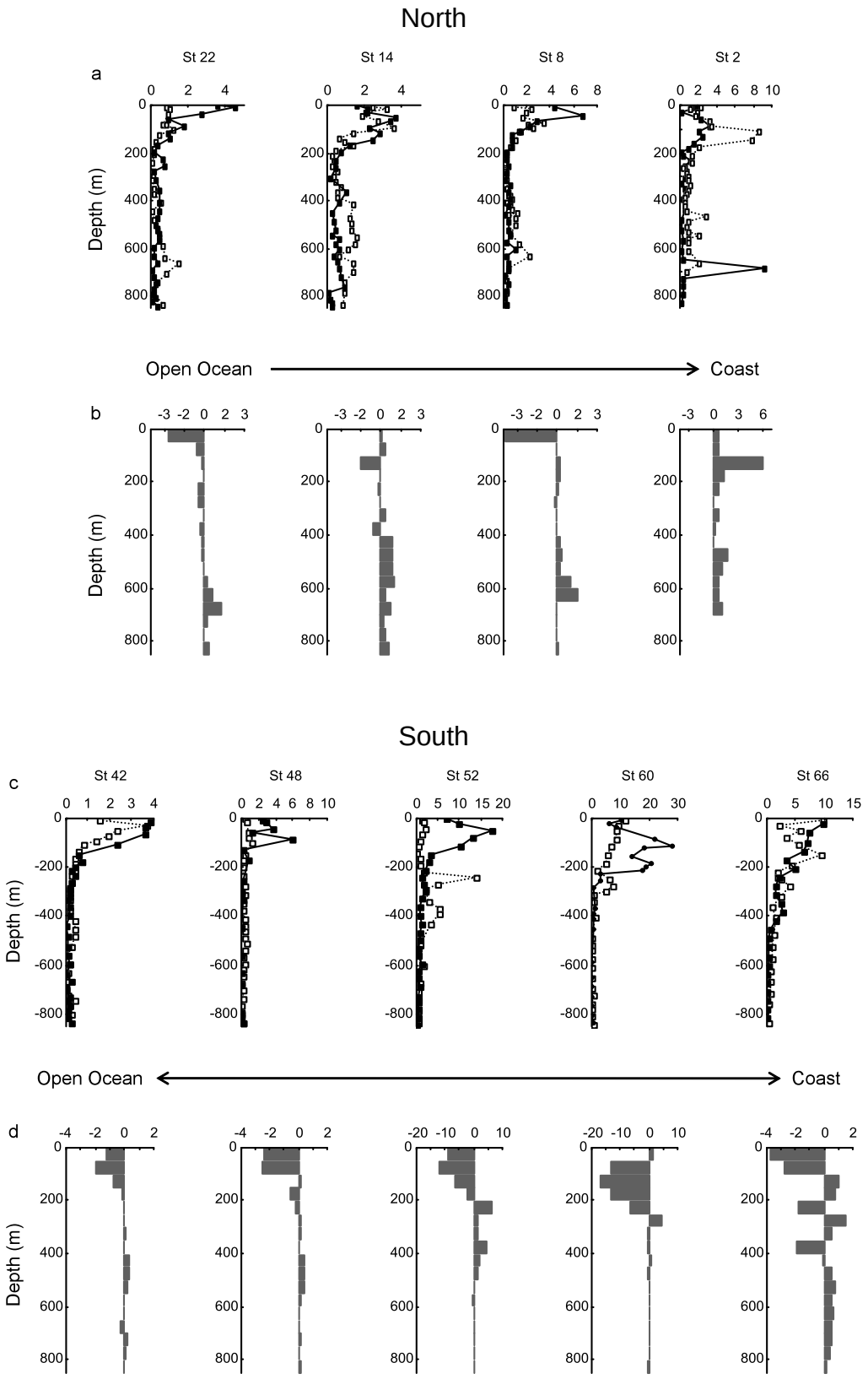

Figure 3.4.3. Biomass vertical profiles (mg protein·m^{-3}) in transects **N** and **S** (a, c; open circles: day, closed circles: night). Day-minus-night variations profiles in transects **N** and **S** (b, d).

Table 3.4.1. Biomasses and fluxes assessed from coast to open ocean during spring 2003 and fall 2002 (previous work). Biomass in mmolC·m^{-2}, Fluxes in mmolC·m^{-2}·d^{-1}, [1] Phytoplankton biomass (in μg chl *a* L^{-1}) from Gutiérrez-Rodríguez *et al.* (2011), [2] Respiratory flux plus pigmented gut flux *versus* POC (mmolC·m^{-2}·d^{-1}). [3] Potential ingestion flux *versus* POC. * Due to the methodology the migrant biomass at St2 was not measurable, the active carbon fluxes showed were non-specific migrant biomass 200-900m integrated values.

Stations	Phytoplankton biomass[1]	Migrant biomass	Epipelagic day biomass	Omnivory index	Pigmented Gut flux	Respiratory flux	Potential ingestion flux	Total carbon flux [2]	Total carbon flux [3]
2	-	0*	134.99	0.99	0.001*	0.002*	0.004*	0.006*	0.004
8	-	34.0	53.34	0.99	0.003	0.14	0.35	0.14	0.35
14	0.068	13.6	65.77	0.91	0.032	0.15	0.36	0.17	0.36
22	0.055	30.96	23.96	0.98	0.012	0.28	0.71	0.29	0.71
66	2.9	55.64	194.99	0.57	0.77	0.71	1.78	1.48	1.78
60	3.1	373.29	257.65	0.74	2.33	3.61	9.03	5.94	9.03
52	-	254.53	30.58	0.92	0.8	4.05	10.13	4.85	10.13
48	0.1	47.94	18.83	0.97	0.057	0.74	1.84	0.79	1.84
42	0.098	35.53	45.8	0.99	0.004	0.23	0.58	0.23	0.58
Spring									
North mean (SD)	0.05 (0.02)	26.19 (11.01)	69.51 (47.04)	0.97 (0.04)	0.02 (0.01)	0.19 (0.08)	0.47 (0.20)	0.21 (0.08)	0.47 (0.20)
South mean (SD)	1.55 (1.68)	153.39 (152.60)	109.56 (109.28)	0.84 (0.18)	0.79 (0.94)	1.87 (1.81)	4.67 (4.53)	2.66 (2.57)	4.67 (4.53)
Fall									
North mean (SD)	0.19 (0.23)	27.12 (12.39)	25.59 (8.01)	0.76 (0.24)	0.06 (0.11)	0.05 (0.05)	0.13 (0.12)	0.18 (0.16)	0.13 (0.12)
South mean (SD)	0.34 (0.35)	71.44 (51.44)	50.12 (18.31)	0.59 (0.21)	1.89 (3.43)	0.54 (0.42)	1.36 (1.06)	1.90 (4.47)	1.36 (1.06)
Spring *versus* fall ratio North	0.26	0.97	2.72	1.28	0.24	3.74	3.74	1.78	3.74
Spring *versus* fall ratio South	4.55	2.15	2.19	1.43	0.42	3.43	3.43	1.09	3.43

Gut fluorescence

The most coastal stations 2 and 66, as well as stations 52 and 60 showed the highest GF values within each transect. Although the GF at station 60 was almost 2-fold higher than at the others, on average, the oceanic stations in **TS** (stations 42, 48) presented a similar gut pigment content than in **TN** (station 22). Community gut pigment content vertical distribution (ng pigments·m^{-3}) in **TN** was quite different from **S** (Figure 3.4.4 a, c). In **TN** (Figure 3.4.4 a), the maximum values were found in the epipelagic zone for stations 2, 8 and 14. Opposite to this, in **TS** (Figure 3.4.4 c), GF at the coastal station 66 presented higher values in the mesopelagic zone (200-600 m) while the oceanic stations presented maximums above 250 m depth.

The day-minus-night profiles (Figure 3.4.4 b, d) showed marked differences between day and night periods and between **TN** and **TS**. On average, the estimated pigmented gut flux was 50-fold higher in the South than in the North (0.79 ± 0.94 and 0.02 ± 0.01 mmolC·m^{-2}·d^{-1} respectively, Table 3.4.1). In **TN** at station 2, the 200-900m day-minus-night positive values were integrated to give an indicative gut flux value due to the missing migrant biomass data.

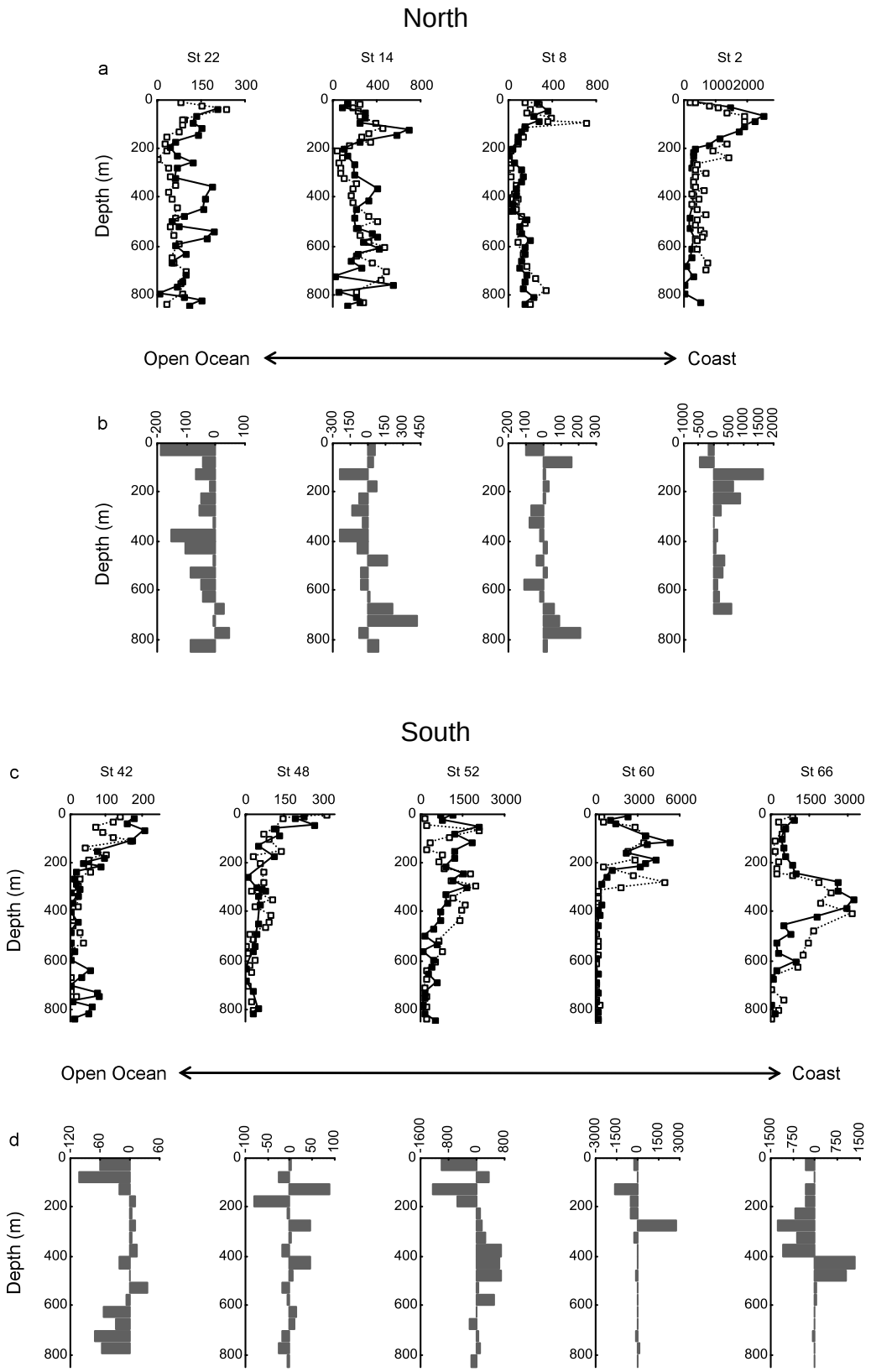

Figure 3.4.4. Gut fluorescence vertical profiles (µg pigments·m^{-3}) in transects **N** and **S** (a, c; open circles: day, closed circles: night). Day-minus-night variations profiles in transects **N** and **S** (b, d).

Electron transfer system activity

ETS activity was higher above 200 m depth at all stations (Figure 3.4.5 a, c). However, the ETS activity was not as sharp as biomass distribution at the depth of the DSL. As observed for biomass and GF, ETS activity was highest at the coastal stations (2, 66) and also at stations 52 and 60. The maximum ETS activity by night was located at station 60, which was double than at stations 2, 60 and 52 (note the change of axis scale in Figure 3.4.5 c).

Respiratory fluxes obtained in **TN** ranged between 0.14 and 0.28 mmolC·m^{-2}·d^{-1}, whereas in **TS**, varied between 0.23 and 4.05 mmolC·m^{-2}·d^{-1}. On average the respiratory flux in **TS** was 10-times higher than in **TN** (Table 3.4.1).

Using the respiratory fluxes we calculated the potential ingestion requirements of the migrant community. In **TN**, the potential ingestion was 2-fold lower within the CTZ (stations 8, 14; 0.35 ± 0.01 mmolC·m^{-2}·d^{-1}) than at station (22, 0.71 mmolC·m^{-2}·d^{-1}). In **TS**, the potential ingestion at stations 60 and 52 was 6.8-fold higher than at the other stations (9.58 ± 0.77 and 1.39 ± 0.71 mmolC·m^{-2}·d^{-1} respectively). The omnivory index of the migrant community was similar in **TN** (0.97 ± 0.04) and in **TS** (0.84 ± 0.18). In **TS**, the omnivory index showed a slight and gradual increase from coast to open ocean (0.57 at station 66 to 0.99 at station 42). In **TN** at station 2, the 200-900m day-minus-night positive values were integrated to give a respiratory flux, which is only an indicative value (Table 3.4.1).

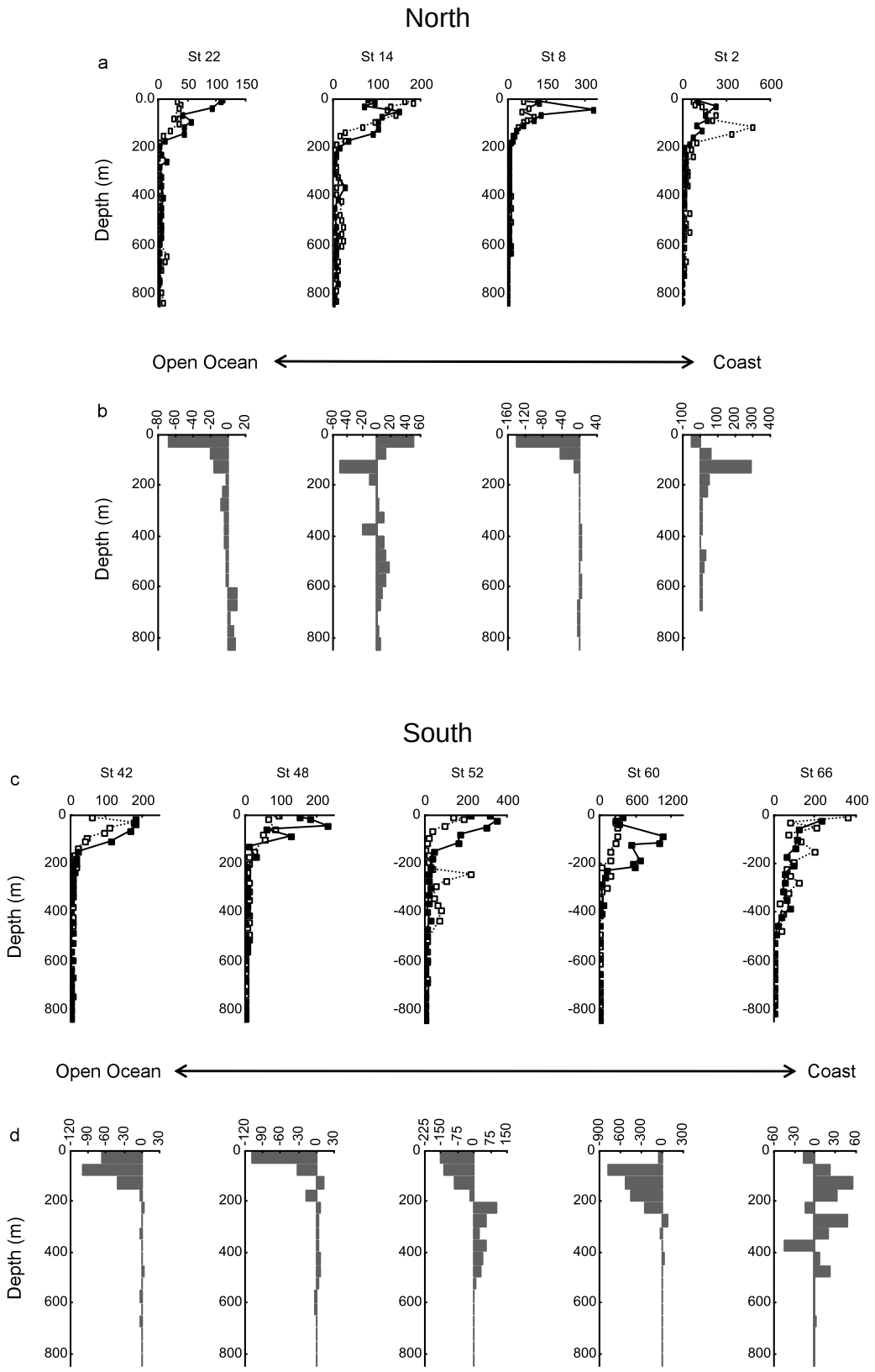

Figure 3.4.5. ETS activity vertical profiles ($\mu lO_2 \cdot m^{-3} \cdot h^{-1}$) in transects **N** and **S** (a, c; open circles: day, closed circles: night). Day-minus-night variations profiles in transects **N** and **S** (b, d).

Seasonality

In order to compare both seasons a spring *versus* fall ratio was calculated dividing the average value during spring by the corresponding average value during fall (Table 3.4.1). All the variables measured in spring were higher than during fall except the pigmented gut flux, as well as the migrant biomass in **TN** (Table 3.4.1, Figure 3.4.6). In **TN**, the spring *versus* fall ratios showed a value of 0.97 for the migrant biomass. The amount of epipelagic biomass was double (2.19-2.72) during spring, both in **TN** and **TS**. The omnivory index values showed an omnivory/carnivory behavior during spring (0.97) while this index indicated an omnivory/herbivory behavior during fall (0.76). The pigmented gut flux values were 50% lower during spring than at fall. However, the respiratory flux, potential ingestion flux as well as the total carbon contribution were 3.6 higher during spring than during fall (Figure 3.4.7).

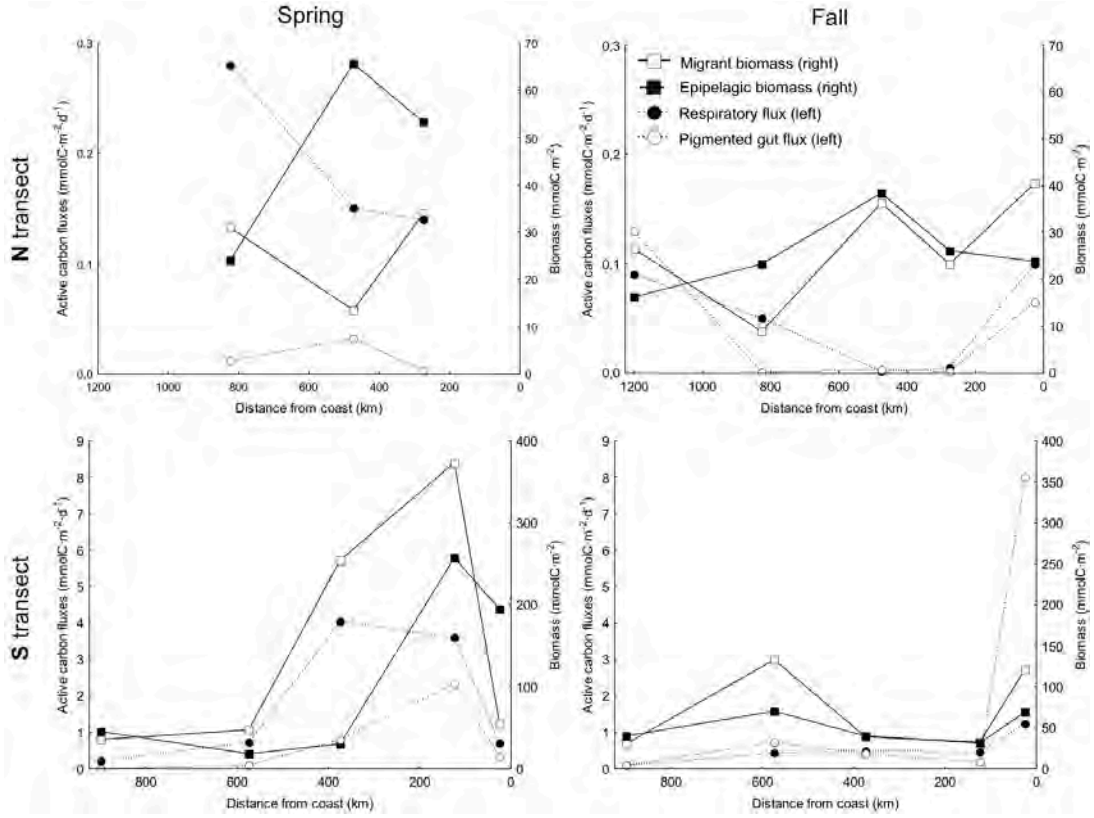

Figure 3.4.6. Fluxes (mmolC·m^{-2}·d^{-1}) and biomass (mmolC·m^{-2}) measured in the Canary Current in fall 2002 and spring 2003. Open circles: Pigmented Gut flux, filled circles: Respiratory flux, Close square: Epipelagic biomass, Open square: Migrant biomass. Note the change of axis scale between **TN** and **TS**.

In **TS**, the spring *vs* fall ratios showed higher values during spring except for the pigmented gut flux. The migrant biomass and the epipelagic biomass showed a double value in spring *vs* fall period. The respiratory flux, potential ingestion flux and total contribution to the total carbon flux showed values 3.4-fold higher in spring *vs* fall. The omnivory index in **TS** still indicates the same omnivory/carnivory behavior as for the northern transect. Also the pigmented gut flux was 42% lower during spring compared to fall. On average, the potential ingestion flux as well as the total active carbon contribution were 3.4-fold higher in spring *vs* fall (Figure 3.4.7).

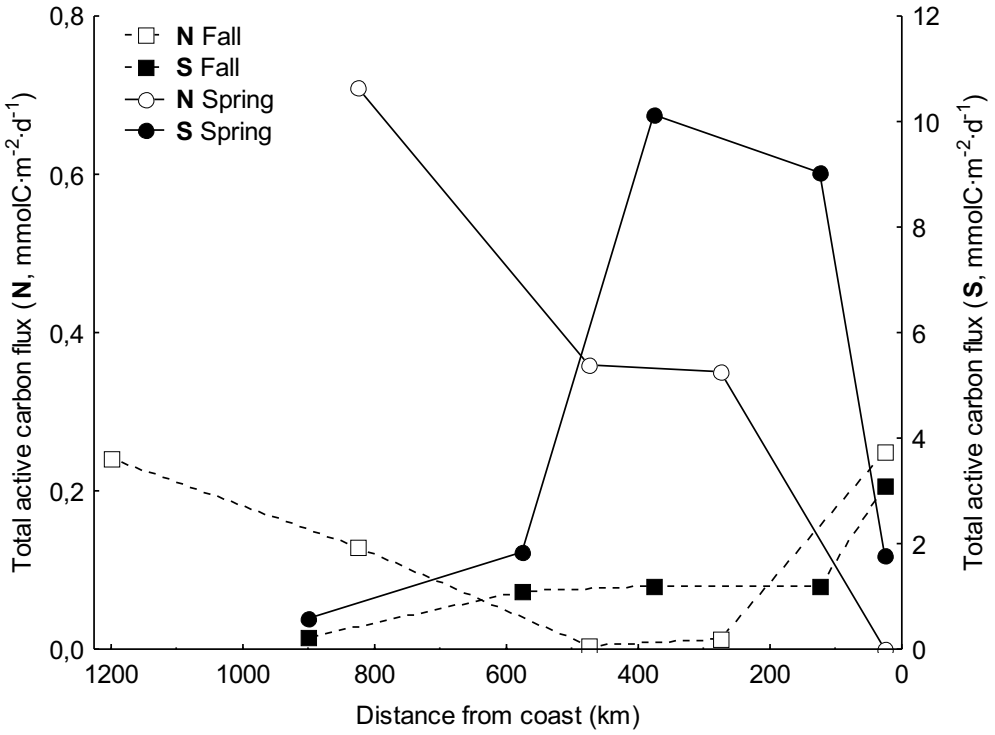

Figure 3.4.7. Total active carbon flux in the Canary Current in fall 2002 and spring 2003. Open circles: **TN** spring, filled circles: **TS** spring, Close square: **TS** fall, Open square: **TN** fall. Note the change of axis scale between **TN** and **TS**.

A slight decreasing tendency was observed for migrant biomass, epipelagic biomass and also for the carbon fluxes measured from coast to open ocean in **TN** and **TS** and also during both fall and spring (Figure 3.4.6, 3.4.7). This decreasing tendency was clear in **TS** more than in **TN** during both spring and fall.

Discussion

The sampling area is a region of high mesoscale activity due to the strong disruption of the Canary current flow by the Canary Archipelago. The disruption generates eddies leeward of the archipelago and connect the highly productive upwelling system with the oligotrophic open ocean waters of the eastern subtropical North Atlantic gyre. The **N** transect (26ºN) extended 1200 km offshore from the boundary of the African coastal upwelling. Hence, the coastal stations 2 and 8 were affected by the presence the Cape Bojador recurrent filament (Barton *et al.*, 2004). The **N** transect crossed also the well-described Canary transition zone (CTZ, Mittelstaeds, 1991; Hernández-Guerra *et al.*, 1993; Arístegui *et al.*, 1994, 1997; Barton *et al.*, 1998). Finally, the **N** transect ended in oligotrophic waters of the subtropical Eastern Atlantic gyre as observed by Gutiérrez-Rodríguez *et al.* (2011).

The **S** transect (21ºN) extended from the quasi-permanent upwelling area of Cape Blanc (Hagen, 2001; Pelegrí *et al.*, 2006), which influenced the coastal station 66 where the chlorophyll values were 29-fold higher than offshore (Gutiérrez-Rodríguez *et al.*, 2011). Close to the upwelling cell, the station 60 was located next to the Cape Vert Frontal Zone (Stramma, 1984), which increases slightly the phytoplankton biomass (Gutiérrez-Rodríguez *et al.*, 2011). However, the primary production in the upwelling cell was 2-fold higher than at stations 60. The station 52 was located in a cyclonic eddy, which raised the deep nutrient rich waters and the chlorophyll maximum from 100 m depth to 50 m depth.

Vertical biomass distribution presented a layered pattern with well-defined deep scattering layer as showed in previous studies in this area (Hernández-León *et al.*, 2001; Yebra *et al.*, 2005; Putzeys *et al.*, 2011; chapter 3.3, unpublished). At night organisms from the DSL migrated to upper layers to feed on the epipelagic zooplankton crop. Most of the night biomass was concentrated in the uppermost 300 m. Moreover, biomass in the DSL by day was in the same range or higher than in the upper 200 m. The observed increases in biomass by night due to vertical migration have also been well documented in the Canary area (Hernández-León *et al.*, 2001; Yebra *et al.*, 2005; Putzeys *et al.*, 2011; Chapter 3.3). Also, the biomass peaks observed

below 700m depth during the night are consistent with measurements made by Plueddemann and Pinkel (1989), Hernández-León *et al.* (2001), Yebra *et al.* (2005), Putzeys *et al.* (2011) and Chapter 3.3.

The influence of upwelled waters and the presence of a frontal zone in the transects had a larger impact on the zooplanktonic community in terms of distribution, abundance, metabolism and carbon fluxes as observed in previous studies (see Yebra *et al.*, 2004, 2005, 2009; Isla and Anadón, 2004, Putzeys *et al.*, unpublished). The epipelagic mesozooplankton in **N** and **S** transects were characterized by the presence of a longitudinal biomass gradient from the upwelling influenced coastal area to the oligotrophic open ocean. Gutiérrez-Rodríguez *et al.* (2011) showed, on average, a higher and positive phytoplanktonic carbon synthesis in the upwelling area (net $C_{synthesis}$ = 15 ± 37 µg C $L^{-1}\cdot d^{-1}$) compared to open ocean (net $C_{synthesis}$ = 2.3 ± 2.3 µg C $L^{-1}\cdot d^{-1}$). Moreover, the filaments associated to the upwelling could export the local production, zooplankton and larvae to more than 400 km in some cases (Postel, 1985; Hernández-León *et al.*, 2002; Rodriguez *et al.*, 1999; Bécognée *et al.*, 2009). The epipelagic mesozooplankton biomass showed also a latitudinal biomass gradient with values 1.6-fold higher in the meso-eutrotrophic transect (South) than in the oligotrophic transect (North). This was probably due to the upwelling productivity (Carr, 2002; Gutiérrez-Rodríguez *et al.*, 2011). Gutiérrez-Rodríguez *et al.* (2011) reported values of phytoplankton daily carbon synthesis of approximately 5 µg C $L^{-1}\cdot d^{-1}$ in **N** transect and approximately 100 µg C $L^{-1}\cdot d^{-1}$ in **S** transect.

The migrant biomass observed for stations of both transects were in the range of values previously reported for this area (Hernández-León *et al.*, 2001; Yebra *et al.*, 2005; Chapter 3.3; see Table 3.4.2), except the migrant biomass observed at station 60, which is the highest reported until now in the literature (Table 3.4.2). The migrant biomass observed during this study was 5.8-fold higher in the meso-eutrophic than in the oligotrophic transect. However, the small or nonexistence of data dealing with zooplankton dynamics, seasonal and inter-annual variability in this area does not allow a reference point for comparison.

Table 3.4.2. Zooplankton active flux estimated in different oceanic regions.

Location	Time of year	Migrant biomass (mg C·m^{-2})	Respiratory flux (mg C·m^{-2}·d^{-1})	Gut flux (mg C·m^{-2}·d^{-1})	% of POC flux	References
Oligotrophic area						
HOT		30.2 - 33.8	1.3-1.7	-	4[a]	Roman et al., 2002
Equator divergence		2.8 - 21.8	0.9-1.2	-	<1-2[a]	Roman et al. (2002)
BATS	March/April	192 (84–540)	14.5 (6.2-40.8)	-	34 (18-70)[a]	Dam *et al.* (1995)
BATS	year-round	50 (0-123)	2.0 (0-9.9)	-	8 (0-39)[b]	Steinberg *et al.* (2000)
BATS	year-round	83 (0.7-468)	-	0.8 (0.007-4.5)	4 (0.03-21)[c]	Schnetzer and Steinberg (2002)
Western Equator	October	46.9	3	-	6	Le Borgne and Rodier (1997)
North (Oceanic)	Oct-Nov	30 ± 10	2.2 ± 0.3	-	-	Isla and Anadón (2004)
Eastern Equator	March - April	96 ± 25.2	4.2 ± 1.2	-	18[a]	Zhang and Dam (1997)
Eastern Equator	October	154.8 ± 32.4	7.3 ± 1.4	-	25[a]	Zhang and Dam (1997)
ALOHA	Year-round	162 (108-216)	3.6 (2.6 - 19.1)	-	15 (12-18)[a]	Al-Mutairi and Landry (2001)
ALOHA	June - July	157.9	3.7	-	18[a]	Steinberg et al. (2008)
Eu- Meso-trophic area						
Central Equator (HNLC)	October	52.9	6	-	4[a]	Le Borgne and Rodier (1997)
North (coastal)	Oct-Nov	360 ± 70	30.3 ± 1.9	-	-	Isla and Anadón (2004)
North (poleward current)	Oct-Nov	270 ± 210	10.4 ± 6.3	-	-	Isla and Anadón (2004)
Western Equator	October	46.9	3	-	6[a]	Le Borgne and Rodier (1997)
Western Equator	February	367 (144 - 447)	22.7 (7.3-19.1)	4.8 (2.6-4.4)	24 (13-35)[a]	Hidaka et al. (2001)
Canary Current						
Canary Islands	March	204 (108 - 341)	0.8 (0.5-1.4)	0.1 (0.05-0.18)[e]	1.8 (1.1-2.7)[d]	Chapter 3.2
Canary Islands	June	580 - 1280	1.8 - 8.3	0.1 - 0-4[e]	15-53[d]	Yebra et al. (2005)
Canary Islands	August	247 - 125	4.2 - 1.9	0.3 - 2.4[e]	20-45[d]	Hernández-León et al. (2001a)
26ºN	Sept-Oct	325 (106 - 486)	0.6 (0.02 - 1.2)	0.8 (0.01 - 3.0)[e]	3.3 (0.1-9.0)[f]	Chapter 3.3
	May-June	314 (163.2 - 408)	2.3 (1.7 - 3.4)	0.2 (0.03 - 0.4)[e]	47.8 (26.9-64.4)[f]	Present chapter
21ºN	Sept-Oct	857 (368 - 1601)	6.5 (1.1 - 14.9)	22.7 (1.3-96.1)[e]	66.0 (0.1-149.5)[f]	Chapter 3.3
	May-June	314 (426.4 - 4480)	2.3 (2.7 - 48.6)	9.5 (0.05-28.0)[e]	118.6 (29.1-273.7)[f]	Present chapter

[a] %POC flux represents only respiratory flux. [b]Active flux includes DOC. [c]Active flux represents only gut flux. [d]Respiratory flux plus gut flux. [e]Gut flux assessed with GF.

[f]Potential ingestion assessed from respiration.

Moreover, the migrant biomass values observed in **N** and **S** transect were lower in the open ocean than in the coastal upwelling influenced area. The migrant biomass differences observed between **N** and **S** transect were probably due to the latitudinal and longitudinal distribution of the potential food sources (phytoplankton, epipelagic zooplankton).

As observed during this study, the diel vertical migrants were responsible for a net transport of carbon to the mesopelagic zone. The pigmented gut flux determined during this cruise was 50-fold lower in **N** than in **S** transect (0.02 ± 0.01 *vs* 0.79 ± 0.94 $mmolC \cdot m^{-2} \cdot d^{-1}$ respectively) coinciding with the results of phytoplankton net carbon synthesis of Gutiérrez-Rodríguez *et al.* (2011). However the results of the net downward transport based on the gut fluorescence method should be considered . In fact, the omnivory index calculated for **N** and **S** transects showed mean values of 0.97 and 0.84 indicating omnivore/carnivore behaviour. The omnivory index values extend the results of Hernández-León *et al.* (2001, 2002, 2004) showing that non-pigmented organisms (e.g. protista) could constitutes 35-80% of the diet of the zooplankton in Canary Island waters. The potential ingestion flux calculated showed to be 10-fold higher in the meso-eutrophic transect than in the oligotrophic transect. The determination of the gut flux due to migrants should be assessed through the potential ingestion to avoid underestimation since the gut flux depend on migrant community diet. Thus, the gut flux due to vertical diel migrants will depend on phytoplankton biomass and non-pigmented food (e.g. protista), as observed from the estimated values for the omnivory index, pigmented gut flux and potential ingestion flux. This extend also the results of Gutiérrez-Rodríguez *et al.* (2011) from phytoplankton net carbon synthesis experiments suggesting the daily phytoplankton growth that escapes to microzooplankton grazing represents the particulate carbon potentially available for export pathways via mesozooplankton grazing or direct sinking.

The diel vertical migrants were also responsible for a net carbon transport to depth through the respiratory flux. The flux values obtained for this cruise were similar or slightly higher than values observed for similar areas (see Table 3.4.2 and references therein). However, the meso-eutrophic

transect showed values 9-fold higher than the oligotrophic transect (1.87 ± 1.81 and 0.19 ± 0.08 mmolC·m^{-2}·d^{-1}, respectively). Also the respiratory carbon flux followed a decreasing tendency from the coast to the ocean in the **S** transect, except for the station 66 located in the upwelling cell.

Using the data of particulate organic carbon flux (POC flux) we estimated the contribution of the active carbon export flux due to the diel vertical migrant to the passive POC flux (Table 3.4.3).

Table 3.4.3. Summary of the POC flux measured at 200 m depth (mmolC·m^{-2}·d^{-1}) and contribution percentage of the total active carbon flux to the POC flux. [1] Respiratory flux plus gut flux. [2] Potential ingestion flux. (nd, not determined). [3] Passive plus active flux

	POC flux (0-200 m)	Active flux		% contribution to POC[1]		Total export flux[3]	
Stations	mmolC·d^{-1}	1	2	1	2	1	2
2	nd	0.006	0.004	nd	nd	nd	nd
8	1.3	0.14	0.35	10.97	26.91	1.44	1.65
14	0.7	0.17	0.36	25.40	52.11	0.87	1.06
22	1.1	0.29	0.71	26.86	64.36	1.39	1.81
66	6.1	1.48	1.78	24.29	29.12	7.58	7.88
60	9.8	5.94	9.03	60.66	92.14	15.74	18.83
52	3.7	4.85	10.13	131.24	273.72	8.55	13.83
48	1.1	0.79	1.84	72.19	167.60	1.89	2.94
42	1.9	0.23	0.58	12.40	30.41	2.13	2.48

The total contribution to the POC flux was quite variable (26.91 to 273.72 %) and the values assessed in the meso-eutrophic transect were the highest values reported until now in the literature (Table 3.4.2). The phytoplankton productivity and the high microzooplankton grazing rate in upwelling compared to oceanic waters observed by Gutiérrez-Rodríguez *et al.* (2011) could explain the high active carbon export flux values of this study. Unfortunately, samples for microzooplankton were not available, precluding any analysis of the potential relationship between microzooplankton biomass and epipelagic mesozooplankton biomass.

A similar study performed in 2002 in the same area allowed us to determine the impact of the seasonality on the trophic food web and on the active carbon export flux. Almost all the variables under study showed to be higher during spring than during fall (Table 3.4.1) and also higher than those previously reported (Table 3.4.2 and references therein). Both migrant

biomass and epipelagic biomass were higher or showed similar values from spring to fall. This link between the seasonality of the upwelling and the mesozooplankton biomass was previously observed by Postel (1990) and Hernández-León *et al.* (2007). Besides the increase of biomass, a possible switch of the trophic food web functioning could affect the intensity of the active carbon export flux. During spring, the phytoplanktonic productivity enhance the epipelagic mesozooplankton which is preyed by the diel vertical migrants (large zooplankton and mesopelagic micronekton). The high omnivory index of the migrant community indicated omnivorous/carnivorous behaviour and combined to the low pigmented gut flux observed could justify this hypothesis. Thus during the spring scenario, the energy and matter produced in the epipelagic zone was probably passing through the so-called macrobial pathway (Hernández-León, 2009) and was directly shunted to the mesopelagic zone due to diel vertical migrants. This hypothesis could explain their high values in relation to the POC flux. By opposite, during fall the lower phytoplanktonic productivity was not able to sustain a large epipelagic mesozooplankton community. Also, the migrant community showed a low omnivory index indicating omnivory/ herbivory behaviour and the pigmented gut flux was higher than during spring. During fall scenario, the energy and matter produced in the epipelagic zone was probably passing through the microzooplankton and to the microbial pathway (Hernández-León, 2009) reducing the amount of energy and matter available for the migrant community. This hypothesis could explain the lower active export flux observed compared to spring.

In summary, this study presents measurements of active carbon flux due to the diel vertical migrant community across strongly contrasting physico-chemical conditions of the subtropical northeast Atlantic Ocean. These environmental differences were clearly reflected in the active export flux. In the eutrophic high productive waters of the upwelling area the matter and energy was channelled from phytoplankton toward large zooplankton and to the migrants and subsequently increased the active carbon flux. While in oligotrophic waters the matter and energy produced were channelled through the microbial pathway and subsequently reduced the amount of carbon

available for the migrant community and the active carbon flux. In addition to the functional aspect of the oligotrophic and meso-eutrophic realms, the contribution of the active carbon flux due to migrant to the POC flux responded coherently to the contrasting seasonal conditions showing higher active export during spring than during fall. The seasonality probably influences the structure of the epipelagic communities and the migrants adapt their diet, which could have consequences on the carbon pathway (macrobial or microbial) and on the amount of carbon actively exported. Overall, our results revealed the active carbon flux due to the diel vertical migrant seems to be more variable than previously thought with contributions values ranging from 1 to 119% of the POC flux.

Acknowledgements

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CARBON SEQUESTRATION AND ZOOPLANKTON LUNAR CYCLES: COULD WE BE MISSING A MAJOR COMPONENT OF THE BIOLOGICAL PUMP?

Santiago Hernández-León, Gara Franchy, Marta Moyano, Inmaculada Menéndez, Claire Schmoker, and Sébastien Putzeys (2010). Limnology and Oceanography, 55(6), 2503-2512.

Abstract:

The plankton outburst during the so-called late winter bloom in subtropical waters was studied in relation to lunar illumination in the Canary Island waters. Nutrient enrichment by mixing and dust deposition promoted a bloom of phyto- and zooplankton. Mesozooplankton biomass increased as the winter mixing progressed but peaked in every full moon and decreased thereafter because of the effect of predation by interzonal diel vertical migrants (DVMs). The pattern was similar to the one described in lakes due to predation by fishes and confirms that this phenomenon is important in the sea. The estimated consumption and subsequent transport of epipelagic zooplankton biomass by DVMs after every full moon is on the order of the mean gravitational export and is an unaccounted flux of carbon to the mesopelagic zone that may play a pivotal role in the efficiency of the biological pump.

Keywords: Canary Islands, lunar cycle, carbon flux, metabolism, respiratory flux, vertical migration, zooplankton, late winter bloom.

Introduction

Most of the research about the downward flux of carbon in the ocean has centered on the so-called gravitational flux, the transport due to the sedimentation of the particulate organic carbon production from the euphotic layer to the mesopelagic zone. In tropical and subtropical regions this flux is a low number, normally less than 10% of primary production (Karl *et al.*, 1996). Another component of the biological pump is the so-called active flux due to the transport of carbon by vertical migrants. These organisms feed on the shallower layers of the ocean at night and return to their daytime residence at depth where they metabolize carbon or simply are eaten by other organisms. The role of these rather large organisms (mesozooplankton and micronekton) in the ocean carbon sequestration has been almost neglected. Active flux is a rather complex mechanism that involves the gut flux (Angel, 1989) (the transport due to the release of feces below the mixed layer), carbon dioxide respiration (Longhurst *et al.*, 1990), dissolved organic carbon excretion (Steinberg *et al.*, 2000), and mortality (Zhang and Dam, 1997) at depth. The few values available at present mainly based on respiration at depth indicate that the active downward carbon flux is highly variable, ranging from 4% to 70% of the gravitational flux (Hernández-León and Ikeda, 2005a). However, diel vertical migrants (DVMs) account for the control of 5-10% of the daily epipelagic zooplankton production (Hopkins *et al.*, 1996), and this ingested food is efficiently transported downward (Pearre, 2003). The consumption of epipelagic zooplankton by these organisms and their role in the fate of a bloom are at present poorly known.

A way to study the biological pump in subtropical waters is to understand the development of the bloom during winter, when nutrients are present in the euphotic zone. The late winter bloom in subtropical waters is produced by cooling of the shallower layers of the ocean, eroding the thermocline and allowing a small flux of nutrients to the euphotic zone. This process promotes the increase in primary production and the growth of micro- and mesozooplankton. Atmospheric Saharan dust deposition during the winter in the Canary Current also increases the availability of carbon, nitrogen, silica, and iron, among other nutrients (Duarte *et al.*, 2006), while promoting blooms

of phyto- and zooplankton (Hernández-León *et al.*, 2004). In experiments using this dry deposition of dust, phytoplankton (mainly diatoms) and primary production increased seven- and tenfold, respectively (Duarte *et al.*, 2006).

Two scenarios were observed during the winter bloom in the Canary Island waters. The first was the increase in mesozooplankton as the effect of higher primary production due to vertical mixing. The second scenario was the decrease in mesozooplankton due to predation by DVMs. The consumption of epipelagic zooplankton and the transport of this organic matter to the mesopelagic zone constitute the total active flux since this carbon is then defecated, excreted, and respired. Diel migrants can also be eaten at depth; thus growth due to feeding at the surface layers is also transported to depth. The control by these migrators on epipelagic mesozooplankton (Hopkins *et al.*, 1996) gives rise to a succession of zooplankton biomass peaks in shallower layers (Hernández-León *et al.*, 2004). Mesozooplankton abundance and biomass were observed to change with the lunar cycle in the oceanic waters of the Canary Current (Hernández-León, 1998; Hernández-León *et al.*, 2002, 2004). This pattern is similar to the changes observed in lakes (Gliwicz, 1986), where zooplankton show a lunar cycle decreasing due to predation by zooplanktivorous fish during the dark phase of the moon. During the illuminated phase, these fishes remain near the bottom of the lake to avoid carnivores, allowing zooplankton to grow free of predation. Diel vertical migration in the ocean is also a mechanism to avoid predation. Migrants remain in the dark during the daytime and migrate to shallower layers at night to feed. To avoid predation, during the illuminated period of the lunar cycle, DVMs do not reach the shallower layers (< 100 m), as observed long ago (Moore, 1950). The absence of DVMs in the upper layers of the ocean during this lunar phase (Pinot and Jansà, 2001) results in a decrease in the predatory pressure and allows oceanic epipelagic (nonmigrating) zooplankton to increase in abundance (Hernández-León, 1998; Hernández-León *et al.* 2001) and biomass (Hernández-León *et al.*, 2002, 2004). By contrast, during the dark period, the interzonal migrants reach the upper layers of the ocean (< 100 m) preying upon the epipelagic zooplankton crop. The variability in abundance was observed as proportional changes in the main species of

copepods (Hernández-León, 1998), but depending on season, as also observed in lakes (Gliwicz, 1986).

The different predatory scenarios during the winter bloom in the Canary Current provide an opportunity to study the response of plankton communities to the winter enrichment, as well as the predatory cycle related to the lunar phase. The results presented here show a clear lunar pattern in the outburst of mesozooplankton during winter. We also estimated an important consumption of carbon by the migrant biota, which suggests that we could be missing a major component of the biological pump if this active flux is not considered.

Methods

Hydrological parameters, chlorophyll, and zooplankton biomass were measured weekly at five stations around Gran Canaria Island (Canary Islands). Sampling was performed from October 2005 to June 2006 at the edge of the island shelf (Figure 3.5.1). Dust deposition rates were measured fortnightly following standard procedures (Goossens and Offer, 1994) at three sites on Gran Canaria Island: one to the north at an altitude of 300 m and two at the south of the island at 15 and 140 m (Figure 3.5.1). Briefly, simple dry glass trays (Pyrex) were used to collect dust particles. In order to fully detach dust grains adhered to the collection surface, the trays were rinsed with deionized water into glass bottles, scraping the material adhered to the glass with a rubber spatula. The sample was dried at 50ºC in an oven.

Vertical profiles of temperature, conductivity, and fluorescence were obtained using a conductivity, temperature, depth probe (SBE25 Sea-Bird Electronics) equipped with an *in situ* fluorometer. Phytoplankton chlorophyll was derived from depth profiles of *in situ* fluorescence, calibrated with samples collected at 15-m depth with a Niskin bottle. Chlorophyll was determined filtering 500 mL of seawater through Whatman GF/F filters, which were preserved in liquid nitrogen until analysis in the laboratory. Pigments were extracted in cold acetone (90%) for 24 h. These extracts were acidified, allowing chlorophyll and phaeopigments to be independently measured in a Turner Design fluorometer previously calibrated with pure chlorophyll.

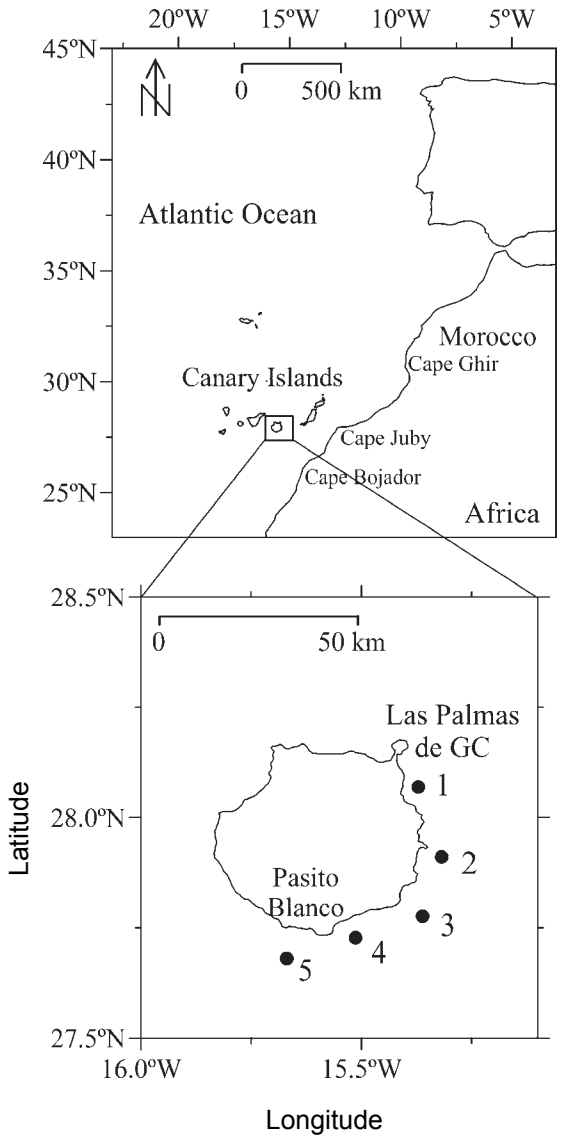

Figure 3.5.1. Map of the study area showing the location of the five sampling stations over 100-m depth at the edge of the shelf break around Gran Canaria Island. The dust deposition devices were installed in the north (Las Palmas de Gran Canaria) and south of the island (Pasito Blanco).

Zooplankton was captured in oblique hauls with a Bongo net equipped with 200-mm mesh nets. The sampler was hauled during daylight hours from 90-m depth to the surface at a speed of about 2–3 knots. A General Oceanics flowmeter was used to measure the volume of water filtered by the net. One of the zooplankton samples was preserved in 4% buffered formalin and used for taxonomic collection. The second sample was transported cold to the laboratory and dry weight measured using a standard procedure (Lovegrove,

1966). Samples were dried at 60ºC for 24 h and later weighed, first allowing the sample to reach room temperature and avoiding humidity.

In order to estimate predation by DVMs, we performed a simple and conservative model to simulate zooplankton biomass during the winter bloom using the criteria of previous works (Hernández-León *et al.*, 2002, 2004), considering

$$P=(B_1 - B_0) + M \quad (1)$$

where P is production of zooplankton, B_1 and B_0 are their biomass at time 1 and 0, respectively, and M is mortality. Then,

$$B_1 = B_0 + (B_0 \cdot g) - (B_0 \cdot m) \quad (2)$$

where g is the growth rate and m the mortality rate.

The model was tested for a rather large set of growth and mortality rates, but only the best simulations are presented for obvious reasons. The bloom was first simulated using a conservative value of daily growth of 0.1 d^{-1} and mortality as a function of the lunar illumination. Different minimum values of mortality were set during the full moon and maximum values during the new moon, coinciding with the presence of DVMs in the epipelagic zone. A second simulation set was performed by increasing maximum growth and mortality rates in order to find the best fit between observed and predicted biomass. Maximum growth rates were obtained from Hirst and Lampitt (1998) and ranged from 0.1 to 0.3 d^{-1}, the latter value being the growth rate predicted by Huntley and Lopez (1992) for a water temperature of 18ºC, the average temperature in the euphotic layer during the bloom. Minimum values of growth and mortality rates were taken from the literature (0.01 to 0.04 d^{-1}; Hirst and Lampitt, 1998). A third simulation set was made ascribing different maximum growth rates to each observed peak during the bloom. Finally, the daily community mortality was estimated as B·m each day. The estimated consumption of epipelagic mesozooplankton by DVMs was calculated assuming that daily mortalities were promoted by these organisms (see Discussion).

Results

Mixing in the water column started in December-January, and the higher values of chlorophyll were observed at the end of January (Figure 3.5.2A), coinciding with temperature below 19ºC, which indicate the suitable mixing conditions for the bloom (Hernández-León *et al.*, 2004; Moyano *et al.*, 2009).

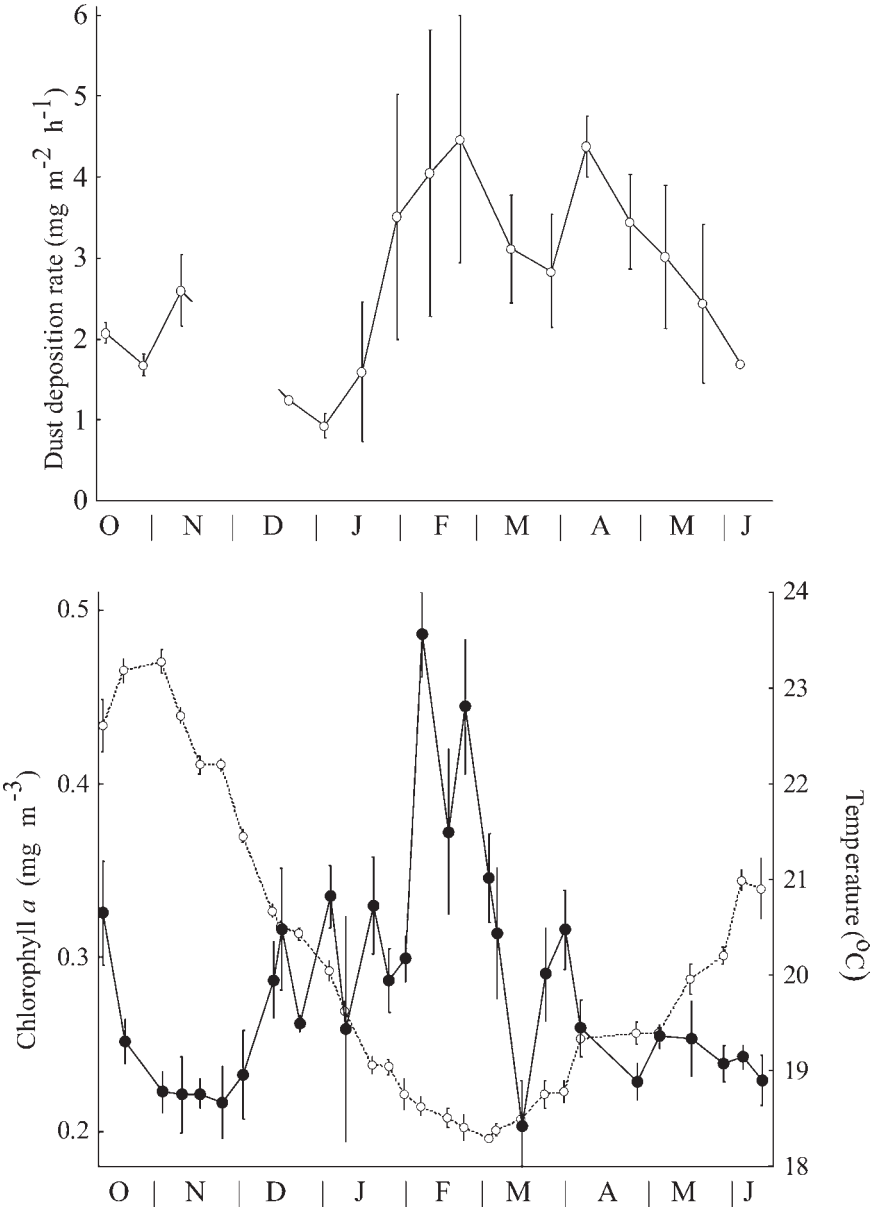

Figure 3.5.2. (A) Dust deposition rates from October 2005 to June 2006, and (B) time series of temperature and chlorophyll in the mixed layer. Vertical bars represent standard error. Observe the increase in chlorophyll coinciding with the increase in dust deposition rates.

This bloom also coincided with the highest dust deposition during winter. This event occurred from the end of January to mid-April (Figure 3.5.2B), in agreement with the high deposition observed by other authors during the same year in the Atlantic Ocean (Lau and Kim, 2007). Mesozooplankton biomass, however, showed an increasing trend from December through March, displaying a clear lunar cycle pattern (Figure 3.5.3). Zooplankton should continuously increase during the development of the phytoplankton bloom. However, a periodic increase and decrease in epipelagic mesozooplankton biomass coupled with every lunar cycle was observed.

Standardizing the biomass values during the winter bloom (from January to March), taking maximum values of biomass in every lunar cycle as 100%, we observed that biomass was significantly lower during the first quarter of the moon (from new moon to crescent moon) and maxima during the illuminated phases of the lunar cycle (Figure 3.5.4). A significant positive correlation (r^2 = 0.533, $p < 0.05$) was also found between lunar illumination and mesozooplankton biomass.

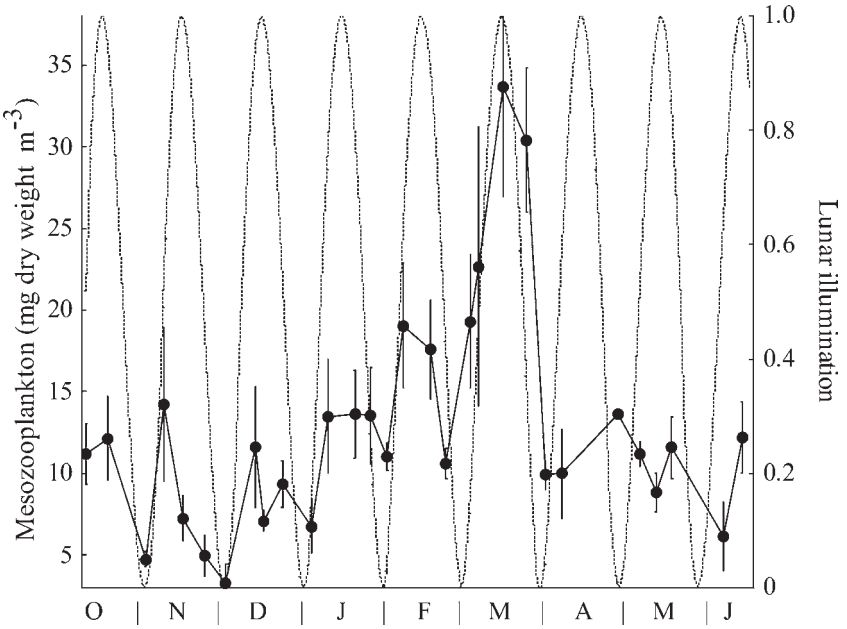

Figure 3.5.3. Time series of mesozooplankton biomass and lunar illumination (dashed line) from October 2005 to June 2006. Vertical bars represent standard error. Lunar illumination is scaled relative to maximum brightness. Observe the lunar cycle in mesozooplankton biomass as the mixing develops through winter (from December to March).

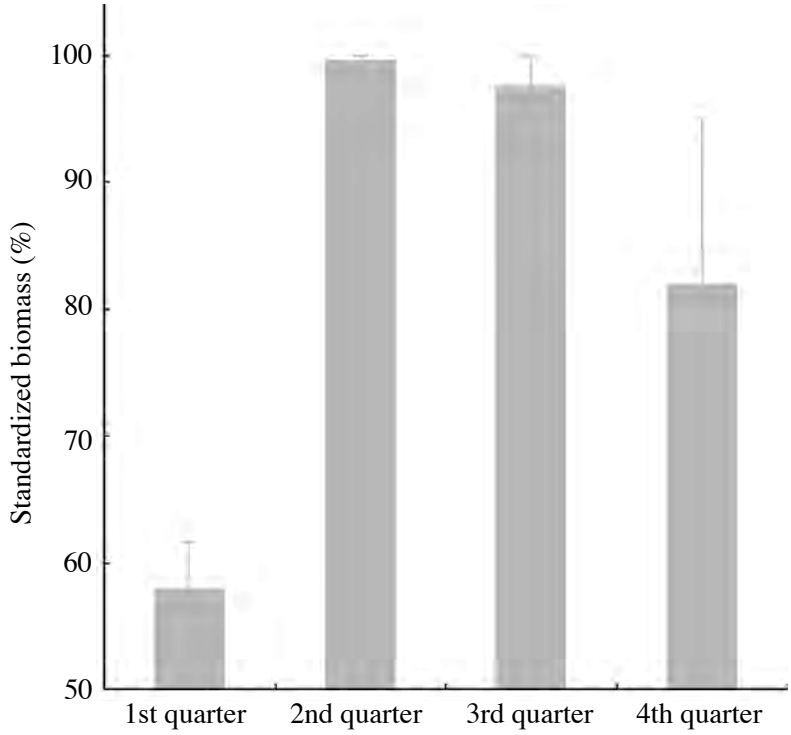

Figure 3.5.4. Standardized biomass (maximum value of biomass in each lunar cycle converted to 100%) during the late winter bloom in the Canary Island waters.

The results of the model to estimate DVM-induced mesozooplankton mortality showed a lag of 11 d between true and predicted biomass when growth rate was set constant and mortality as a function of lunar illumination. This lag only disappeared when maximum growth rate was set 10 d before full moon following a sinusoidal pattern (Figure 3.5.5A, B). Using different maximum growth rates for every peak, we obtained a more realistic match between true and predicted biomass (Figure 3.5. 5C). In any case, good agreement was observed between the predicted and the measured mesozooplankton biomass in both cases (Table 3.5.1). The obtained values of community mortality also followed the lunar pattern as expected (not shown). The use of maximum growth and mortality rates for the three mesozooplankton biomass peaks (Table 3.5.1, upper panel) or different maximum growth rates for every peak (Table 3.5.1, lower panel) did not promote markedly different values of community mortality. Those values ranged between 1.6 and 2.8 mmol C m^{-2}·d^{-1} for the first peak, before the bloom, and between 2.7 and 6.3 mmol C m^{-2}·d^{-1} during the bloom.

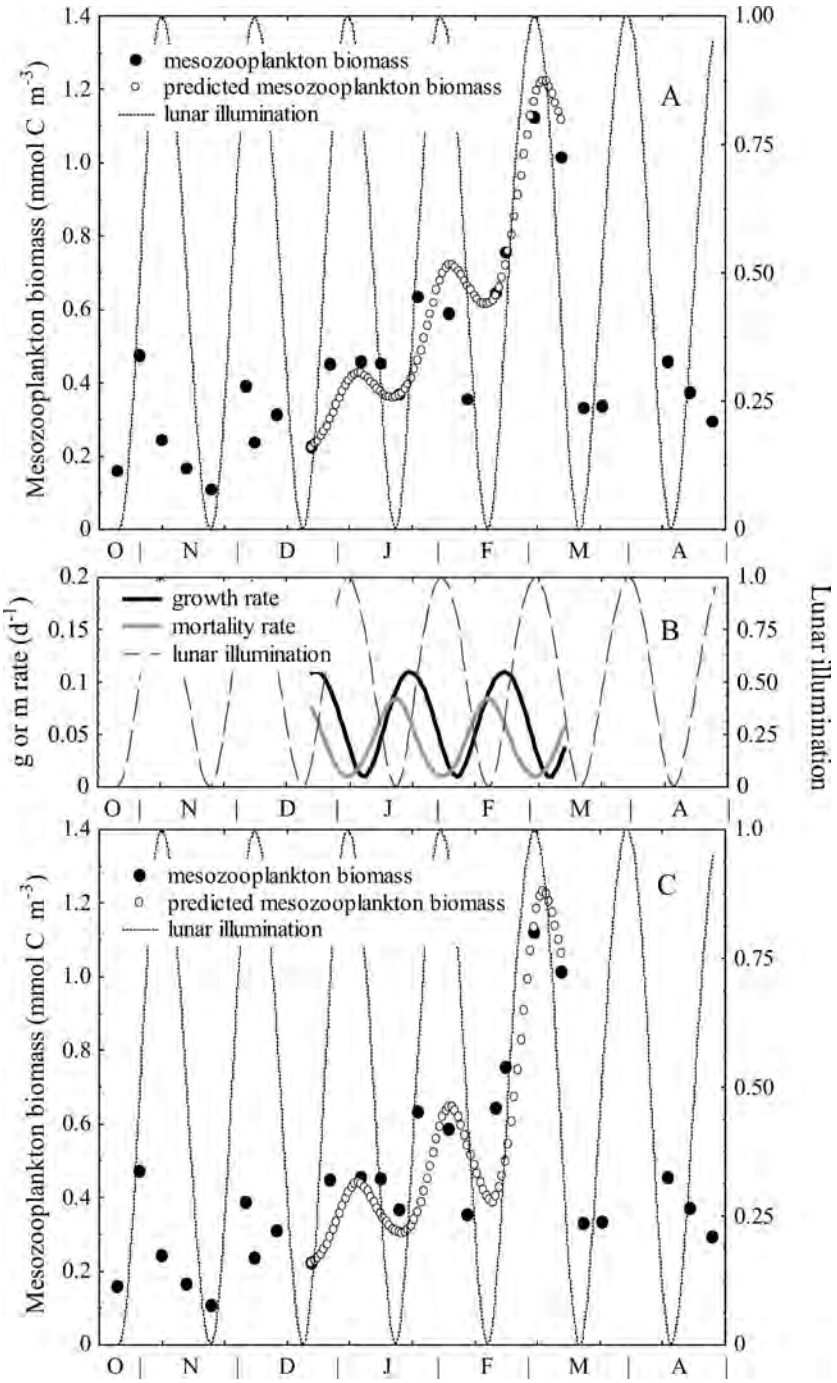

Figure 3.5.5. (A) True (filled circles) and predicted (open circles) mesozooplankton biomass (*r* = 0.902, p < 0.001) according to the lunar illumination (dashed line). (B) Growth and mortality rates used to simulate the biomass in (A). Maximum growth rate was set within waxing moon (g = 0.11 d^{-1}) and maximum mortality rate was set within new moon (m 5 0.08 d21). Minimum mortality and growth rates were 0.01 d^{-1} within full and waxing moon, respectively. (C) True (filled circles) and predicted (open circles) mesozooplankton biomass (r = 0.873, p < 0.001) according to the lunar illumination (dashed line). Maximum growth rate was set within waxing moon and it was different for every peak (first peak, g_1 = 0.13 d^{-1}; second peak, g_2 = 0.15 d^{-1}; third peak, g_3 = 0.18 d^{-1}). Maximum mortality rate was set within new moon and it was

different for every peak too (first peak, m_1 = 0.12 d^{-1}; second peak, m_2 = 0.15 d^{-1}; third peak, m_3 = 0.13 d^{-1}). Minimum mortality and growth rates were 0.01 d^{-1} within full moon and waning moon, respectively.

Discussion

The results show a clear lunar cycle in mesozooplankton biomass during the late winter bloom in these subtropical waters. The phytoplankton outburst was rather low compared with previous studies in the area despite the important dust deposition events observed. During the winter bloom in 2005, chlorophyll a (Chl *a*) values reached almost 1 mg Chl *a* m^{-3} (Moyano *et al.*, 2009), while in 2006 the highest values were around 0.5 mg Chl *a* m^{-3}. The difference could be explained by temperature differences between both years. Neuer *et al.* (2007) found that some years with lower temperatures during the timing of the bloom showed large chlorophyll values (see their Figure 8). However, the mesozooplankton boost was of the same magnitude in 2005 (Moyano *et al.*, 2009) compared with 2006. The different peaks of mesozooplankton were always linked to the lunar cycle (Hernández-León *et al.*, 2002, 2004; Moyano *et al.*, 2009), although these increases were not always observed during the same months. For instance, the two lunar-linked peaks observed in January and February in the present work were not found during the previous year (Moyano *et al.*, 2009). The latter authors found an increase in chlorophyll almost coinciding with the zoo- plankton bloom in March, while in the present work the increase in chlorophyll was observed at the end of January, coinciding with temperatures below 19ºC, but also with the increase in dust deposition, allowing the availability of iron and other nutrients (Duarte *et al.*, 2006). However, although the bloom coincided in time with the dust deposition, the phytoplankton outburst was rather low. It is known that microzooplankton is able to control a rather large portion of primary production in the world oceans (Calbet and Landry, 2004), and the waters around the Canary Islands are not an exception. Therefore, we wonder whether an increase in microzooplankton was also able to control primary production. The processes engaged in the development of the bloom in subtropical waters are rather complex and still not fully understood.

Table 3.5.1 Daily community mortality values modeled in accordance with different growth and mortality rates in the case that the same maximum rate values were used during the bloom (upper panel) and in the case that different maximum rate values were used for every peak (lower panel) (g_1, m_1, and M_1 are first peak values; g_2, m_2, and M_2 are second peak values; and g_3, m_3, and M_3 are third peak values).

Minimum growth and mortality rate (d^{-1}), bloom	Maximum growth rate (d^{-1}) g	Maximum mortality rate (d^{-1}) m	Correlation (r)	Significance (p)	Daily community mortality (mmol C m^{-2} d^{-1})		
					M_1	M_2	M_3
0.01	0.11	0.08	0.902	<0.001	1.6	2.7	3.1
0.02	0.13	0.09			2.0	3.4	4.1
0.03	0.14	0.10			2.4	4.1	5.2
0.04	0.15	0.11			2.8	4.8	6.3

Minimum growth and mortality rate (d^{-1}), peak	Maximum growth rate (d^{-1})			Maximum mortality rate (d^{-1})			Correlation (r)	Significance (p)	Daily community mortality (mmol C m^{-2} d^{-1})		
	g_1	g_2	g_3	m_1	m_2	m_3			M_1	M_2	M_3
0.01	0.13	0.15	0.18	0.12	0.15	0.13	0.873	<0.001	1.8	2.9	3.3
0.02	0.14	0.16	0.19	0.13	0.16	0.14			2.1	3.4	4.1
0.03	0.15	0.17	0.20	0.14	0.17	0.15			2.4	3.8	4.9
0.04	0.16	0.18	0.21	0.15	0.18	0.16			2.7	4.2	5.7

Moreover, the presence or not of these mesozooplankton biomass peaks during the winter bloom are also unknown. For instance, the mesozooplankton outburst was observed in January and February during 2000 (Hernández-León *et al.*, 2004), as in the present work, but not in 2005 (Moyano *et al.*, 2009). In contrast to some previous works, the zooplankton lunar pattern observed during late winter in the present work showed biomass peaks that were centered near the full moon (Figures 3.5.3, 3.5.4). Hernández-León *et al.* (2004) found the biomass increase during the illuminated phase of the lunar cycle and the maximum near the waning moon. They explained this pattern as the effect of high growth rates of zooplankton counteracting mortality until the latter surpassed the former as darkness progressed through the lunar cycle. Thus, the interplay between both rates promotes the biomass to peak around the full moon. Using the simple model described in the methods section, we were able to assess mortality during the different mesozooplankton lunar cycles. Growth rates used to simulate the bloom (Table 3.5.1) were approximately half the value of 0.3 d^{-1} predicted by Huntley and Lopez (1992) for the average temperature in the euphotic layer during the bloom. Therefore, we consider our approach to be conservative. The match between true and predicted biomass was found when maximum growth rates were set 10 d before the maximum biomass. Previous estimations of grazing by mesozooplankton in relation to the lunar cycle showed sharp increases in gut fluorescence about 10 d before the maximum biomass (Hernández-León *et al.*, 2004; see their figure 3.5.6). Thus, an increase in growth rates should also be expected to coincide with maximum grazing. The estimated values of consumption during the first biomass peak observed before the bloom (range 1.6-2.8 mmol C $m^{-2}·d^{-1}$ in January, Table 3.5.1) were comparable with two previous estimations (Hernández-León *et al.*, 2002, 2004) obtained north of the Canary Islands, which gave average values of 1.9 for May 1999 and 2.9 mmol C $m^{-2}·d^{-1}$ for February–March 2000. The second and third peaks found in the present work showed considerably larger average values (range 2.7-6.3 mmol C $m^{-2}·d^{-1}$). In the oceanic zone of the Canary Current, north of the Canaries, gravitational flux estimates (Neuer *et al.*, 2007) using sediment traps average 0.7 mmol C $m^{-2}·d^{-1}$, compared with

2.4 mmol C $m^{-2}·d^{-1}$ in Bermuda (Michaels and Knap, 1996) and 2.3-2.4 mmol C $m^{-2}·d^{-1}$ in Hawaii (Karl *et al.*, 1996). Thus, our estimates of mortality during the first peak (similar to previous ones) are similar to average values of gravitational flux in Hawaii and Bermuda in a nonbloom scenario. However, these values of mortality are two- to fourfold greater than the average values of gravitational flux in the Canary Current given by Neuer *et al.* (2007) and on the order of or higher than export flux (0.7-2 mmol C $m^{-2}·d^{-1}$) found by Alonso-González *et al.* (2009) also in the Canary Current from spring to autumn. Moreover, our average values during the bloom were two- to fourfold greater than the highest value of gravitational flux (~ 1.3 mmol C $m^{-2}·d^{-1}$) recorded in the Canary Current by Neuer *et al.* (2007), and on the order of or higher than the highest records of gravitational flux observed in the Canary basin (3-4 mmol C $m^{-2}·d^{-1}$) by Alonso-González *et al.* (2009), and in Bermuda (Michaels and Knap, 1996) and Hawaii (Karl *et al.*, 1996) of about 6 mmol C $m^{-2}·d^{-1}$. Different observations, reviewed by Pearre (2003), indicate that diel migrants reach the shallower layers at dusk, feed until their guts are full, and then, asynchronously, migrate downward to avoid predation. Moreover, gut clearance rates in micronekton were observed to be long enough for the downward migration to have been completed before evacuation occurs (Baird *et al.*, 1975). In addition, fecal matter of mesopelagic fish show fast sinking rates (average of 1028 $m·d^{-1}$), much higher than copepod or euphausiid fecal pellets (Robison and Bailey, 1981). The latter authors also observed that the release of dissolved organic compounds is low and does not represent a significant output during sinking. This rapid sinking and slow dissolution promote a higher efficiency in the flux of carbon to the deep sea. Moreover, this community is composed of a large percentage of fishes, and these organisms produce precipitated carbonates that are defecated and transported downward (Wilson *et al.*, 2009). We wonder whether these large pellets are efficiently sampled by sediment traps. Thus, if we assume that a high percentage of the mesozooplankton consumed at shallower layers is transported to the mesopelagic zone by DVMs, the estimated active flux values are, at least, of the same magnitude as the gravitational flux normally found in subtropical waters. The role of this rather large fauna has scarcely been considered in previous works about active flux. Diel migrants are

normally sampled using unsuitable nets for micronektonic organisms. This bias in the measurement of DVM biomass could give rise to an important underestimation of the active flux in the ocean. In this sense, Hidaka *et al.* (2001) assessed active flux by mesozooplankton and micronekton in the western equatorial Pacific Ocean. Their results showed that flux due to micronektonic organisms was 56-60% of total active flux. Therefore, values of this flux based only on the mesozooplankton fraction (Hernández-León and Ikeda, 2005a) are clear underestimates. Micronekton biomass in the mesopelagic zone has not been well evaluated. As an exception, the biomass of myctophid fishes were estimated to be 0.7-18.5 g wet weight·m^{-2} (average of 7.2) in the world oceans (Hernández-León and Ikeda, 2005a). Assuming that dry weight of myctophids is 20% of wet weight and carbon forms 40% of dry weight, only myctophid biomass should be on the order of 48.3 mmol C m^{-2}. Hernández-León and Ikeda (2005b) in their review of respiration in the ocean found an average biomass of mesopelagic mesozooplankton of 33.4 mmol C m^{-2} (± 25.5, n = 53). Although highly variable, these numbers indicate that micronekton is an important component of the mesopelagic fauna and should be included in studies of active flux. Unfortunately, sampling this community is rather difficult and time consuming, but, as indirectly observed in the present work, their transport is of paramount importance for the assessment of the role of the biological pump in the ocean.

Understanding of water column ecosystem functioning has also gained knowledge from iron fertilization experiments. However, most of the experiments performed were too short to unveil the role of mesozooplankton and micronekton on the biological pump. Very few measurements of zooplankton have been done in tropical and subtropical experiments, and the role of micronektonic organisms has been even more neglected. A high growth rate of mesozooplankton was observed during the iron fertilization experiment IronEx II, but a declining trend in their biomass was found (Rollwagen Bollens and Landry, 2000). The authors explained the declining trend in biomass as a probable effect of predation. Now, we know that this experiment was performed during the new moon, in a high predation scenario caused by DVMs. Similarly, Tsuda *et al.* (2005) did not find any increase in

mesozooplankton biomass in the Subarctic Pacific Iron Experiment for Ecosystem Dynamics Study (SEEDS) 2001 during summer. They only observed an increase of copepodite I of large copepods after waxing moon (day 9 after iron enrichment) at the end of sampling. However, during the SEEDS II experiment in summer 2004 (Tsuda *et al.*, 2007), copepod biomass increased inside and outside the fertilized patch to reach maximum values around waning moon (day 19 after iron enrichment). This biomass maximum after the full moon was also observed by Hernández-León *et al.* (2004) during the late winter bloom north of the Canary Islands. They explained the lag to reach the maximum values of biomass to the interplay between growth and mortality as argued above. The SERIES iron fertilization experiment showed also a clear increase of *Oithona similis* following the lunar cycle (new and full moon during days 1 and 15 after iron enrichment, respectively), especially in the mixed layer (Sastri and Dower, 2006). In this fertilization, the increase in biomass of large copepods was observed to peak around the waning moon (Tsuda *et al.*, 2006), as in the SEEDS II experiment. Accordingly, the role of predation on epipelagic zooplankton by DVMs and its biogeochemical consequences to the biological pump in the ocean should be seriously considered. In summary, we show that downward carbon transport in subtropical waters does not end with the sinking of the organic carbon produced in the shallower layers. In fact, the process is much more complex, and part of the production is shunted to the mesopelagic zone by DVMs. Our results shed some light on the uncoupling between primary production and particle export flux in the ocean (Michaels *et al.*, 1994; Karl *et al.*, 1996) and explain the 30-d periodicity in the gravitational flux observed in the oceanic waters of the Canary Current (Khripounoff *et al.*, 1998). In addition, this active flux could explain, at least in part, the unaccounted downward organic flux promoting the carbon demands of bacteria and zooplankton in the mesopelagic zone (Steinberg *et al.*, 2008). Moreover, geochemical estimates of new production are in the range of 6.8-14.6 mmol C $m^{-2} \cdot d^{-1}$ (Maiti *et al.*, 2009), much higher than sediment trap measurements, but near the addition of gravitational and our conservative estimates of active fluxes. Thus, our results suggest a pivotal role of epipelagic zooplankton and DVMs in the biological pump and give insights into the fate of a bloom. Because of the

importance of micronektonic migrants in the active flux (Hidaka *et al.*, 2001) it is important to assess the biomass, feeding, and metabolism of this community, which in fact is a gap in our knowledge of the ocean. In any case, the lunar cycle-linked active flux described here for subtropical oligotrophic waters represents an important and unaccounted flux of carbon to the mesopelagic zone that deserves further research. The finding of DVM movements at 800-1300 m depth following the lunar cycle (van Haren, 2007) also gives insight into a ladder of migration (Vinogradov, 1970) of valuable consequences for carbon transport to the deep sea.

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IV· DISCUSSION

Diel vertical migration behaviour of marine zooplankton represents the largest biomass movement on earth. Previous studies evidenced the high variable contribution of the diel vertical migrants (DVMs) to the biological pump. Compared to the passive particulate organic carbon flux, the values of active flux ranged from <1 to >70% (Table 4.1 and references therein). Theses studies mainly used size-specific metabolic rates based on a multivariate regression (Dam *et al.*, 1995; Zhang and Dam, 1997; Roman *et al.*, 2002), taxon-specific incubations (Steinberg *et al.*, 2000), mixed crustacean incubations (Isla and Anadón, 2004) and very few studies used the ETS enzymatic assay on the total zooplanktonic community to determine the active carbon flux (Hernández-León *et al.*, 2001; Yebra *et al.*, 2005). In this work, active fluxes due to the DVMs were estimated in the Northeast Atlantic subtropical gyre using the ETS activity as a routine method jointly with a community metabolic budget approach. The results of this work extended the previously published estimations of zooplankton active flux and suggest that diel vertical migration impact on the biological pump is much more variable than previously thought with values ranging from <1% to 119% of the passive POC flux. Causes for this high variability are mainly related to productivity in the upper layers, seasonality, mesoscale structures, feeding behaviour, and the moonlight influence.

The production cycle in subtropical waters is characterized by the late winter bloom (Menzel and Ryther, 1961). This bloom is produced due to the erosion of the thermocline driven by surface cooling in winter that enhances vertical diffusion of nutrients from below the mixed layer. Its influence in relation to the particle formation, transformation and passive POC flux is already known (Neuer *et al.*, 2002). The late winter bloom in the Canary Island waters is also fairly well known from the standpoint of plankton biomass and production (De León and Braun, 1973; Arístegui *et al.*, 2001; Hernández-León, 2004).

Table 3.4.2. Zooplankton active flux estimated in different oceanic regions.

Location	Time of year	Migrant biomass (mg C·m^{-2})	Respiratory flux (mg C·m^{-2}·d^{-1})	Gut flux (mg C·m^{-2}·d^{-1})	% of POC flux	References
Oligotrophic area						
HOT		30.2 - 33.8	1.3-1.7	-	4[a]	Roman et al., 2002
Equator divergence		2.8 - 21.8	0.9-1.2	-	<1-2[a]	Roman et al. (2002)
BATS	March/April	192 (84–540)	14.5 (6.2-40.8)	-	34 (18-70)[a]	Dam *et al.* (1995)
BATS	year-round	50 (0-123)	2.0 (0-9.9)	-	8 (0-39)[b]	Steinberg *et al.* (2000)
BATS	year-round	83 (0.7-468)	-	0.8 (0.007-4.5)	4 (0.03-21)[c]	Schnetzer and Steinberg (2002)
Western Equator	October	46.9	3	-	6	Le Borgne and Rodier (1997)
North (Oceanic)	Oct-Nov	30 ± 10	2.2 ± 0.3	-	-	Isla and Anadón (2004)
Eastern Equator	March - April	96 ± 25.2	4.2 ± 1.2	-	18[a]	Zhang and Dam (1997)
Eastern Equator	October	154.8 ± 32.4	7.3 ± 1.4	-	25[a]	Zhang and Dam (1997)
ALOHA	Year-round	162 (108-216)	3.6 (2.6 - 19.1)	-	15 (12-18)[a]	Al-Mutairi and Landry (2001)
ALOHA	June - July	157.9	3.7	-	18[a]	Steinberg et al. (2008)
Eu- Meso-trophic area						
Central Equator (HNLC)	October	52.9	6	-	4[a]	Le Borgne and Rodier (1997)
North (coastal)	Oct-Nov	360 ± 70	30.3 ± 1.9	-	-	Isla and Anadón (2004)
North (poleward current)	Oct-Nov	270 ± 210	10.4 ± 6.3	-	-	Isla and Anadón (2004)
Western Equator	October	46.9	3	-	6[a]	Le Borgne and Rodier (1997)
Western Equator	February	367 (144 - 447)	22.7 (7.3-19.1)	4.8 (2.6-4.4)	24 (13-35)[a]	Hidaka et al. (2001)
Canary Current						
Canary Islands	March	204 (108 - 341)	0.8 (0.5-1.4)	0.1 (0.05-0.18)[e]	1.8 (1.1-2.7)[d]	Chapter 3.2
Canary Islands	June	580 - 1280	1.8 - 8.3	0.1 - 0-4[e]	15-53[d]	Yebra et al. (2005)
Canary Islands	August	247 - 125	4.2 - 1.9	0.3 - 2.4[e]	20-45[d]	Hernández-León et al. (2001a)
26ºN	Sept-Oct	325 (106 - 486)	0.6 (0.02 - 1.2)	0.8 (0.01 - 3.0)[e]	3.3 (0.1-9.0)[f]	Chapter 3.3
	May-June	314 (163.2 - 408)	2.3 (1.7 - 3.4)	0.2 (0.03 - 0.4)[e]	47.8 (26.9-64.4)[f]	Present chapter
21ºN	Sept-Oct	857 (368 - 1601)	6.5 (1.1 - 14.9)	22.7 (1.3-96.1)[e]	66.0 (0.1-149.5)[f]	Chapter 3.3
	May-June	314 (426.4 - 4480)	2.3 (2.7 - 48.6)	9.5 (0.05-28.0)[e]	118.6 (29.1-273.7)[f]	Present chapter

[a] %POC flux represents only respiratory flux. [b]Active flux includes DOC. [c]Active flux represents only gut flux. [d]Respiratory flux plus gut flux. [e]Gut flux assessed with GF.

[f]Potential ingestion assessed from respiration.

The influence of this productive pulse on the active carbon export flux mediated by diel vertical migration has been quantified for the first time in the present study. An increase in the proportion of active flux compared to the POC flux at the end of the bloom was observed (Chapter 3.1; Figure 3.2.6). This increase of the active carbon export flux could determine the transport and fate of the organic matter annually produced in the subtropical ocean.

The link between the seasonality of the upwelling and the mesozooplankton biomass was previously observed by Postel (1990) and Hernández-León *et al.* (2007). However, the effect of seasonality in the active carbon export flux mediated by the DVMs has not been assessed until now (Chapter 3.4). The average migrant biomass and the epipelagic biomass (0-200 m) were 2 to 5.8-fold higher during spring compared to fall (Chapter 3.4, Table 3.4.1), and the total contribution of the migrant community to the active carbon flux was 3.4 to 3.7-fold higher during spring (Table 3.4.1). The contribution of the active carbon flux by DVMs to the POC flux responded coherently to the contrasting seasonal conditions, showing higher active export during spring than in fall. On average, the drawdown of carbon increased approximately 4 folds in spring compared to the fall period. The intensity of the upwelling enhance productivity during spring and, consequently, increase locally the amount of carbon drained to deep waters by migrant zooplankton.

Another cause for a higher contribution of DVMs to the active carbon flux is the high variability promoted by mesoscale hydrographic structures such as eddies, the upwelling areas along the African coast, filaments, meanders and fronts, which are typical features of the area studied. The Canary Current flow is characterized by the strong disruption promoted by the Canary Archipelago, forming a downstream region of high mesoscale and macroscale activity. This area was recently described as the Canary Eddy Corridor (CEC; Sangrà *et al.*, 2009). The CEC is an area of high variability in productivity that convey water masses and export the planktonic production from the meso-eutrophic coastal upwelling system to the oligotrophic ocean. Further south, the Cape

Vert Frontal Zone (CVFZ) is a highly productive area influenced by the quasi-permanent upwelling off Cape Blanc and a thermohaline front.

The active carbon fluxes found in the area not influenced by the mesoscale structures, north off the Canary Islands, showed to be 1 to 5-fold lower than in the southern part of the archipelago (Chapter 3.2; Table 4.1). Only few estimates accounted for more than 25% of the POC flux, and those were mostly related to estimations carried out in areas characterized by the presence of mesoscale structures identified in this work (upwelling, thermohaline front, meanders, eddies; Figure 4.1).

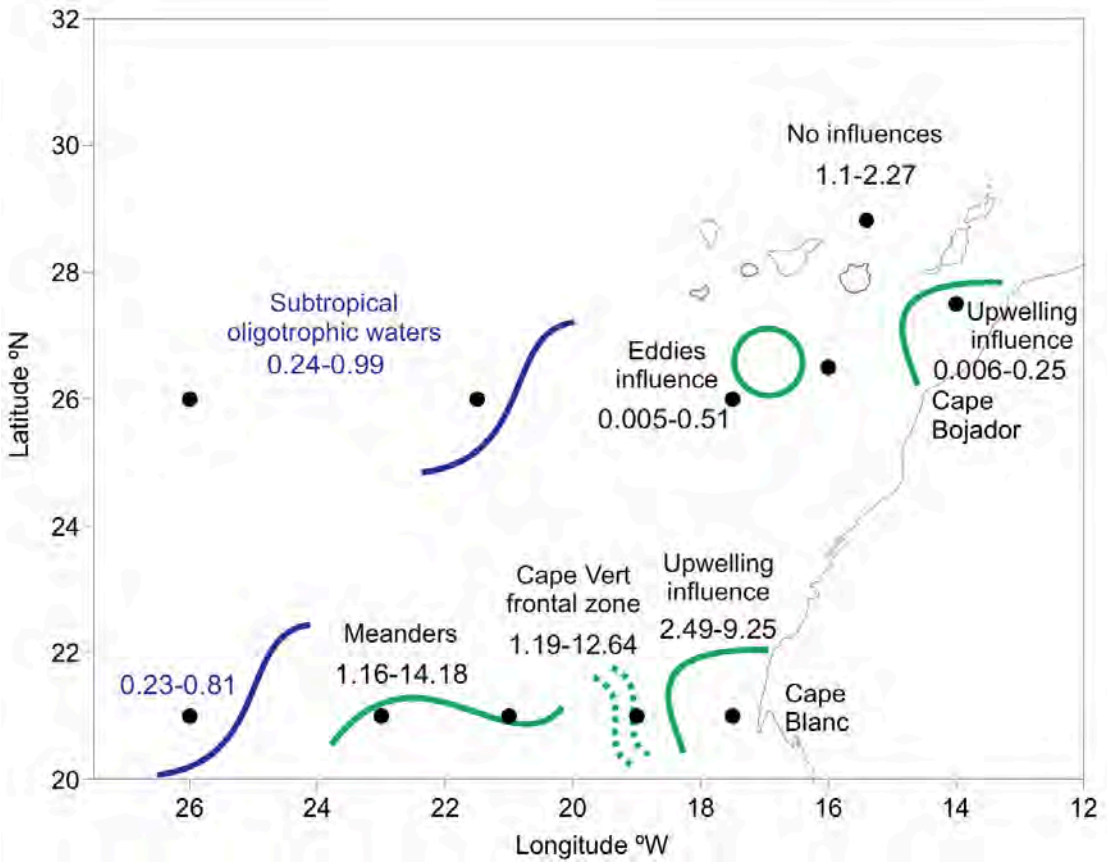

Figure 4.1. Main mesoscale structures, influence areas and maximum active carbon flux values measured (in mmolC·m^{-2}·d^{-1}) during spring and fall period respectively.

These hydrological structures could enhance primary production, concentrate the epipelagic biomass and allow a higher amount of prey for the migrant community.

The importance of seasonality and mesoscale structures is rather clear in the high variability observed in zooplankton active flux values. However, it

is not always evident which process contributes at any given location as the effects interact among them.

Thus, the variability is difficult to trace. However, the use of the metabolic budget (respiration, potential ingestion and the omnivory index) of the migrant community compared to the epipelagic community showed to be a powerful tool to assess the effect of the migrant community (Chapters 3.2; 3.3; 3.4). In fact, food availability is the starting point of metabolism and the influence of the diet and and changes in feeding have been shown to modify the active carbon fluxes (Chapter 3.2; Figure 3.2.6). The zooplanktonic epipelagic community, as a food source, could be conditionning the migrant community in terms of low/high prey abundance. South of the Canary Archipelago was observed a latitudinal and longitudinal productivity gradient from North to South and from the African coastal upwelling area toward the open ocean, which affected the carbon fluxes mediated by DVMs (Chapters 3.3; 3.4). In the eutrophic waters of the upwelling area, the phytoplanktonic productivity is enhanced and large phytoplankton and zooplankton develops there, favouring migrants and shunting energy and matter through the macrobial pathway (Hernández-León, 2009), increasing the active carbon flux (Chapter 3.3; 3.4). By opposite, in oligotrophic waters the matter and energy produced is channelled through the microzooplankton toward the microbial pathway, reducing the amount of carbon available for the migrant community and active carbon flux (Chapter 3.3; 3.4). This explanation is plausible since >60% of the primary production in the Canaries region, as well as in other oligotrophic areas, can be attributed to picoplanktonic cells (<2 µm, Arístegui *et al.*, 2001), which are below the size of copepod food detection or preference (Calbet and Landry 1999). Non-pigmented organisms constitute a large portion (35-80%) of the diet of zooplankton in oligotrophic waters (Hernández-León *et al.*, 2001, 2002, 2004, Chapter 3.2; 3.3; 3.4), which agrees with the results of other authors working in oligotrophic waters (Dam *et al.*, 1995; Gaudy *et al.*, 2003).

Thus, the food availability of DVMs could be another cause for the high variability of the active carbon flux, depending at large on the productivity, the

structure of the food web of the areas under study and probably on the taxonomic composition.

The downward carbon transport in subtropical waters does not end with the sinking of the organic carbon produced in the shallower layers. In fact, the process is much more complex, and part of the production is shunted to the mesopelagic zone due to the predatory activity of DVMs on epipelagic zooplankton (Chapters 3.2; 3.3; 3.4; 3.5). Calculations based on the biomass disappearance of the zooplankton epipelagic biomass during the moon cycle showed values of active flux due to predation of 63% of the gravitational flux (Hernández-León *et al.*, 2002; Chapter 3.5). The estimated consumption and subsequent transport of epipelagic zooplankton biomass by DVMs after every full moon is on the order of the mean gravitational export and is an unaccounted flux of carbon to the mesopelagic zone, which may play a pivotal role in the efficiency of the biological pump. The biogeochemical consequences of the moonlight cycle to the biological pump in the ocean should be seriously considered. Moreover, the lunar cycle influence could explain also the 30 days periodicity in the gravitational flux (Khripounoff *et al.*, 1998) as well as the uncoupling between primary production and particle export flux in the ocean (Michaels *et al.*, 1994; Karl *et al.*, 1996).

Therefore, the model developed (Chapter 3.1) linked for the first time the vertical biomass movements, the metabolic processes and the active carbon fluxes. The light influence on the vertical distribution of zooplankton was sucessfully reproduced and the hypotheses used for this purpose support the effect of the interzonal fauna on epizooplankton during the moon cycle observed (Hernández-León, 1998; Hernández-León *et al.*, 2001, 2002; Chapter 3.5). In fact, these hypotheses could also explain the influence of the sunlight and the moonlight on the vertical migrations (Casper and Thorp, 2007; Van Haren, 2007; Hernández-León *et al.*, 2010); as well as the DVMs distribution during events such as eclipses (Sherman and Honey, 1970; Tarling *et al.*, 1999; Strömberg *et al.*, 2002; Economou *et al.*, 2008).

Thus, the results suggest a pivotal role of the epipelagic zooplankton and DVMs in the biological pump and give insights into the fate of a bloom.

Because of the importance of micronektonic migrants in the active flux (Hidaka *et al.*, 2001) it is important to assess the biomass, feeding, and metabolism of this community, which in fact is a gap in our knowledge of the ocean. In any case, the lunar cycle-linked active flux described for subtropical oligotrophic waters (Chapter 3.5) represents an important and unaccounted flux of carbon to the mesopelagic zone that deserves further research. The finding of DVM movements at 800-1300 m depth following the lunar cycle (van Haren, 2007) also gives insight into a ladder of migration (Vinogradov, 1970) of valuable consequences for carbon transport to the deep sea.

Finally, the data gathered in this work could be used to prove the robustness of the model proposed in Chapter 3.1. The preliminary results obtained from initial simulations (Figure 4.2 and Table 4.2) showed to fit accurately with *in situ* profiles. The integrated fluxes (Table 4.2) obtained with the model showed several differences compared to the *in situ* data, requiring further analysis. In this sense, the present work contributes about 70% of the information available for the Canary Current and 20% of the total published data about active carbon flux attributed to DVMs at a global scale. The use of all this information coupled to the above mentioned model will improve our knowledge of the importance of active flux in the ocean.

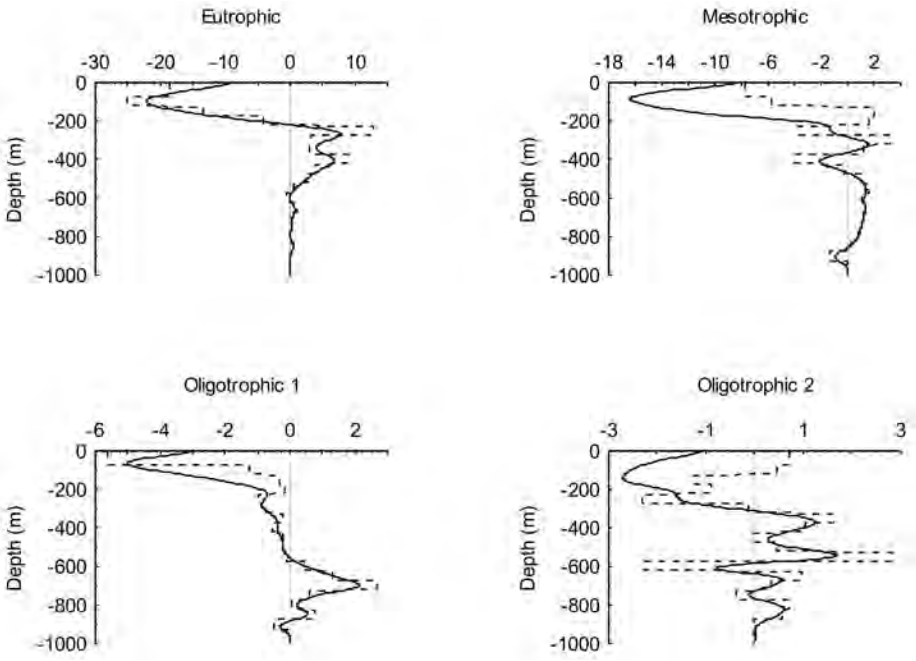

Figure 4.2. Day-minus-night comparison between zooplankton biomass from simulations (continuous line) and from *in situ* data (dashed line) for different trophic conditions.

Table 4.2. Comparison between simulations and *in situ* data for different trophic conditions. Migrant biomass (MB) in mmolC·m^{-2}, Respiratory flux (RF) in mmolC·m^{-2}·d^{-1}.

	Eutrophic		Mesotrophic		Oligotrophic 1		Oligotrophic 2	
	Simulated	*In situ*	Simulated	*In situ*	Simulated	*In situ*	Simulated	*In situ*
MB	250.7	254.5	157.1	55.6	55.7	50.1	40.9	47.9
RF	7.1	4.1	2.1	0.7	9.5	0.3	0.22	0.33

V· CONCLUSIONS

The main conclusions of this thesis are:

1. The model built reproduced both the migratory behaviour, in terms of speed and amplitude, as well as the active carbon flux of the large zooplankton. This model can be used as a predictive tool for oligotrophic waters.

2. The light forcing hypotheses used here support the effect of the interzonal fauna on epizooplankton during the lunar cycle and can be used to study the significant impact of this cycle on the active carbon flux.

3. The late winter bloom is much more complex than previously reported. The pelagic food web in the subtropical waters is governed by the interplay between resources and consumers. This interaction showed consequences on both the diet of migrant organisms and on the active carbon flux.

4. The productive pulse during the late winter increased the active carbon export flux due to diel vertical migration. Such increase gives an insight into the fate of a fraction of the organic matter annually produced in the subtropical ocean. This active carbon export during the late winter bloom has been quantified for the first time in this work.

5. The complex hydrological system south of the Canary Archipelago influenced the active carbon flux. The latitudinal and longitudinal high variability observed in the active carbon export flux is related to the local productivity, the food web structure, and the presence of mesoscale structures.

6. The active carbon export flux due to the diel vertical migrants responded coherently to seasonality with higher fluxes during spring. The seasonal differences observed affected both the zooplankton epipelagic biomass and the migrant biomass. This is the first study showing the link between the upwelling seasonal productivity and the active carbon export flux due to diel vertical migrants.

7. The active carbon export flux in the meso-eutrophic area was higher compared to the oligotrophic area, confirming once again the influence of the local productivity. Such local productivity increased the active carbon export flux and determined the transport and fate of a fraction of the organic matter annually produced in the study area.

8. The use of metabolic budget equations showed to be useful to trace the origin of the carbon actively exported by the migrant community. The metabolic budget also showed a diet adaptation of the migrant community to the epipelagic planktonic structure. The amount of carbon actively exported to the deep ocean can be linked to the planktonic structure of the superficial layers

9. During the moon cycle, the migrant community was responsible for a significant increase of the active carbon flux to the mesopelagic zone. This cyclical increase in the active carbon export is on the order of the mean gravitational export and was unaccounted until this study. Thus the lunar cycle should be recurring and it unmask the pivotal role in the efficiency of the biological pump.

VI· FUTURE RESEARCH

The results obtained in this thesis increased our knowledge on the active carbon flux due to the diel vertical migrants in the northeast Atlantic subtropical gyre and could be used as reference for future studies.

This work particularly highlights the high variability of the active carbon flux. The evolution, productivity and trophic relations between the epiplanktonic and the migrants communities deserves further research in order to determine the variability of the active carbon export flux.

A long term study of the active carbon export flux due to migrants (including the micronekton) should be considered in order to quantify the annual variability as well as the influence of the moon cycle on the amount of carbon annually transported to the mesopelagic layer.

The amount of data collected *in situ* from the different sampled areas and the hydrological conditions could be used to improve the robustness of the model and in addition, to perform a sensibility test to each parameters of the model.

Finally, the model proposed should be implemented and should include the moonlight influence. Also, the possible incorporation of this migration model to a regional model (Regional Ocean Modeling System, ROMs) should deserve further study.

VII · SPANISH SUMMARY

RESUMEN

Los océanos constituyen un sistema regulador clave del clima y también un depósito activo de carbono lo cual aumenta el interés general por el estudio del ciclo del carbono oceánico. En el contexto actual de control de las emisiones de CO_2 y su influencia sobre el cambio climático, las estimaciones del carbono transportado desde la atmósfera hacia las aguas profundas por la migración vertical diaria del zooplancton son críticos. En efecto, los organismos migradores juegan un papel clave en el flujo vertical de la materia particulada y disuelta en la columna de agua. Este trabajo contribuye a incrementar el conocimiento y la comprensión de los flujos activos de carbono debidos a los migradores verticales en aguas subtropicales. Este trabajo destaca como el impacto de la alimentación así como el flujo metabólico de los migradores deben ser considerados seriamente ya que este puede llegar a ser equivalente al flujo gravitacional en aguas subtropicales. El transporte de carbono hacia las capas profundas en aguas subtropicales no termina con el hundimiento del carbono orgánico producido en superficie. De hecho, el proceso es mucho más complejo, y parte de la producción es transportada a la zona mesopelágica por los migradores. Los resultados sugieren un papel fundamental del zooplancton epipelágico y de los migradores verticales en la bomba biológica y nos permiten comprender el destino de la materia producida durante un *bloom* de producción. Además, el pulso productivo debido al *bloom* de finales de invierno puede aumentar el flujo digestivo y debe también, ser considerado. En el área influenciado por la Corriente de Canarias, el gradiente de productividad así como la compleja diversidad hidrodinámica tiene un impacto profundo en términos de abundancia, actividad metabólica y composición del ecosistema epipelágico. La variabilidad mesoescalar, estacionalidad y también la abundancia de comida y la dieta de la comunidad migradora desempeña un papel importante en el transporte y destino de la materia orgánica producida anualmente en el océano subtropical. También, el vínculo entre el flujo activo y el ciclo lunar descrito en aguas oligotróficas subtropicales representa un importante, y hasta ahora no suficientemente valorado, flujo de carbono hacia la zona mesopelágica que requiere una mayor investigación en el futuro.

PRESENTACIÓN DE LA TESIS

El presente trabajo, titulado “Flujo activo de carbono en el giro subtropical del Atlántico Noreste” forma parte de una serie de estudios encuadrados dentro de los proyectos de investigación BREDDIES (REN2001-2650/ANT), MESOPELAGIC (CICYT, MAR97-1036), COCA (REN2000-1471-C02-02 MAR) y CONAFRICA (CTM2004-02319/MAR) realizados por el Grupo del Instituto de Oceanografía y Cambio Global (IOCAG), perteneciente a la Facultad de Ciencias del Mar (Universidad de Las Palmas de Gran Canaria, España). El Dr. Santiago Hernández-León ha dirigido y supervisado esta tesis doctoral junto con la Dra. Lidia Yebra Mora.

Esta tesis está dividida en dos partes. La primera ha sido escrita íntegramente en inglés y está dividida en Introducción, Metodología, Resultados, Discusión, Conclusiones y Líneas Futuras de Investigación. Por tanto, el resumen y las conclusiones de esta tesis están escritas de acuerdo a la normativa para la obtención de la Mención europea del Título de Doctor (BOULPGC. Art. 1 Capítulo 4, a 5 de noviembre 2008).

La segunda parte de la tesis está escrita en español y, de este modo, contiene 50 páginas en este idioma requeridas por el Reglamento de Elaboración, Tribunal, Defensa y Evaluación de Tesis Doctorales de Universidad de Las Palmas de Gran Canaria (BOULPGC. Art. 2 Capítulo 1, a 5 de noviembre 2008). Además, sigue la estructura exigida por este Reglamento: Introducción, Objetivos de la investigación y aportaciones originales, Planteamiento y Metodología, Resultados, Discusión, Conclusiones y Futuras Líneas de Investigación.

VII·1 INTRODUCCIÓN

7.1.1 El dióxido de carbono, importancia y problemática

El dióxido de carbono (CO_2), aunque se encuentra a baja concentración en la atmósfera (0,3%), actúa reteniendo la radiación infrarroja en las capas bajas de la atmósfera (Figura 7.1.1). El dióxido de carbono combinado con el vapor de agua y otros gases presentes en la atmósfera son responsables del llamado "efecto invernadero", esencial para el mantenimiento de una temperatura idónea para la vida en el planeta.

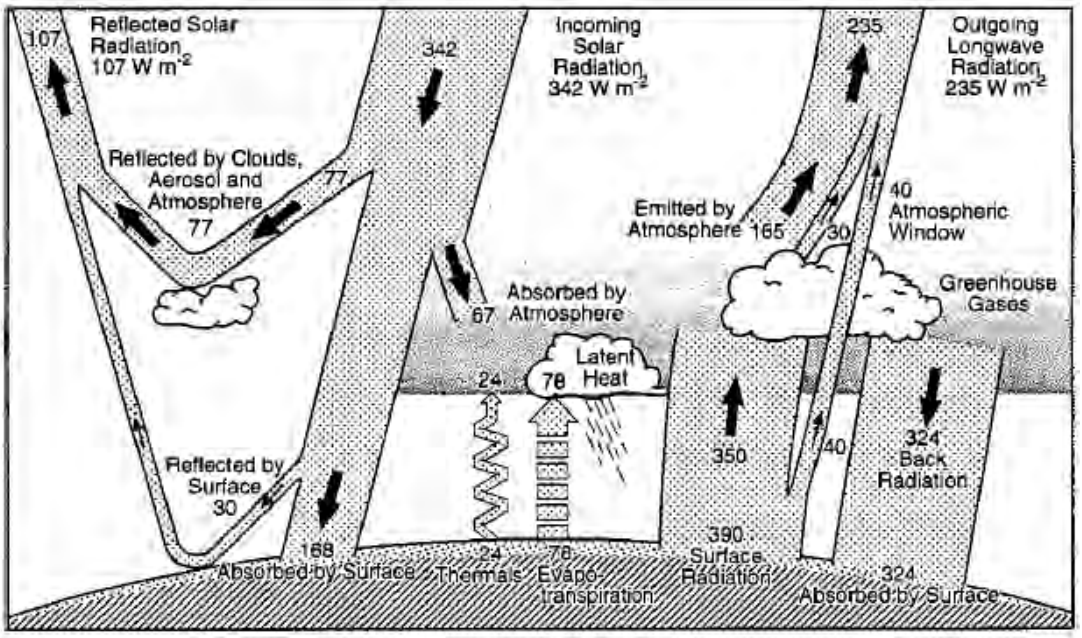

Figura 7.1.1. Balance energético medio del planeta (Unidades en $W \cdot m^{-2}$, Kiehl y Trenberth, 1997).

No obstante, la explotación y la quema de combustibles fósiles con el fin de sustentar las actividades industriales y de transporte libera grandes cantidades de dióxido de carbono hacia la atmósfera. Dicha emisión es hoy en día una preocupación para la humanidad y también una de las mayores agresiones que sufre el planeta, ya que el dióxido de carbono es un gas de efecto invernadero y el aumento de su concentración en la atmósfera es uno de los factores que provocan el "cambio climático". El término cambio climático está estrechamente vinculado al aumento de la concentración de dióxido de carbono en la atmósfera y al consecuente incremento del efecto invernadero al haberse modificado de forma drástica la concentración de CO_2. Este incremento en la concentración de CO_2 es debido a las emisiones derivadas de las actividades antropogénicas durante el último siglo (Figura 7.1.2).

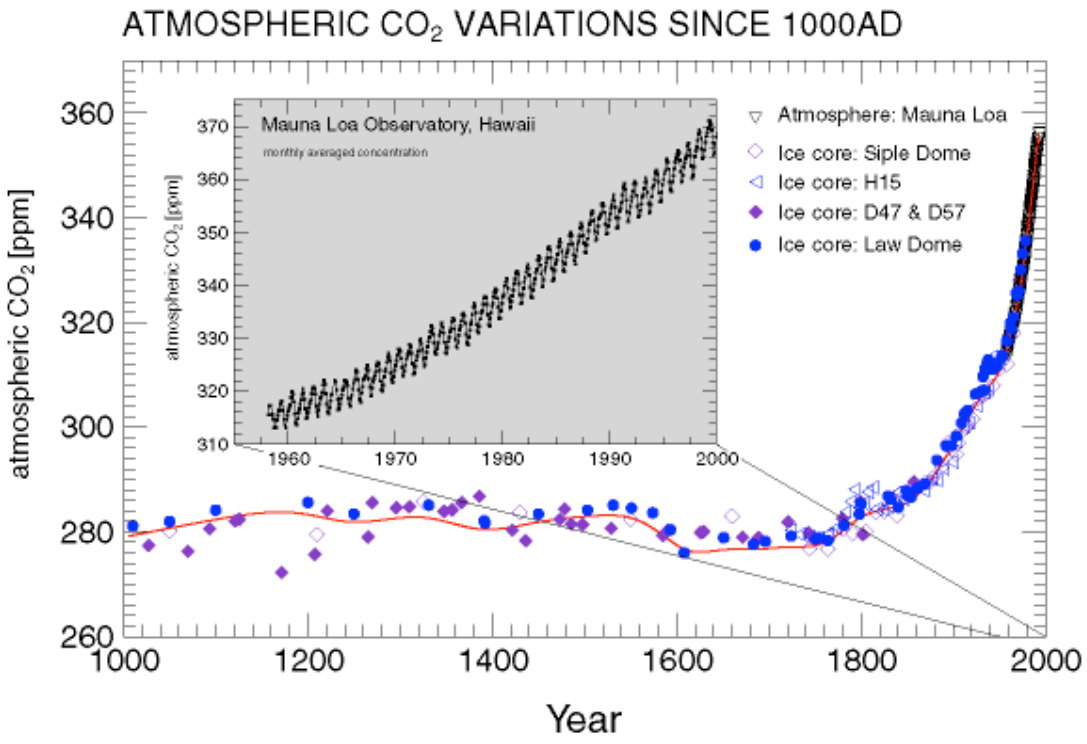

Figura 7.1.2. Evolución de los niveles de dióxido de carbono (Sarmiento y Gruber, 2002).

Datos procedentes de los glaciares indican que los niveles de CO_2 en al atmósfera han cambiado a lo largo de la historia. En el periodo pre-industrial (1000-1800) la concentración de CO_2 se situaba alrededor de 280 ppmv (590 Pg C, Etheridge *et al*., 1996), pero subieron drásticamente desde entonces para alcanzar los 366 ppmv en 1998 (775 Pg C, Holmén, 2000) y superar los 380 ppmv en 2004 (Varotsos *et al.*, 2007). Actualmente, la cantidad de CO_2 en la atmosfera según el *National Oceanic and Atmospheric Administration* es de 393 ppmv (Agosto 2012, Figura 7.1.3).

Por otra parte el dióxido de carbono también es vital para el crecimiento de los organismos autótrofos. Además, el carbono es el elemento que permite el transporte de la energía primaria, ya sea solar o química, a través de las redes tróficas de la biosfera. En la atmósfera, la hidrosfera y la litosfera el carbono circula en forma de materia y energía, tanto a través de los seres vivos (biosfera) como de la materia inerte (necromasa). El flujo de carbono a través del sistema litosfera-océano-atmósfera-biosfera, así como los procesos biológicos, geológicos, físicos y químicos que lo regulan, determinan y caracterizan el complejo ciclo de los compuestos orgánicos e inorgánicos del carbono.

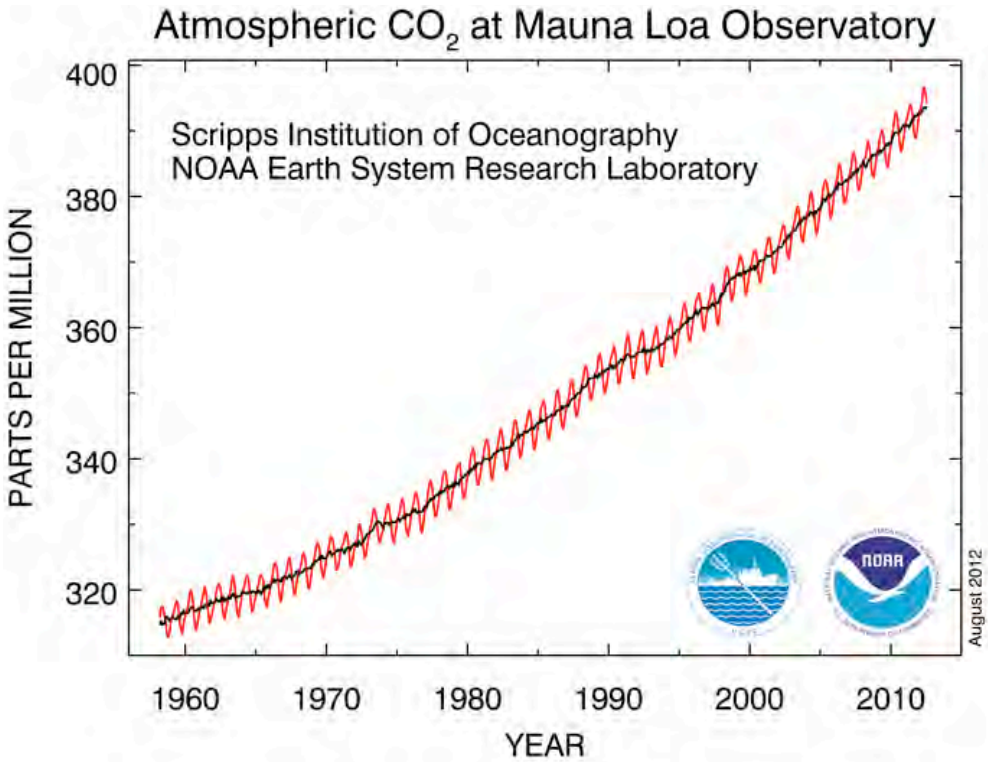

Figura 7.1.3. Evolución de los niveles de dióxido de carbono en la atmósfera (NOAA, http://www.esrl.noaa.gov/).

En este ciclo, algunas formas de carbono se acumulan a lo largo del sistema dando lugar a lo que se conoce como los grandes depósitos de carbono que son: la litosfera, el océano, la atmósfera y la biosfera (Figura 7.1.4). El ciclo del carbono, de importancia para la regulación del clima de la Tierra y con grandes implicaciones para el sostenimiento de la vida, ha sido y sigue siendo ampliamente estudiado. Se define como una sucesión de transformaciones que sufre el carbono a lo largo del tiempo. Además de la dimensión espacial, el ciclo del carbono comprende dos ciclos que suceden en escalas de tiempo diferentes:

- El ciclo biológico, que incluye los intercambios de carbono (CO_2) entre los organismos y la atmósfera (Field *et al.*, 1998; Joos *et al.*, 1999). Este ciclo es relativamente rápido y se estima que la renovación del carbono atmosférico se produce cada 20 años.
- El ciclo biogeoquímico que regula la transferencia de carbono entre la atmósfera, la hidrosfera y la litosfera (océanos y suelos), el cual es de larga duración que el ciclo biológico al verse implicados los mecanismos geológicos. La retención del carbono en este caso se cuenta en miles hasta millones de años (Falkowski *et al.*, 2000).

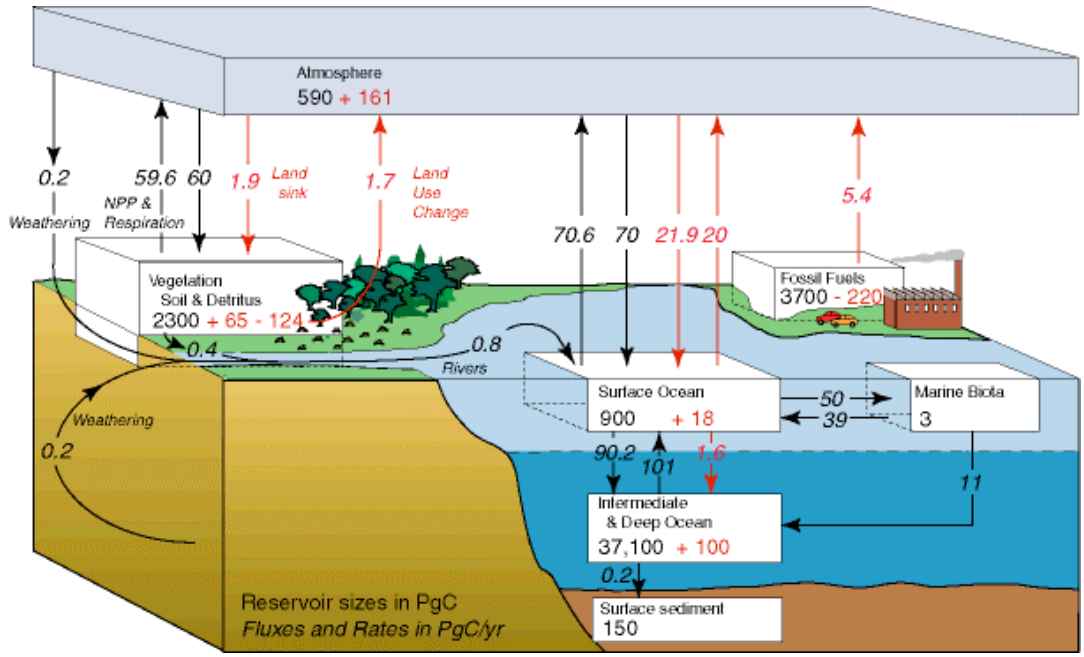

Figura 7.1.4. Ciclo global del carbono, flujos y principales depósitos. Las flechas indican los flujos (en petagramos de carbono por año, 1Pg =10^{15} gC) entre la atmosfera y los dos principales sumideros, la tierra y el océano, promediado durante los años 1980. Los flujos antropogénicos están en rojo; los flujos naturales en negro. El flujo neto entre los depósitos esta equilibrado por los procesos naturales pero no para los flujos antropogénicos. En las cajas, los números en negro dan el tamaño preindustrial de los depósitos y los números en rojo muestran los cambios resultantes de la actividad humana desde los tiempos preindustriales. Para el sumidero del continente, el primer numero en rojo representa un valor infravalorado cuyo origen es especulativo; el segundo representa la disminución debido a la deforestación. Los números están ligeramente modificados comparados con los que fueron publicados por el *Intergovernmental Panel on Climate Change*. NPP es la producción primaria neta. (Sarmiento and Gruber, 2002).

7.1.2 El ciclo del CO_2 en el océano

El estudio del ciclo del carbono cobra en los océanos una gran importancia ya que juegan un papel fundamental en el sistema climático. Esto no es debido únicamente a los intercambios de calor o al transporte de masas de agua, sino también a su impacto sobre el ciclo biogeoquímico del carbono de todo el planeta. De hecho el océano es el principal reservorio activo de carbono del planeta, superando en un orden de magnitud a la biosfera continental y a la atmósfera. Su capacidad para intercambiar el CO_2 con la atmósfera y para almacenar el carbono, especialmente en las capas más profundas de agua, le otorga un papel clave en el control del contenido atmosférico de dióxido de carbono. Así, para conocer el ciclo del carbono en

el sistema oceánico es crítico determinar el destino del dióxido de carbono antropogénico sustraído a la atmósfera. Además, la interfaz atmósfera-océano es el punto de unión entre el efecto invernadero y la oceanografía. Como consecuencia y debido al interés creciente por conocer los factores que podrían paliar o incrementar el efecto invernadero, se han desarrollado en los últimos años programas de investigación internacionales tales como JGOFS (Joint Global Ocean Flux Study), GLOBEC (Global Ocean Ecosystem Dynamics) y, desde 2007 IMBER (Integrated Marine Biogeochemistry and Ecosystem Research). Estos programas tienen por objeto incrementar el conocimiento sobre la estructura y el funcionamiento del ecosistema oceánico global así como sus posibles respuestas al cambio climático y la influencia del mismo sobre los océanos.

7.1.3 Las bombas de carbono

Los intercambios de CO_2 entre la atmosfera y el océano son altamente dependientes de la temperatura de las aguas superficiales, la circulación atmosférica y las corrientes; así como de los procesos de fotosíntesis y de respiración. Dos grandes mecanismos influyen sobre el ciclo del carbono en sus formas tanto orgánicas como inorgánicas. Estos dos procesos son conocidos como la bomba física (también llamada bomba de solubilidad) y la bomba biológica (Raven y Falkowski, 1999). Ambos mecanismos son responsables de la captación del dióxido de carbono atmosférico y de su incorporación al sistema oceánico.

1.3.1 La bomba física

La bomba física está relacionada con los procesos físicos y termodinámicos que permiten la captación y el almacenamiento del carbono de origen atmosférico. La bomba de solubilidad se compone de dos elementos. El primero de ellos es la solubilidad del dióxido de carbono en la interfaz aire-agua, siendo mayor la solubilidad cuanto más fría es el agua. Además dependiendo de la temperatura, la capacidad de almacenamiento es función del reservorio alcalino y de la cantidad de CO_2 presente en el océano. La velocidad del viento conjuntamente con la mezcla y la evaporación del agua, lo cual enfría la capa superficial del océano, contribuye a los

intercambios océano atmosfera.

El segundo componente esta vinculado a la circulación del océano también llamada circulación termohalina. Las aguas profundas se forman por hundimiento de masas de agua en altas latitudes donde las condiciones son favorables a la solubilidad del dióxido de carbono. Estas masas de agua profundas contienen una gran concentración de carbono inorgánico disuelto. Este proceso permite a las densas y frías aguas polares transferir CO_2 atmosférico al océano profundo donde se queda durante siglos. Así, el hundimiento de aguas polares juega un papel clave en la captura del carbono.

La solubilidad del CO_2 en el agua junto con la circulación general de los océanos son capaces de bombear el carbono de la atmosfera hacía el interior del océano. Las aguas profundas circulan hasta latitudes ecuatoriales, más cálidas, donde emergen a la superficie y, al aumentar su temperatura, disminuye la solubilidad del CO_2. De esta manera, las aguas ecuatoriales emiten grandes cantidades de dióxido de carbono a la atmósfera, siendo fuentes de CO_2. Los afloramientos, y en nuestro caso el afloramiento norafricano actúan como fuentes de CO_2.

El reservorio alcalino es regulado por reacciones químicas entre el dióxido de carbono y el agua de mar. Estas reacciones son un balance entre varias especies iónicas y no iónicas, conocidas como carbono inorgánico disuelto. Estas especies son: dióxido de carbono libre disuelto (CO_2), ácido carbónico (H_2CO_3), bicarbonato (HCO_3^-) y carbonato (CO_3^{2-}).

$$CO_2 + 2\ H_2O \leftrightarrow H_2CO_3 \leftrightarrow HCO_3^- + H^+$$

$$HCO_3^- \leftrightarrow CO_3^{2-} + H^+$$

Este equilibrio químico, llamado también sistema de carbonatos o alcalinidad, depende de factores tales como el pH, que depende a su vez del balance de carga entre cationes (Na^+, K^+, Mg^{2+}, Ca^{2+}) y aniones (CO_3^{2-}, Cl^-, SO_4^{2-}, Br^-). Así una alteración del pH puede conducir a una mayor o menor absorción de dióxido de carbono desde la atmósfera para mantener el balance. Por tanto cuanto mayor es el desequilibrio de carga positiva, mayor es la solubilidad del dióxido de carbono. Este balance puede verse alterado por otros procesos como, por ejemplo, la disolución / precipitación de $CaCO_3$,

o actividades biológicas como la fotosíntesis, la respiración o la calcificación. Cada uno de estos procesos tiene diferentes efectos sobre la alcalinidad y juntos ejercen una gran influencia en el ciclo global del carbono.

1.3.2 La bomba biológica

La bomba biológica comprende la transferencia de la producción primaria hacía las aguas sub-superficiales por sedimentación del carbono orgánico particulado (POC, el flujo pasivo o gravitacional) y además por las migraciones verticales de los organismos planctónicos (el denominado flujo activo). La bomba biológica es responsable del transporte del carbono atmosférico a través de los sistemas biológicos. Una vez incorporado al sistema biológico, el carbono circula entre los diferentes niveles de la cadena trófica y su destino final depende de actividades biológicas tales como el crecimiento, la ingestión, la respiración, la excreción y la mortalidad.

La bomba biológica se basa en la capacidad de los organismos autótrofos, principalmente fitoplancton, para sintetizar moléculas orgánicas complejas como glúcidos, lípidos y prótidos, a partir de compuestos minerales simples como el dióxido de carbono, el amonio, los fosfatos y los nitratos. Dicha síntesis exige una cantidad de energía considerable, que es proporcionada al ecosistema por la radiación solar. Los pigmentos fotosintéticos aseguran la captura de la radiación solar. Dichos pigmentos convierten la radiación solar en una forma de energía (ej. ATP, NADPH) que los organismos pueden emplear para realizar la reacción fotosintética. Escrita de manera generalizada y tomando en cuenta la relación de Redfield (1934; C:N:P=106:16:1) la fotosíntesis sigue la ecuación siguiente:

$$106\ CO_2 + 16\ HNO_3 + H_3PO_4 + 122\ H_2O \xrightarrow{\text{ATP / NADPH}} (CH_2O)_{106}(NH_3)_{16}H_3PO_4 + 138\ O_2$$

La fotosíntesis es el proceso base de casi toda la cadena trófica ya que genera de materia orgánica también denominada en términos generales biomasa. A través de la fotosíntesis, una parte del CO_2 atmosférico se almacena en la biomasa y podrá ser utilizado por los eslabones superiores de la red trófica pelágica (Chisholm, 1992). La actividad fotosintética retira el dióxido de carbono de la capa superficial y determina los niveles de carbono

orgánico disuelto en las aguas superficiales y el intercambio de carbono entre el océano y la atmosfera. La cantidad anual de carbono capturado se estima a 2,2 Pg C·año^{-1} (Takahashi *et al.*, 2002). De esta manera el océano actúa, en general, como sumidero para el dióxido de carbono atmosférico. No obstante, Del Giorgio y Duarte (2002) mostraron que la respiración oceánica (55 hasta 76 Gt C·año^{-1}) representa la mayor fuente de CO_2 en la biosfera, comparable a los 70-80 Gt C·año^{-1} de la respiración del suelo.

Existen evidencias que muestran que la respiración del océano abierto es al menos del mismo orden de magnitud que la respiración del suelo, la incertidumbre en la magnitud del anterior es también mucho más grande, y su importancia como fuente de CO_2 a la atmosfera es hasta ahora confusa. Del Giorgio y Duarte (2002) también comentan que la consideración de la respiración oceánica puede ayudar a explicar la distribución de las regiones fuentes de CO_2 en el océano. Particularmente, el papel del océano subtropical como fuente de CO_2 a la atmosfera es consistente con el hecho de que la respiración en la capa fótica excede la producción primaria. Estos autores concluyen diciendo que “después de todo no podemos pretender comprender todo el ciclo global del carbono cuando no sabemos si el biota de los océanos globales es una fuente o un sumidero de carbono”.

La cadena trófica en el océano es compleja (Figura 7.1.5) y la materia orgánica producida en la capa superficial circula entre los diferentes elementos de la red trófica. No obstante, una parte de la biomasa generada por los autótrofos se pierde en el océano profundo debido a la gravedad. Este flujo de carbono orgánico se conoce como flujo gravitacional (flujo de POC) y representa el primer elemento de la bomba biológica. Honjo *et al.* (2008) mostraron que el flujo de POC varia desde 25 (en el Pacifico) hasta 605 mmolC m^{-2}·año^{-1} en el mar de Arabia. La zona oceánica que muestra el flujo de POC mas alto en una región amplia es la zona de los giros boreales en el Pacifico Norte donde el flujo medio de POC es de 213 mmolC m^{-2}·año^{-1}. El flujo de POC es particularmente alto en las zonas de afloramiento, incluyendo la divergencia en el mar de Arabia y la zona de Cabo Verde. El flujo de POC mas bajo en una región amplia se encuentra en el Pacifico Norte en los giros subtropicales y tropicales (39 mmol m^{-2}·año^{-1}, Honjo *et al.*, 2008).

El carbono ingerido por cada nivel trófico será excretado y defecado en parte (30% del carbono total ingerido) y el resto será respirado o se incorporará a los organismos como crecimiento. En total se asimila aproximadamente un 70% del carbono ingerido. El segundo elemento de la bomba biológica es el flujo activo. Este flujo activo está compuesto por i) el flujo digestivo, ii) el flujo respiratorio, iii) el flujo por excreción, y finalmente iv) el flujo por mortalidad. Este trabajo se enfoca hacia los flujos de carbono en la columna de agua y en particular se centra en los flujos digestivos y respiratorios mediados por los organismos mesozooplanctónicos migradores.

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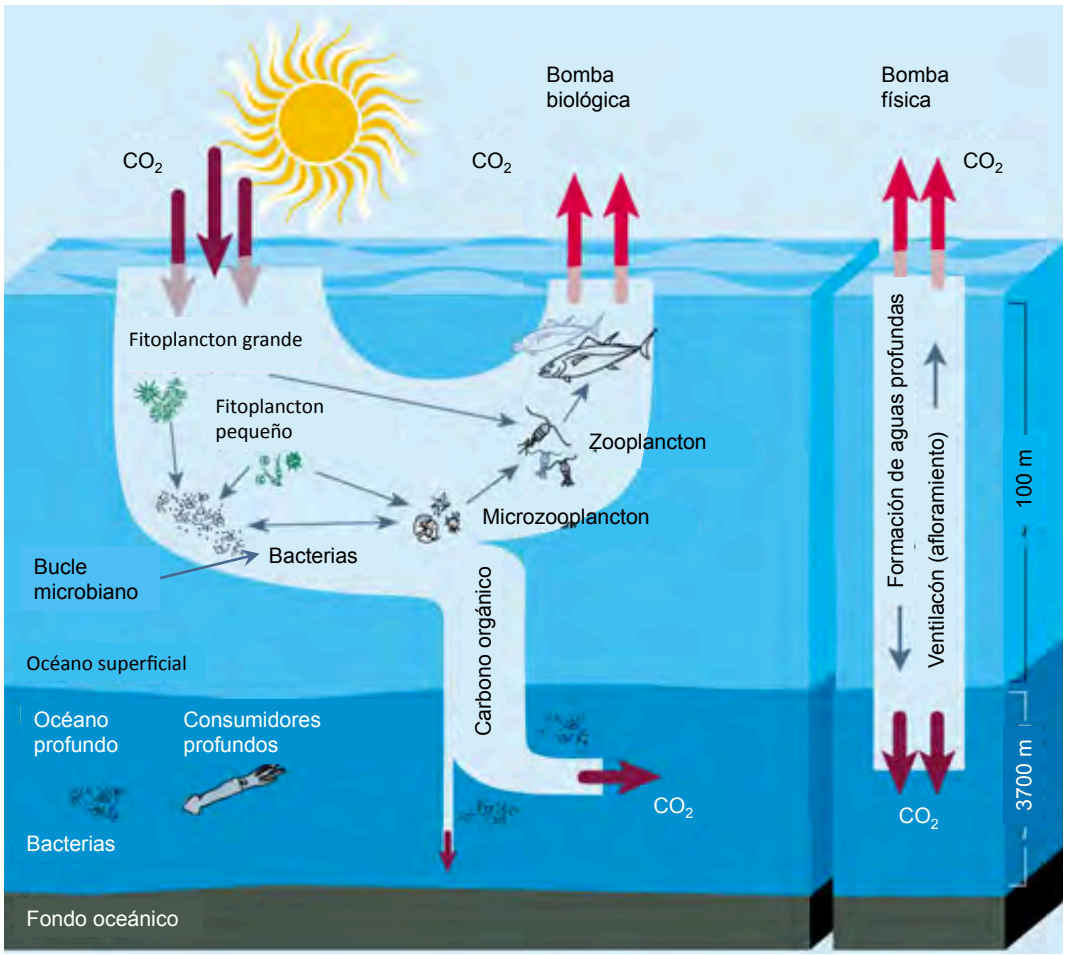

Figura 7.1.5. Diagrama de los componentes y procesos internos de la bomba biológica. Notar que el CO_2 es incorporado por el fitoplancton y transformado en materia orgánica en la zona eufótica (u océano superficial), esta materia orgánica es procesada y una parte de ella se hunde a las aguas profundas (Modificado de Chisholm, 2000).

Además de su efecto en la formación de materia orgánica, la radiación solar tiene un importante impacto fisiológico (tanto sobre los organismos

autótrofos como los heterótrofos) y también de carácter etológico en los animales marinos. Numerosos autores han demostrado la influencia de la iluminación tanto solar como lunar en el comportamiento del zooplancton (Cushing, 1951; Mc Naught *et al.*, 1964; Ringelberg, 1964; Boden y Kampa, 1967; Forward, 1988; Hernández-León *et al.*, 2001a, 2002, 2004, 2007, 2009, 2010). Debido a la importancia de la iluminación solar y también a su periodicidad, el comportamiento de los animales es ciclico y éstos presentan unas adaptaciones correspondientes a dicha periodicidad, tales como una sincronización de los ciclos biológicos o la estacionalidad de las épocas favorables y desfavorables.

En el océano, muchos organismos zooplanctónicos realizan migraciones verticales (Longhurst, 1976; Youngbluth, 1976; Sameoto, 1984; Laval, 1989; Hernández-León *et al.*, 1999, 2001a, 2001b, 2002, 2004, 2010; Yebra *et al.*, 2005). Este fenómeno ha sido estudiado observando las diferencias entre los perfiles de distribución vertical del zooplancton de día y de noche. Estas diferencias existen tanto en términos de biomasa como en la composición taxonómica. Atendiendo a su desplazamiento en la columna de agua, el zooplancton puede ser dividido en cuatro grupos; (1) los no migradores, (2) los migradores nocturnos hacia la superficie, (3) los migradores ocasionales y (4) los migradores inversos que descienden de noche hacia las profundidades.

Esta tesis, se centra en los organismos migradores del segundo grupo. Estos organismos zooplanctónicos realizan movimientos verticales nocturnos a diario. De día se encuentran concentrados formando las capas profundas de reflexión (500 m de profundidad aproximadamente) para evitar ser depredados (Zaret y Suffern, 1976; Frost, 1988; Dawidowicz *et al.*, 1990). Al anochecer ascienden hacía los estratos más superficiales (0-200 m) (Angel, 1985; Fowler y Knauer, 1986; Hernández-León *et al.*, 2001a, 2001b, 2002, 2004; Yebra *et al.*, 2005) para alimentarse de fitoplancton, microplancton o consumir zooplancton no migrador. La ingestión en la capa eufótica y posterior migración implica un transporte de materia orgánica desde la superficie hacia los estratos profundos (Figura 7.1.5; Angel, 1985; Fowler y Knauer, 1986; Longhurst y Harrison, 1988, 1989; Hernández-León *et al.*, 2001b, 2002, 2004, 2010; Yebra *et al.*, 2005; Steinberg, 2008; Shatova,

2012). Cuando el tiempo de digestión es mayor que el tiempo que tardan los migradores en retornar a las zonas profundas, el contenido del tracto digestivo se transporta hacia las profundidades donde la egestión, la respiración y la excreción tiene lugar. Este transporte de material fecal se denomina flujo digestivo (Angel, 1985, 1989). La respiración en las capas profundas es también un transporte neto de carbono hacia las capas profundas del océano. Este transporte se denomina flujo respiratorio. Los cálculos realizados por varios autores (Longhurst y Harrison, 1988; Longhurst *et al.*, 1989, 1990; Zhang y Dam, 1997; Hernández-León *et al.*, 2001b, 2004; Yebra *et al.*, 2005; Steinberg, 2008) sugieren que el flujo respiratorio debido a los migradores puede representar una parte significativa del flujo total de carbono en los océanos. El flujo respiratorio junto con el flujo digestivo son los principales componentes del flujo activo y pueden representar una parte importante de la bomba biológica en comparación con el flujo pasivo (del 0 al 100% del flujo de POC; Longhurst y Harrison, 1988; Longhurst *et al.*, 1989, 1990; Zhang y Dam, 1997; Hernández-León *et al.*, 2001b, 2002, 2004, 2010; Yebra *et al.*, 2005; Steinberg, 2008).

Además de los flujos respiratorios y digestivos existen otros flujos activos como el de mortalidad debido a la muerte de los migradores en las capas profundas, y, la excreción de material orgánico disuelto (amonio, nitrógeno orgánico disuelto y carbono orgánico disuelto; ver Steinberg *et al.*, 2000). Incluso si la excreción de material orgánico disuelto tiene una proporción relativamente baja comparada con la producción primaria, dicho flujo representa entre el 2 y el 19% de la producción primaria (Steinberg *et al.*, 2000).

La migración vertical del zooplancton y del micronecton representa el movimiento de biomasa más importante en el océano (Enright, 1977; Buskey and Swift, 1983; Atkinson *et al.*, 1992). Como consecuencia, el zooplancton promueve un importante flujo de materia y energía hacía los estratos más profundos del océano y su estudio reviste un gran interés. En este contexto, esta tesis doctoral presenta el estudio de los flujos activos de carbono en la columna de agua como consecuencia de las migraciones verticales del mesozooplancton en el giro subtropical del Atlántico Noreste y particularmente en la zona de la corriente de Canarias.

En el contexto actual de un cambio global del clima, los modelos asociados océano-atmósfera evidencian profundos cambios en la circulación oceánica, en la productividad marina así como en la eficacia del océano para absorber el carbono de origen antropogénico. Para predecir la evolución de las concentraciones de dióxido de carbono en la atmósfera y para definir estrategias creíbles de estabilización (p.e. los acuerdos del protocolo de Kyoto, 1997), es necesario estudiar y comprender las interacciones entre los ciclos biogeoquímicos marinos y el clima. La creación de modelos biogeoquímicos marinos a gran escala y más específicamente de la actividad biológica ha experimentado un desarrollo importante durante los últimos años gracias a los avances de observaciones y estudios de procesos llevados a cabo principalmente por los programas JGOFS y GLOBEC. A pesar de todos los avances realizados, el “Intergovernmental Panel for Climate Change” (IPCC) concluyó en 2007 que “los modelos oceánicos actuales están severamente limitados por la falta de ecuaciones caracterizando las actividades biológicas y para especificar las variaciones temporales y espaciales en dichas ecuaciones” (ver informes, http://www.ipcc.ch/). Esto es particularmente acusado en el caso de la respiración oceánica, donde la reducción de dichas incertidumbres sobre la respiración del océano abierto requeriría un esfuerzo internacional concertado a gran escala.

Debido a la importancia que tienen las migraciones verticales sobre el transporte de materia y energía, así como la importancia que están tomando los modelos informáticos como herramienta de predicción, como primer paso de esta tesis se ha desarrollado un modelo unidimensional para simular las migraciones verticales del mesozooplancton y los flujos de carbono asociados a estas en las aguas Canarias, usando para ello datos de estudios publicados. Como segundo paso, y con el propósito de verificar la solidez del modelo desarrollado, así como para su posterior aplicación, ha sido necesario obtener más datos de campo procedentes de distintas regiones, condiciones hidrográficas y épocas del año.

En el área de Canarias (Figure 7.1.6), se han identificado estructuras mesoescalares al sur de las islas, como remolinos inducidos por ellas debido a sus interacciones con la Corriente de Canarias o la presencia de filamentos procedentes del afloramiento africano.

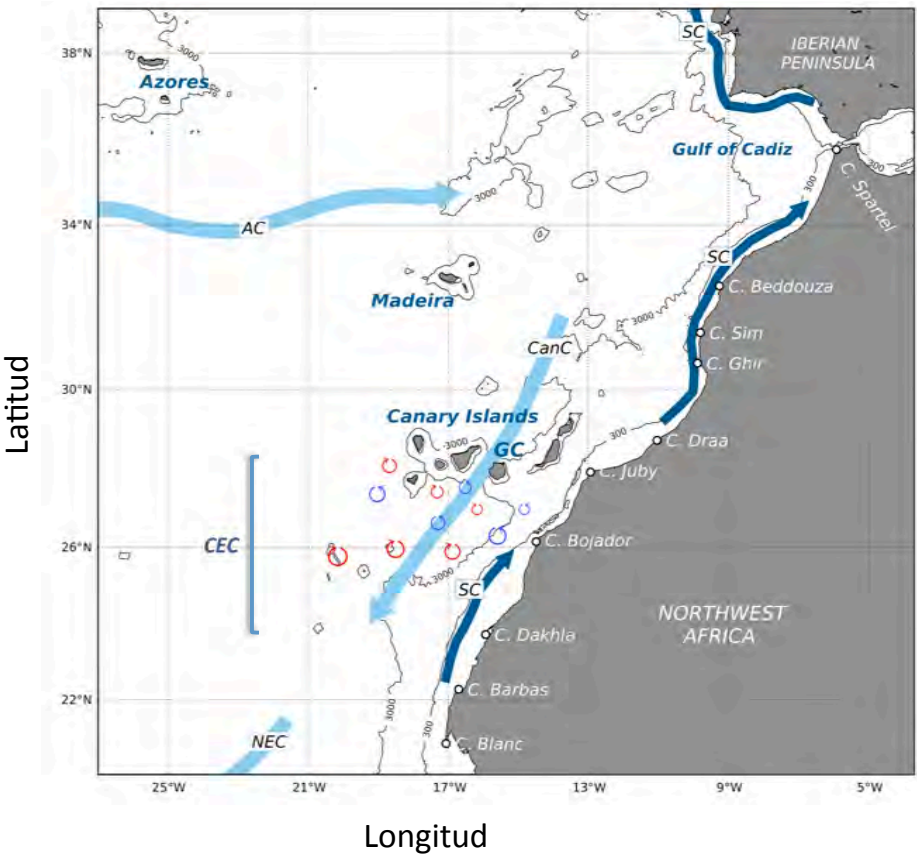

Figure 7.1.6. Mapa esquemático de la Cuenca Canaria que muestra las corrientes principales (azul claro: corrientes superficiales; azul oscuro: corrientes profundas) y giros mesoscalares (azul: ciclónico; rojo: anticiclónico) al sur de las Islas Canarias. AC: Corriente de las Azores; CanC: Corriente de Canarias; NEC: Corriente norecuatorial; Sc: Corriente profunda (Dibujado por E. Masson a partir de Arístegui *et al.*, 2009).

Estas estructuras presentan altos valores de producción primaria (Arístegui *et al*., 1989, 1994, 1997) y así promueve una zona de transición entre el afloramiento Africano (sistema eutrófico) y el oceánico abierto oligotrófico. Así, y para completar nuestros conocimientos sobre los flujos activos de carbono en la zona del giro subtropical del Atlántico Noreste y para determinar la influencia de las estructuras mesoescalares sobre los flujos activos se realizaron varios estudios de campo en distintas zonas de la Corriente de Canarias.

El primer estudio de campo se realizó en una estación al norte de la isla de Gran Canaria donde la columna de agua no está sometida a perturbaciones ocasionadas por el efecto de islas. Esta área fue elegida como base para la construcción del modelo numérico porque es estable, tal

como se describe en el primer capitulo de la sección de resultados. Además se realizaron otros dos estudios al sur del Archipiélago Canario en periodos estacionales diferentes. En cada uno de estos estudios se realizaron dos transectos localizados a 21 y 26º Norte, respectivamente. Ambos transectos se iniciaron cerca de la costa Africana y se prolongaron hacia el océano Atlántico abierto. Este muestreo cruza así varias zonas con productividad diferentes. Primero, la zona costera está afectada por el afloramiento costero Africano y por fenómenos mesoescalares tales como los filamentos procedentes del afloramiento. La segunda zona se encuentra al sur del Archipiélago y está influenciada por los remolinos inducidos por la presencia de las islas afectando la estabilidad de la columna de agua. Algunos de estos remolinos son estructuras cuasi-permanentes mientras otros se van generando al sur de las islas pero son llevados hacia el océano abierto por la Corriente de Canarias. Los muestreos terminan en el océano abierto donde la columna de agua está influenciada por la actividad mesoescalar del “Canary Eddy Corridor” (Sangrá *et al.*, 2009).

Finalmente, el incremento del plancton durante el bloom tardío de invierno en aguas subtropicales fue estudiado en relación a la iluminación lunar en aguas de las Islas Canarias. La biomasa mesozooplanctónica epipelágica incrementa mientras la mezcla invernal progresa pero presenta un incremento cada luna llena y disminuye después debido al efecto de la predación por parte de los migradores verticales interzonales (DVMs). Con el fin de estimar el impacto de la predación de los DVMs sobre el zooplancton epipelágico, y sobre los flujos activos de carbono, se desarrolló un modelo simple y conservativo empleando los criterios de estudios previos.

VII·2 OBJETIVOS DE LA INVESTIGACIÓN Y APORTACIONES ORIGINALES

Dada la importancia que tienen las migraciones verticales sobre el transporte de materia y energía, así como la importancia que están tomando los modelos matemáticos como herramienta de predicción, el objetivo de esta tesis ha sido responder a la siguientes cuestiones:

1. ¿Podemos desarrollar un modelo matemático simulando las migraciones verticales y los flujos activos de carbono asociados?
2. ¿Podemos emplear este modelo matemático para predecir los movimientos de biomasa y los flujos activos de carbono en una zona determinada de Canarias?
3. ¿Podemos aplicar este modelo numérico para predecir los flujos activos en toda la zona de la Corriente de Canarias?

Con el propósito de contestar a las dos primeras preguntas, se revisaron los trabajos realizados anteriormente sobre modelos numéricos. La mayoría de ellos se desarrollaron tratando de reproducir el comportamiento migratorio empleando la influencia de los factores externos. No obstante no tomaron en cuenta el impacto que tiene este comportamiento migratorio sobre los flujos activos de carbono. Así, se ha desarrollado un modelo unidimensional para simular las migraciones verticales y los flujos de carbono asociados.

La respuesta a la tercera pregunta planteada es negativa. En efecto, la cantidad de datos publicados sobre flujos activos y distribución de biomasa de migradores en la zona de Canarias, era cuando se planteó esta pregunta, del todo insatisfactorio. Por lo tanto, se realizaron una serie de estudios de campo con el propósito de incrementar nuestros conocimientos y comprensión de este fenómeno en la zona. Además de la adquisición de datos para alimentar el modelo previamente desarrollado, los objetivos de estos trabajos tuvieron como objetivo responder a las preguntas siguientes:

4. ¿ Afecta el *bloom* de finales del invierno al comportamiento migratorio y a los flujos activos de carbono?
5. A lo largo de la gran variabilidad encontrada en los paisajes físicos entre el afloramiento norafricano hasta el océano abierto, ¿Existe una variación de la distribución vertical de los migradores y de los flujos activos de carbono?

6. ¿La variabilidad estacional tiene influencia sobre el flujo activo de carbono?
7. ¿Cuáles son las consecuencias del ciclo lunar sobre los flujos activos de carbono debidos a los migradores?

Los resultados aportados con el fin de responder los objetivos expuestos previamente constituyen en sí mismo las aportaciones originales de este trabajo. Las respuestas a las cuestiones planteadas se presentan en resultados y están recogidos en las siguientes aportaciones científicas:

3.1 A model of zooplankton diel vertical migration off the Canary Island: Implication for active carbon flux (2005) Putzeys, S. and S. Hernández-León. *Journal of Sea research*, 53: 213-222.

3.2 Carbon fluxes due to migrant zooplankton movements during the late winter bloom in the Canary Islands waters (2011) Putzeys, S., Yebra L., Almeida C., Bécognée P. and S. Hernández-León. *Journal of Marine Systems*, 88: 53-562.

3.3 Active carbon flux by diel migrant zooplankton in eutrophic and oligotrophic waters of the Canary Current. Putzeys, S., Almeida C., Bécognée P., Yebra, L. Marrero Diaz A., Arístegui J. and S. Hernández-León. En preparación.

3.4 Seasonality effect on active carbon flux by diel migrant zooplankton in eutrophic and oligotrophic waters of the Canary Current. Putzeys, S., Almeida C., Bécognée P., Yebra, L. Marrero Diaz A., Arístegui J. and S. Hernández-León. En preparación.

3.5 Carbon sequestration and zooplankton lunar cycles: Could we be missing a major component of the biological pump? (2010) S. Hernández-León, G. Franchy, M. Moyano, I. Menéndez, C. Schmoker and S. Putzeys. *Limnology and Oceanography*, 55(6): 2503-2512.

VII·3 PLANTEAMIENTO Y METODOLOGÍA

7.3.1 La zona de estudio

La zona de estudio constituye una región de transición costa-océano compleja caracterizada por una fuerte variabilidad espacial, temporal y escalar, determinando así una gran variedad de condiciones hidrodinámicas y como consecuencia una gran variedad de condiciones biológicas en una zona cercana al archipiélago. En efecto, el archipiélago Canario perturba el flujo normal de la corriente de Canarias (Arístegui *et al.*, 1994; 1997; Barton *et al.*, 1998) e induce la formación de una zona, al sur, con una gran actividad mesoescalar. Esta zona se denomina Zona de Transición Costera (ZTC, o CTZ Coastal Transition Zone, en inglés). La ZTC conecta de una de las zonas más productiva, el afloramiento norafricano, con un sistema oligotrófico, las aguas del océano abierto del giro subtropical noratlántico. En la zona de estudio encontramos remolinos (ciclónicos y anticiclónicos), filamentos procedentes del afloramiento, zonas oligotróficas y frentes. El estudio de la interacción de las aguas eutróficas costeras y las aguas oligotróficas de Canarias ha permitido cambiar la visión que se tenía de la ZTC como una región típicamente oligotrófica (Barton *et al.*, 1998). En efecto, debido al transporte de las aguas eutróficas del afloramiento norafricano en forma de filamentos (Barton *et al.*, 1998) y la interacción de dichos filamentos con los remolinos, se produce una exportación de materia orgánica (Arístegui *et al.*, 1997; Basterretxea, 1994; Hernández-Guerra *et al.*, 1993), de mesozooplancton (Hernández-León *et al*., 2002) y de larvas neríticas (Rodríguez *et al.*, 1999) hacia el archipiélago Canario.

Estudios anteriores realizados en Canarias (Yebra *et al*., 2005) y otros estudios realizados en zonas de afloramiento y de frentes (Isla y Anadón, 2004) demostraron que las estructuras mesoescalares influyen en los flujos activos de carbono, pero la zona de Canarias carece de estudios exhaustivos que permitan alimentar de forma adecuada a modelos predictivos. El incremento de los conocimientos del ciclo del carbono y particularmente de los flujos activos en la zona de Canarias es un paso necesario para la validación de modelos predictivos en esta región.

7.3.2 El diseño del modelo numérico

3.2.1 Descripción general de la construcción del modelo

El modelo desarrollado es unidimensional basado en el trabajo realizado por Andersen y Nival (1991) y consiste en una ecuación diferencial de derivadas parciales de segundo orden que describe la variación espacial y temporal de la biomasa. Se han aportado a la ecuación de Andersen y Nival (1991) ciertas modificaciones a fin de poder calcular las tasas metabólicas y, posteriormente, cuantificar los flujos activos de carbono simulados.

Se ha considerado una columna de agua de 1000 m de profundidad dividida en capas de 4 m. La iluminación es considerada como la variable forzante y varía según las horas del día ya que es uno de los factores más influyentes (Forward, 1988). La temperatura ha sido también tenida en cuenta para poder calcular las tasas metabólicas *in situ*. Se ha supuesto que los movimientos verticales como la difusión son de menor importancia comparado con la velocidad de migración de los organismos. La ecuación resultante que describe los cambios en la biomasa en función del tiempo y de la profundidad se expresa de la siguiente manera:

$$\frac{\partial B}{\partial t} = \frac{\partial (w \times B)}{\partial z}$$

donde w es tanto la variable forzante del sistema como la velocidad de migración (negativa o positiva según el movimiento sea ascendente o descendente); B es la biomasa de los migradores, y δz, δt son las dimensiones dependientes de la profundidad y del tiempo. La Tabla (7.3.1) presenta las variables y los factores que se utilizaron para inicializar el modelo. La ecuación anterior se puede aproximar a la ecuación diferencial siguiente:

$$\frac{B_{t+1} - B_t}{\Delta t} = \frac{-d_1 \times w_{i-1} \times B_{i-1}^t - |w_i| \times B_i^t + d_2 \times w_{i+1} \times B_{i+1}^t}{\Delta z}$$

donde i son las diferentes capas de la columna de agua (de i=0 a i=n con un Δz=4 m), B la biomasa, t el tiempo (con un Δt= 90 s) y w la velocidad de migración del zooplancton.

Tabla 7.3.1. Variables y coeficientes del modelo. (- sin unidades)

Variables		Unidades
B	Biomasa zooplanctónica (fracción 1000-2000 μm)	$mgC \cdot m^{-3}$
I_z	Irradiancia a la profundidad z	$W \cdot m^{-2}$
I_{L1}	Influencia de la intensidad absoluta de la luz	-
I_{L2}	Influencia de la tasa de cambio de la irradiancia	-
w	Velocidad de migración	$m \cdot h^{-1}$

Parámetros de migración		Unidades	Valores
I_s	Irradiancia óptima	$W \cdot m^{-2}$	10
I_e	Irradiancia en la superficie	$W \cdot m^{-2}$	0.10
α	Coeficiente de la curva de foto-inhibición	-	0.012
I_v	Limite de la variación relativa de la irradiancia	%	3
w_m	Velocidad inicial de migración	$m \cdot h^{-1}$	87.5

En la ecuación aproximada, la velocidad de migración de los organismos (w) se define como $w = w_m.I_{L1}.I_{L2}$ con w_m la velocidad de migración inicial, I_{L1} la influencia de la intensidad absoluta de la luz y I_{L2} la influencia de la tasa de cambio de la irradiancia (Tabla 7.3.1).

Los coeficientes d_1 y d_2 han sido definidos como en Andersen y Nival (1991):

Si $w_{i-1} < 0$ entonces $d_1 = 1$

Si $w_{i-1} \geq 0$ entonces $d_1 = 0$

Si $w_{i+1} < 0$ entonces $d_2 = 1$

Si $w_{i+1} \leq 0$ entonces $d_2 = 0$

Se ha considerado Δz=4 m y Δt= 90 s para conservar el esquema de estabilidad del modelo $\left(\Delta t \leq \frac{\Delta z}{w}\right)$.

3.2.2 Descripción de la construcción de la variable forzante

Al contrario que en el modelo de Andersen y Nival (1991), la irradiancia ha sido enteramente simulada gracias a la ecuación de Basterretxea y Arístegui (1999) y usando la constante solar de Iqbal (1983). La intensidad y la variación de la radiación solar pueden ser simuladas en

función del día juliano y de la hora del día. Las ecuaciones empleadas incorporan también la posición geográfica del punto simulado (Spencer, 1971), las condiciones atmosféricas y su influencia en la transmisión de la luz (Paltridge y Platt, 1976). Así, el modelo construido puede ser aplicado en zonas concretas y para horas determinadas.

Ya que sólo parte de la luz atraviesa la atmósfera y que otra parte se pierde al cruzar la interfaz aire-océano, debido a las perdidas por reflectancia, se empleó la ecuación siguiente para determinar la cantidad de luz por debajo de la interfaz aire-mar:

$$I^{m}_{surf} = I^{m}_{t} \times (R - 1)$$

donde R es la dependencia de la reflectancia, calculada como:

$$R = \frac{1}{2} \times \frac{\sin^2(\theta_a - \theta_w)}{\sin^2(\theta_a + \theta_w)} + \frac{1}{2} \times \frac{\tan^2(\theta_a - \theta_w)}{\tan^2(\theta_a + \theta_w)}$$

donde θ_a es el ángulo de incidencia de la luz en el aire y θ_w es el ángulo de incidencia de la luz en el agua.

La reflectancia (R) como porcentaje fue tomada de la relación de Fresnel que interviene en el fenómeno de reflexión-refracción de las ondas electromagnéticas. El hecho de que la reflectancia sea función del ángulo cenital y de la velocidad del viento (Gordon, 1969) no ha sido considerado en el modelo. La parte de la luz que puede atravesar la superficie del océano puede cambiar de dirección debido a la refracción. El ángulo de refracción puede ser determinado empleando la relación de Snell (1621):

$n_a \times \sin \theta_a = n_w \times \sin \theta_w$

donde n_w y n_a son los índices de refracción del agua de mar y del aire, respectivamente. El valor del ratio n_w/n_a es de 1,341 (Kirk, 1983) tanto para el agua de mar como para el agua dulce a temperatura ambiente y para longitudes de onda útiles para la fotosíntesis. El angulo θ_a se calcula empleando la ecuación del ángulo de elevación solar:

$\sin \beta = \cos \theta_a$

y $\sin \beta = \sin \phi \times \sin \delta - \cos \phi \times \cos \delta \times \cos \tau$

entonces $\cos \theta_a = \sin \phi \times \sin \delta - \cos \phi \times \cos \delta \times \cos \tau$

con τ la hora del día en radianes.

El modelo también calcula la intensidad de la luz desde la sub-superficie hasta los 1000 m de profundidad (I_z) utilizando la relación clásica de Beer-Lambert (1852) con un coeficiente de atenuación K(z) determinado a partir de una distribución simulada de la biomasa fitoplanctónica C(z) como se describe a continuación:

$$K(z) = 0{,}0384 + 0{,}0088 \times C(z) + 0{,}054 \times C(z)^{2/3}$$

$$\text{con } C(z) = C_o + \frac{h}{\sigma\sqrt{2\pi}} \times e^{-\left[\frac{(z - z_m)^2}{2\sigma^2}\right]}$$

donde C(z) es la distribución de la biomasa de clorofila (mg $C \cdot m^{-3}$) en función de la profundidad, z; σ, la desviación estándar en el rango de profundidad del máximo de clorofila (50 m en este caso); $C_o + \frac{h}{\sigma\sqrt{2\pi}}$, la concentración en clorofila en el máximo (65,79 mg$C \cdot m^{-3}$) y z_m la profundidad del máximo de clorofila (100 m).

3.2.3 Procedimiento para la estimación de la tasa de respiración

El modelo inicial de Andersen y Nival (1991) consideraba las tasas fisiológicas como la ingestión, la excreción, la mortalidad y la tasa de muda como un solo parámetro fijo que dependía de la biomasa. En el presente modelo, se utilizo la ecuación de Ikeda (1985) que se basa en la biomasa y la temperatura para generar datos de tasa respiratoria y se define como sigue:

$$\text{Ln } Y = a_0 + a_1 \times \text{Ln } X_1 + a_2 \times \text{Ln } X_2$$

siendo Y la cantidad de oxígeno utilizado (µl $O_2 \cdot ind^{-1} \cdot h^{-1}$); a_0, a_1, y a_2 son coeficientes definidos en la Tabla 7.3.2; X_1, la biomasa individual (mg C) y X_2 la temperatura correspondiente a la capa de donde se extrajo el dato de biomasa simulado.

Tabla 7.3.2. Coeficientes de la ecuación de Ikeda (1985). (** p<0,01, R^2=0,95)

Símbolo	Valor	Test t para a=0
a_0	0,5254	23,91**
A_1	0,8354	130,01**
a_2	0,0601	39,87**

El consumo de oxígeno determinado a través de la relación de Ikeda ha sido convertido en unidades de carbono empleando para ello un cociente respiratorio de 0,97 (Omori y Ikeda, 1984). En cuanto a la tasa de ingestión, está derivada también de esta relación de Ikeda, considerando una asimilación del 70% y que la mitad de la comida asimilada se utiliza para el crecimiento y la otra mitad para la respiración.

3.2.4 Procedimiento de inicialización

El modelo fue inicializado utilizando perfiles de biomasa migradora procedentes de una campaña realizada en el sur de Gran Canaria en agosto de 1993 (Hernández-León *et al.*, 2001b). Los valores brutos de los perfiles de biomasa (mg proteína·m^{-3}) han sido procesados antes de poder ser incorporado en el modelo. Los datos iniciales (mg proteínas·m^{-3}) fueron convertidos a carbono. Para ello se utilizó, en primer lugar, la relación dada por Hernández-León *et al.* (2001b) que permite transformar de proteínas a peso seco y, en segundo lugar, una relación utilizada por varios autores (Båmsted, 1986; Dam y Peterson, 1993) que considera que el contenido en carbono equivale a un 40% del peso seco, así se obtienen mg C·m^{-3}. Los perfiles de biomasa convertidos fueron a continuación promediados.

Después de este primer paso y con el fin de determinar la fracción de la biomasa implicada en la migración vertical, se sustrajeron los perfiles de día de los de la noche. Así se crearon los perfiles sintéticos de organismos migradores que se emplearon en el modelo. Los perfiles de temperatura de esta campaña fueron promediados antes de ser introducidos en el modelo para poder calcular las tasas metabólicas.

7.3.3 Obtención de muestras de zooplancton y metodología de análisis

3.3.1 Obtención de muestras

Las muestras biológicas recogidas en este trabajo fueron adquiridas utilizando una red de tipo Longhurst Hardy Plankton Recorder (LHPR; Longhurst *et al.*, 1966). La LHPR se basa en el principio de Hardy para recoger el plancton y puede ser arrastrado en un solo perfil en forma de V en la columna de agua. El marco de aluminio esta equipado de una red cónica y

de un cono frontal. El marco canaliza el agua a través de la red cónica de 200 µm hacia un copo que contiene dos cilindros de gasa, que enrollan alrededor de un carrete cada dos minutos, intercalando las muestras de zooplancton entre ellas y permitiendo un muestreo semi-discreto. Atado al marco, en cada lado, se encuentran dos cilindros que contienen una batería recargable y la electrónica para dirigir el colector, supervisar los instrumentos (CTD Seabird y un flujómetro) y comunicar con la superficie. Para ayudar a mantener la estabilidad y la posición horizontal de la LHPR, un peso depresor de 45 kilogramos fue atado a la parte frontal inferior del marco de aluminio.

La eficiencia de pesca con la LHPR comparada con otros métodos de muestreo se ha determinado en estudios anteriores (e.g. Brander y Thompson, 1989; Halliday *et al.*, 2001; Richardson *et al.*, 2004; Stehle *et al.*, 2007) en los cuales los factores de calibración o la eficiencia de diferentes métodos de muestreo fueron determinados. Estos estudios mostraron que la LHPR entre otros aparatos era la red más adecuada para muestrear los migradores verticales.

Generalmente, las muestras fueron obtenidas desde 0 hasta 800 m y cada muestra cubría una capa de entre 20 y 40 m lo que representa una media de 30 muestras por pesca. La conductividad, temperatura, fluorescencia y profundidad fueron también medidas, usando un sensor CTD. Una vez a bordo, las muestras se limpiaron y se conservaron rápidamente en nitrógeno líquido (-196ºC) para su posterior tratamiento.

Antes de recibir un tratamiento específico para cada análisis, las muestras recibieron un pre-tratamiento común. Primero fueron homogeneizadas utilizando un triturador sónico durante 45 segundos y a una frecuencia de 75 Hz, a una temperatura por debajo de los 4ºC y en condiciones de luz reducida. Estas condiciones permiten reducir la degradación de clorofila y de las proteínas y también disminuye la posibilidad de pérdida de actividad enzimática.

3.3.2 Determinación de la biomasa.

El contenido proteico de las muestras se determinó utilizando el sobrenadante de las muestras homogeneizadas y centrifugadas a 4000 rpm.

Para ello se siguió una modificación del método de Lowry *et al.* (1951) ajustada para microanálisis por Rutter (1967), usando suero de albúmina bovina (BSA) como estándar. A partir del contenido proteico (mg proteinas·m^{-3}) utilizamos la ecuación dada por Hernández-León *et al.* (2001b) obtenida de una recopilación de estudios en aguas de las Islas Canarias para obtener el peso seco de cada una de una de las muestras (mg peso seco·m^{-3}). Asumiendo una relación carbono/peso seco de 0,4 (Båmstedt, 1986; Dam y Peterson, 1993) se convirtío el peso seco a carbono (mg C·m^{-3}).

3.3.3 Contenido del tracto digestivo

La fluorescencia en el tracto digestivo (GF o Gut Fluorescence) se empleó como índice del contenido en pigmentos del tracto digestivo del zooplancton. La fluorescencia se midió a partir de 200 µl de homogeneizado crudo diluído en 10 ml de acetona al 90% durante 24h a -20 ºC y guardado en oscuridad. Los extractos fueron centrifugados y las mediciones de fluorescencia se realizaron a partir del sobrenadante en un fluorómetro Turner Design (modelo 10-005 R) antes y después de acidificación con una gota de acido clorhídrico puro (37%). El fluorómetro fue calibrado empleando clorofila *a* pura (procedimiento de Yentsch y Menzel, 1963). Los pigmentos del tracto digestivo se calcularon usando las ecuaciones de Parsons *et al.* (1984).

Los valores obtenidos fueron corregidos por fluorescencia residual del exoesqueleto de los organismos capturados de la capa de reflexión profunda. En este estudio se considero una fluorescencia debida al exoesqueleto de 0,1 µg de pigmentos por gramo de peso húmedo (Willason y Cox, 1987) y se usó un ratio peso seco/peso húmedo de 0,2 (Mauchline, 1969).

3.3.4 Actividad ETS (Electron Transfer System ó sistema de transporte de electrones)

Los ensayos de la actividad ETS se realizaron utilizando el método de Packard (1971) modificado por Gómez *et al.* (1996) donde pueden verse los detalles del procedimiento. La actividad ETS se corrigió para la

temperatura *in situ* para cada una de las profundidades muestreadas utilizando la ecuación de Arrhenius y usando una energía de activación de 15 Kcal·mol^{-1} (Packard *et al.,* 1975).

3.3.5 Determinación de los flujos

Los valores obtenidos en cada estación fueron clasificados y promediados en intervalos de 50 m con el propósito de obtener perfiles verticales de día y de noche de contenido proteico, contenido en pigmentos del tracto digestivo y actividad del sistema de transferencia de electrones.

Utilizando los perfiles de biomasa (mg proteina·m^{-3}), sustraemos los valores de día de los valores nocturnos creando así un perfil de día menos noche (DMN). La utilización de este método de cálculo permite determinar la biomasa de los organismos zooplanctónicos que realizan una migración vertical y así se determinan los flujos activos debidos a dicha migración. Los valores negativos entre 0-200 m representan la biomasa de los migradores que de noche han alcanzado la capa epipelágica. Integrando estos valores, obtenemos la biomasa total de migradores (mg·proteina·m^{-2}):

$$\text{Biomasa de migradores} = \int_{0\text{-}200} \text{valores Biomasa DMN}$$

Este método es utilizado de manera corriente para la determinación de los flujos de carbono (Longhurst y Williams, 1979; Zhang y Dam, 1997; Hernández-León *et al.*, 2001b; Yebra *et al.*, 2005).

Los flujos digestivos (ng pigmento·m^{-2}·d^{-1}) se calcularon realizando una operación en dos pasos. Primero, los valores positivos de los perfiles DMN fueron integrados y divididos por la biomasa a la misma profundidad para obtener el contenido del tracto digestivo específico en profundidad (µg pigmento·mg proteina^{-1}):

$$\text{GF específico} = \left[\int_{200\text{-}850} \text{Contenido del tracto digestivo}\right] \times \left[\int_{200\text{-}850} \text{Biomasa DMN}\right]^{-1}$$

El segundo paso fue multiplicar este contenido digestivo específico en profundidad por la biomasa migradora para obtener el flujo digestivo.

Para determinar el flujo respiratorio se integran los valores positivos de los perfiles DMN de ETS (µl O_2·m^{-3}·h^{-1}) y se divide a continuación por la biomasa correspondiente al mismo intervalo de profundidad:

$$\text{Actividad ETS específica} = \left[\int_{200\text{-}850} \text{ETS}\right] \times \left[\int_{200\text{-}850} \text{Biomasa}\right]^{-1}$$

La actividad ETS especifica (µl O_2·mg proteína^{-1}·h^{-1}) obtenida se multiplica por la biomasa migradora y se divide por 2:

$$\text{Flujo respiratorio} = \text{Actividad ETS específica} \times \text{Biomasa migradora} \times 0{,}5$$

El factor 0,5 aparece en la fórmula porque asumimos un ratio respiración/actividad ETS de 0,5 como en Hernández-León y Gómez (1996).

Los valores obtenidos a través de estos cálculos fueron convertidos a valores de flujo de carbono por día teniendo en cuenta el tiempo de residencia de los organismos en la capa profunda. El flujo digestivo y el flujo respiratorio se suman posteriormente tener un valor aproximado del flujo activo total de carbono.

Para determinar el metabolismo de la comunidad migradora, se ha determinado también la ingestión potencial (I, mgC·m^{-2}·d^{-1}) empleando los valores positivos integrados de los perfiles día-menos-noche de respiración (R) por debajo de 200 m de profundidad. Asumimos que la asimilación es de 0,7 y que la eficacia del crecimiento es de 0,3 antes de aplicar la ecuación propuesta por Ikeda y Motoda (1978):

$$I = 1 \cdot R/(0.7\text{-}0.3) = R \cdot 1/0.4 = 2.5 \cdot R$$

Con el fin de determinar la fuente de alimento empleada por los migradores para sustentar su metabolismo, hemos comparado su ingestión potencial con los valores del contenido del tracto digestivo. Hemos calculado el índice de omnívoria como [(ingestión - contenido del tracto digestivo)·ingestion^{-1}] (Hernández-León *et al.*, 2002).

VII·4 RESULTADOS

Capitulo primero

Un modelo de la migración vertical del zooplancton en aguas canarias y sus implicaciones sobre los flujos activos de carbono.

La migración vertical del zooplancton es conocida como un fenómeno común a todos los medios acuáticos. Muchas especies de zooplancton, como los copépodos y los eufausiáceos, realizan diariamente esta migración vertical yendo y viniendo de la capa epipelágica a la capa mesopelágica. Al parecer y a pesar de que existan muchos factores influyendo en la migración vertical, la influencia de la luz es el factor externo mas aceptado como catalizador de este fenómeno. La realización diaria de las migraciones tiene implicaciones importantes en cuanto al transporte activo de carbono a zonas profundas del océano. Este transporte puede ser evidente como lo es el transporte de material fecal, o más sutil, como lo es el transporte de carbono debido a la respiración en las capas profundas. Este transporte llamado flujo respiratorio junto con el flujo digestivo y el flujo debido a la mortalidad en profundidad constituyen una parte importante de la bomba biológica.

Un modelo matemático de la migración vertical del zooplancton fuera de la zona de influencia de las Islas Canarias ha sido generado. Este modelo simula las variaciones espaciales y temporales de la biomasa zooplanctónica y permite el calculo del metabolismo a través de un ciclo diario en la columna de agua desde 0 hasta 1000 m de profundidad. Los resultados se utilizaron para estimar el flujo activo de carbono debido a la respiración por parte de los migradores verticales. Este modelo depende principalmente de la influencia de la intensidad absoluta de la luz y de la tasa de cambio de la iradiancia. Las respuestas natatorias a las propiedades del campo de luz describen la migración vertical del zooplancton. La distribución vertical simulada de los animales en las aguas cercanas a la superficie (75-112 m) durante la noche y en las capas profundas durante el día (428-436 m) está en acuerdo con los datos *in situ* empleados para inicializar el modelo. La respiración diurna en profundidad obtenida fue comparada con estimaciones *in situ* de la respiración basadas en la actividad ETS (sistema de transferencia de electrones) de estudio previos y también con ecuaciones empíricas relacionando la temperatura y el metabolismo del mesozooplancton

epipelágico. Se descubrió que estas ecuaciones tienden a sobreestimar el flujo activo mientras que los datos derivados del ETS lo subestiman. El modelo muestra que el consumo de carbono en aguas superficiales estimado gracias a las tasas metabólicas y la consecuente producción de grandes empaquetados fecales debería estar considerado en la determinación del flujo activo en el océano.

Capitulo segundo

Influencia del bloom tardío de invierno sobre el metabolismo del zooplancton migrador y sus implicaciones sobre los flujos exportados.

La comprensión de los mecanismos involucrados en el ciclo productivo en las aguas subtropicales es necesario para determinar cual es el destino de la materia orgánica producida en estas extensas áreas del océano. Uno de los procesos involucrados en dicho ciclo productivo es el pulso de producción que ocurre a finales del inverno. En las aguas subtropicales este *bloom* tardío es debido a la erosión de la termoclina lo cual aumenta la difusión de nutrientes hacia las capas superficiales permitiendo el crecimiento del fitoplancton.

A pesar de ser un dato critico para los modelos y las estimaciones biogeoquímicas existen muy pocos estudios referentes al flujo activo de carbono debido a los migradores. Se estudio la variabilidad temporal y la distribución vertical de la biomasa, los índices de alimentación y de respiración de la comunidad zooplanctónica al norte de las Islas Canarias durante el fin del *bloom* tardío de invierno con el fin de determinar los flujos verticales de carbono en este área.

La distribución de la biomasa durante el día presentó dos capas densas de organismos en 0-200m y alrededor de 500m, mientras que durante la noche, la mayor parte de la biomasa se concentró en la capa epipelágica. El flujo digestivo basado en el contenido en pigmentos (0,05-0,18 $mgC \cdot m^{-2} \cdot d^{-1}$) representó un 0,22% del flujo pasivo exportado (flujo de carbono orgánico particulado, COP) mientras que la ingestión potencial representó un 3,91% del COP (1,24-3,40 $mgC \cdot m^{-2} \cdot d^{-1}$). El flujo respiratorio (0,50-1,36 $mgC \cdot m^{-2} \cdot d^{-1}$) fue solamente un 1.57% del flujo pasivo. El flujo total de carbono debido a los migradores (respiración más ingestión potencial) varió entre un 3,37 y un 9,22% del flujo de COP; lo cual es tres veces mayor que calculando el flujo digestivo basándose únicamente en el contenido en pigmentos del tracto digestivo. Los resultados sugieren que los flujos mediados por los migradores juegan un reducido papel en la exportación de carbono hacia las capas profundas del océano abierto durante el periodo final del *bloom*.

El estudio de los flujos activos inducidos por los migradores verticales en una área no influenciada por la actividad mesoescalar generada por las islas Canarias permite establecer un punto de comparación para futuros estudios en esta zona. Los flujos de carbono determinados fueron entre una y cinco veces inferiores comparados con los que se registran en el sur del archipiélago demostrando una vez más la importancia de las estructuras de mesoescala sobre la exportación vertical vinculada a los migradores. La variabilidad mesoescalar, la estacionalidad y probablemente la dieta de la comunidad migrante pueden ser factores determinantes en el transporte y en el destino final de la materia orgánica producida anualmente en el océano subtropical. Además, se observó que los pulsos de producción del *bloom* de finales de invierno combinado con tormentas de polvo sahariano incrementan la importancia del flujo digestivo hacia aguas profundas.

Capitulo tercero

Flujo activo de carbono debido al zooplancton migrador en aguas eutróficas y oligotróficas de la corriente de Canarias.

La Corriente de Canarias está caracterizada por una fuerte disrupción de su flujo por el Archipiélago Canario formando al sur una zona de gran actividad mesoescalar. Esta zona costera de transición Canarias-África (ZCT), conecta el área altamente productivo del afloramiento norafricano (Cabo Bojador) con las aguas oligotróficas del océano abierto del giro subtropical nordeste Atlántico. Otra región altamente productiva es la zona del frente de Cabo Verde, cerca de Cabo Blanco. Esta área está influenciada por un afloramiento casi permanente y por un frente termohalino que genera filamentos y produce una alta variabilidad tanto espacial como temporal. Para determinar el papel del zooplancton sobre la exportación vertical del carbono en estas áreas, se estudió la distribución de la biomasa zooplanctónica y su metabolismo a lo largo de dos secciones a 21 y 26º de latitud norte. La biomasa mostró una distribución típica con dos capas densas de organismos. La primera capa estaba localizada por encima de los 200 m y la segunda por debajo de los 400 m de profundidad coincidiendo con la capa de reflexión profunda. El promedio de biomasa migradora (0-200 m) era 2,6 veces más alto en el transecto sur (71,44 ± 51,44 $mmolC \cdot m^{-2}$) que en el transecto norte (27,12 ± 12,39 $mmolC \cdot m^{-2}$). Esto se ha visto reflejado en el flujo respiratorio exportado siendo 10 veces mayor en el transecto sur comparado con el transecto norte (0,54 ± 0,42 y 0,05 ± 0,05 $mmolC \cdot m^{-2} \cdot d^{-1}$, respectivamente). Además, las estimaciones del flujo digestivo pigmentado fueron 31 veces superiores en el transecto sur comparado con el transecto norte (1,89 ± 3,43 y 0,06 ± 0,11 $mmolC \cdot m^{-2} \cdot d^{-1}$, respectivamente). La contribución del metabolismo zooplanctónico al flujo de carbono particulado varió entre 3,4 % en el transecto norte (oligotrófico) y contrastando con el valor de 66 % en el transecto sur (eutrófico)

Capitulo cuarto

Efectos de la estacionalidad sobre el flujo activo de carbono promovido por zooplancton migrador en aguas eutróficas y oligotróficas de la corriente de Canarias.

El paso de la Corriente de Canarias a través del Archipiélago Canario genera al sur una región con una alta actividad mesoescalar. Esta área influenciada por los procesos mesoescalares, llamada zona costera de transición, conecta la zona productiva del afloramiento norafricano con las aguas oligotróficas del océano abierto del giro subtropical del Atlántico Noreste. Otra región altamente productiva es la zona del frente de Cabo Verde, cerca de Cabo Blanco. Esta área está influenciada por un afloramiento casi permanente y por un frente termohalino que genera filamentos y produce una alta variabilidad tanto espacial como temporal. Para determinar el papel del zooplancton sobre la exportación activa de carbono en estas áreas durante la primavera, se estudió la distribución de la biomasa zooplanctónica de 0 hasta 850 m de profundidad así como y su metabolismo a lo largo de dos secciones a 21 (meso-eutrófico) y 26º N (oligotrófico). La biomasa presentaba una distribución en capas típica en ambos transectos. No obstante el promedio de la biomasa migradora (0-200 m) era 5,9 veces superior en el transecto eutrófico (153,39 ± 152,60 $mmolC \cdot m^{-2}$) que en el transecto oligotrófico (26,19 ± 11,01 $mmolC \cdot m^{-2}$). El flujo de carbono exportado debido a la respiración, era 10 veces mas alto en el transecto eutrófico que en el transecto oligotrófico (1,87 ± 1,81 y 0,19 ± 0,08 $mmolC \cdot m^{-2} \cdot d^{-1}$, respectivamente). Además, las estimaciones del flujo digestivo pigmentado fueron 50 veces superiores en el sur comparado con el norte (0,79 ± 0,94 y 0,02 ± 0,01 $mmolC \cdot m^{-2} \cdot d^{-1}$, respectivamente). La contribución total del metabolismo zooplanctónico al flujo de carbono particulado fue del 64,3% en el transecto oligotrófico, contrastando con el 119% observado en el transecto eutrófico. Estos resultados fueron comparados con una campaña realizada en la misma área durante el otoño con el propósito de determinar el efecto de la estacionalidad. Los flujos así como la biomasa de los migradores fue mas alta durante la primavera comparado con el periodo otoñal. La contribución del zooplancton migrador al flujo de POC fue de 1,8 hasta 14

veces mas alta durante la primavera que durante el otoño resaltando así la alta variabilidad de la contribución entre la primavera y el otoño.

Capitulo quinto

Secuestro de carbono y ciclos lunares del zooplancton: ¿ Podríamos estar perdiéndonos un componente importante de la bomba biológica ?

La explosión de zooplancton durante el *bloom* de finales de invierno en las aguas subtropicales fue estudiada en relación con la iluminación lunar en las aguas de la isla de Canarias. El enriquecimiento en nutrientes por mezcla y los depósitos de polvo promovieron *blooms* de fitoplancton y zooplancton. La biomasa mesozooplanctónica creció mientras progresaba la mezcla invernal pero presentó un máximo durante cada luna llena y disminuyó después, debido al efecto de depredación por parte de los migradores verticales (DVMs). El proceso fue similar al que se describe en lagos debido a la depredación por los peces y confirma que este fenómeno es también importante en el océano. El consumo estimado y el posterior transporte de biomasa zooplanctónica epipelágica por parte de los DVMs después de cada luna llena era del mismo orden de magnitud que el promedio del flujo gravitacional exportado. Además este consumo y transporte conforman un flujo de carbono no contabilizado hacia la zona mesopelágica, y que puede jugar un papel importante en la eficiencia de la bomba biológica.

En resumen, se demuestra que el transporte de carbono hacia los estratos más profundos en las aguas subtropicales no acaba con el hundimiento del carbono orgánico producido en las capas más superficiales. De hecho, el proceso es mucho más complejo, y parte de la producción es transportada hacia la zona mesopelágica por los DVMs. Los resultados arrojan algo de luz sobre el desacople entre la producción primaria y el flujo exportado de partículas en el océano y explica la periodicidad de 30 días observado en el flujo gravitacional en aguas oceánicas de la Corriente de Canarias. Además, este flujo activo puede explicar, por lo menos en parte, una fracción no contabilizada del flujo orgánico que promueve las demandas de carbono de bacterias y zooplancton en la zona mesopelágica. Las estimaciones biogeoquímicas de producción nueva variación en un rango entre 6,8 y 14,6 $mmolC \cdot m^{-2}$, siendo mucho más altas que las medidas de las trampas de sedimento, pero cerca de la suma del flujo gravitacional y de la estimas conservativas de los flujos activos publicados. Los resultados indican

un papel central del zooplancton epipelágico y los DVMs en la bomba biológica y nos acerca a la comprensión del destino de un *bloom*. Debido a la importancia de los migradores micronectónicos en el flujo activo es importante determinar la biomasa, la alimentación y el metabolismo de esta comunidad, algo todavía poco estudiado en el océano. En cualquier caso, el ciclo lunar vinculado al flujo activo descrito en este trabajo para las agua subtropicales oligotróficas representa un flujo de carbono importante hacia la zona mesopelágica y que no ha sido tomado en cuenta hasta ahora, lo cual requiere mas investigación. El descubrimiento de movimientos de DVMs entre 800 y 1300 m de profundidad siguiendo el ciclo lunar también nos hace entrever las distintas fases migratorias con consecuencias importantes en el transporte de carbono el océano profundo.

VII·5 DISCUSSIÓN

El comportamiento migratorio del zooplancton marino representa el transporte de biomasa más grande en la tierra. Estudios anteriores determinaron la alta variabilidad de la contribución de los migradores verticales (DVMs) a la bomba biológica. Comparado con el flujo pasivo de carbono orgánico particulado (flujo de POC), los valores de flujo activo varían desde <1 hasta >70% (Tabla 5.1 y referencias incluidas). Estos estudios utilizaron principalmente tasas metabólicas específicas relativas al tamaño basadas en una regresión multivariable (Dam *et al.*, 1995; Zhang y Dam, 1997; Roman *et al.*, 2002), incubaciones taxonómicas específicas (Steinberg *et al.*, 2000), incubaciones de crustáceos mezclados (Isla y Anadón, 2004) y muy pocos estudios utilizaron métodos enzimáticos como el del sistema de transporte de electrones (ETS) en la comunidad zooplanctónica total para determinar el flujo activo de carbono (Hernández-León *et al.*, 2001; Yebra *et al.*, 2005). En este trabajo, los flujos activos debido a los DVMs fueron determinados en el área del giro subtropical del Atlántico nordeste usando el ETS como método rutinario conjuntamente con un balance metabólico de la comunidad. Los resultados de este trabajo ampliaron los valores previamente publicados sobre el flujo activo del zooplancton y sugieren que el impacto de la migración vertical diaria en la bomba biológica es mucho más variable que lo previamente pensado con valores variando desde <1% hasta 119% del flujo pasivo de POC. Las causas de esta alta variabilidad se relacionan principalmente con la productividad en las capas superiores del océano, la estacionalidad, las estructuras mesoscalares, el comportamiento alimenticio, y la influencia de la iluminación lunar.

El ciclo productivo en las aguas subtropicales se caracteriza por el *bloom* de finales de invierno (Menzel y Ryther, 1961). Este *bloom* se origina con la erosión de la termoclina debido al enfriamiento de la superficie durante el invierno, lo cual aumenta la difusión vertical de nutrientes procedentes de debajo de la capa de mezcla. La influencia del *bloom* sobre la formación de partículas, su transformación y el flujo pasivo de POC es conocida (Neuer *et al.*, 2002).

Tabla 5.1. Flujos activos debidos al zooplancton en diferentes regiones oceánicas.

localización	Época del año	Biomasa migradora (mg C·m^{-2})	Flujo respiratorio (mg C·m^{-2}·d^{-1})	flujo digestivo (mg C·m^{-2}·d^{-1})	% del flujo POC	Referencias
Zona oligotrófica						
HOT		30.2 - 33.8	1.3-1.7	-	4[a]	Roman *et al.*, 2002
Divergencia Ecuatorial		2.8 - 21.8	0.9-1.2	-	<1-2[a]	Roman *et al.* (2002)
BATS	Marzo/Abril	192 (84–540)	14.5 (6.2-40.8)	-	34 (18-70)[a]	Dam *et al.* (1995)
BATS	Ciclo anual	50 (0-123)	2.0 (0-9.9)	-	8 (0-39)[b]	Steinberg *et al.* (2000)
BATS	Ciclo anual	83 (0.7-468)	-	0.8 (0.007-4.5)	4 (0.03-21)[c]	Schnetzer y Steinberg (2002)
Oeste ecuatorial	Octubre	46.9	3	-	6	Le Borgne y Rodier (1997)
Norte (Oceánico)	Oct-Nov	30 ± 10	2.2 ± 0.3	-	-	Isla y Anadón (2004)
Este ecuatorial	Marzo - Abril	96 ± 25.2	4.2 ± 1.2	-	18[a]	Zhang y Dam (1997)
Este ecuatorial	Octubre	154.8 ± 32.4	7.3 ± 1.4	-	25[a]	Zhang y Dam (1997)
ALOHA	Ciclo anual	162 (108-216)	3.6 (2.6 - 19.1)	-	15 (12-18)[a]	Al-Mutairi y Landry (2001)
ALOHA	Junio - Julio	157.9	3.7	-	18[a]	Steinberg *et al.* (2008)
Zona Eu- Meso-trófica						
Centro Ecuatorial (HNLC)	Octubre	52.9	6	-	4[a]	Le Borgne y Rodier (1997)
Norte (costa)	Oct-Nov	360 ± 70	30.3 ± 1.9	-	-	Isla y Anadón (2004)
Norte (corriente)	Oct-Nov	270 ± 210	10.4 ± 6.3	-	-	Isla y Anadón (2004)
Oeste ecuatorial	Octubre	46.9	3	-	6[a]	Le Borgne y Rodier (1997)
Oeste ecuatorial	Febrero	367 (144 - 447)	22.7 (7.3-19.1)	4.8 (2.6-4.4)	24 (13-35)[a]	Hidaka *et al.* (2001)
Corriente de Canarias						
Islas Canarias	Marzo	204 (108 - 341)	0.8 (0.5-1.4)	0.1 (0.05-0.18)[e]	1.8 (1.1-2.7)[d]	Capitulo 3.2
Islas Canarias	Junio	580 - 1280	1.8 - 8.3	0.1 - 0-4[e]	15-53[d]	Yebra *et al.* (2005)
Islas Canarias	Agosto	247 - 125	4.2 - 1.9	0.3 - 2.4[e]	20-45[d]	Hernández-León *et al.* (2001a)
26ºN	Sept-Oct	325 (106 - 486)	0.6 (0.02 - 1.2)	0.8 (0.01 - 3.0)[e]	3.3 (0.1-9.0)[f]	Capitulo 3.3
	Mayo-Junio	314 (163.2 - 408)	2.3 (1.7 - 3.4)	0.2 (0.03 - 0.4)[e]	47.8 (26.9-64.4)[f]	Capitulo 3.4
21ºN	Sept-Oct	857 (368 - 1601)	6.5 (1.1 - 14.9)	22.7 (1.3-96.1)[e]	66.0 (0.1-149.5)[f]	Capitulo 3.3
	Mayo-Junio	314 (426.4 - 4480)	2.3 (2.7 - 48.6)	9.5 (0.05-28.0)[e]	118.6 (29.1-273.7)[f]	Capitulo 3.4

[a] % del flujo de POC flux representa solo el flujo respiratorio. [b] Flujo activo incluye el DOC. [c] Flujo activo representa solo el flujo digestivo. [d] Flujo respiratorio mas flujo digestivo.

[e] Flujo digestivo determinado con GF. [f] Ingestión potencial determinada gracias a la respiración.

El *bloom* de finales de invierno en las aguas de las islas Canarias es también conocido del punto de vista de la biomasa planctónica y de la producción (De León y Braun, 1973; Arístegui *et al.*, 2001; Hernández-León, 2004).

La influencia de este pulso productivo sobre el flujo activo de carbono debido a la migración vertical se ha cuantificado por primera vez en este estudio. Un aumento en la proporción del flujo activo comparado con el flujo de POC al final del bloom fue observado (Capítulo 3.1; Figura 3.2.6). Este aumento del flujo activo de carbono podría determinar el transporte y el destino de la materia orgánica producida anualmente en el océano subtropical.

El vínculo entre la estacionalidad del afloramiento y la biomasa del mesozooplancton fue observado previamente por Postel (1990) y Hernández-León *et al.* (2007). Sin embargo, el efecto de la estacionalidad del afloramiento sobre el flujo activo de carbono debido a los DVMs no se ha mostrado hasta ahora (Capítulo 3.4). El promedio de la biomasa migratoria y la biomasa epipelágica (0-200 m) fue de 2 a 5,8 veces superior durante la primavera comparado con el otoño (Capítulo 3.4, Tabla 3.4.1), y la contribución total de la comunidad migratoria al flujo activo de carbono fue 3,4 hasta 3,7 veces más alta durante la primavera (Tabla 3.4.1). La contribución al flujo activo de carbono debido a los migradores respondió coherentemente al contraste estacional mostrando una exportación activa de carbono más alta durante la primavera que durante el otoño. De manera general, durante la primavera la exportación de carbono aumentó aproximadamente de 4 veces comparado con el período otoñal. La intensidad del afloramiento aumenta la productividad durante el verano y, por lo tanto, aumenta localmente la cantidad de carbono exportada hacia las aguas profundas por el zooplancton migrador.

Otra causa para una contribución más alta al flujo activo del carbono por parte de los migradores verticales es la alta variabilidad promovida por las estructuras hidrográficas de mesoscala tales como remolinos, las áreas de afloramiento presentes a lo largo de la costa africana, filamentos, meandros y frentes, que son características típicas del área estudiada. El flujo de la

Corriente de Canarias se caracteriza por la fuerte disrupción debida al archipiélago Canario, formando a sotavento del mismo, una región de alta actividad macro y mesoscalar. Esta área fue descrita recientemente como *Canary Eddy Corridor* (la CEC; Sangrà *et al.*, 2009). La CEC es una área de alta variabilidad en productividad que transporta masas de agua y exporta la producción planctónica desde el sistema de afloramiento costero meso-eutrófico al océano oligotrófico. Mas al sur, la zona frontal de Cabo Verde (CVFZ) es una área altamente productiva influenciada por el afloramiento cuasi permanente de Cabo Blanco y por un frente termohalino.

Los flujos activos de carbono determinados en la zona no influenciada por las estructuras de mesoscala, al norte de las Islas Canarias, mostraron ser de 1 a 5 veces más bajos que en la parte sur del archipiélago (Capítulo 3.2; Figura 5.1). Solo pocas estimaciones contribuyen más que el 25% del flujo de POC, y esas estimaciones fueron relacionadas sobre todo con las valoraciones realizadas en las áreas caracterizadas por la presencia de estructuras mesoescalares identificadas en este trabajo (afloramiento, frente termohalino, meandros, remolinos; Figura 5.1).

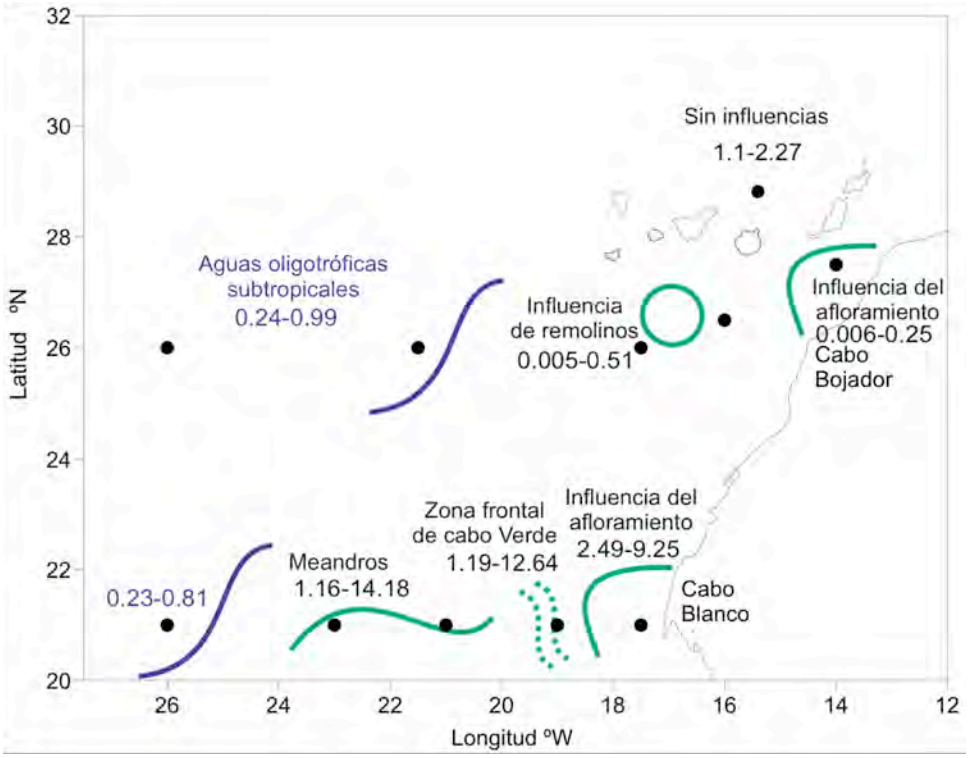

Figura 5.1. Principales estructuras mesoescalares, zonas de influencia y valores máximos de flujos activos medidos durante el verano y el otoño respectivamente (en mmolC·m^{-2}·d^{-1}).

Estas estructuras hidrológicas podrían localmente aumentar la producción primaria, concentrar la biomasa epipelágica y permitir una mayor cantidad de presas para la comunidad de migradores.

La importancia de la estacionalidad y de las estructuras a mesoscala es bastante clara en cuanto se observa la alta variabilidad de los valores del flujo activo debido al zooplancton. Sin embargo, no está siempre claro cual de los procesos contribuye en una área concreta pues los efectos podrían obrar recíprocamente.

Entonces, el origen de la variabilidad del flujo activo de carbono es difícil de determinar. No obstante el uso del balance metabólico (respiración, ingestión potencial y el índice omnivoría) de la comunidad de los migradores comparado con la comunidad epipelágica ha demostrado ser una herramienta potente para determinar qué sucede a la comunidad de los migradores (Capítulos 3.2; 3.3; 3.4). De hecho, la disponibilidad de alimentos es el punto de partida del metabolismo y la influencia de la dieta y los cambios de la dieta han demostrado poder modificar los flujos activos de carbono (capítulo 3.2; Figura 3.2.6). La comunidad zooplanctónica epipelágica, como fuente de comida, podría condicionar la comunidad migratoria en términos de alta/baja disponibilidad de presas de la abundancia. Al sur del Archipiélago Canario se observo un gradiente de productividad latitudinal y longitudinal desde el norte hacia el sur y desde la zona de afloramiento en la costa Africana hacia el océano abierto, que afectó a los flujos activos de carbono debidos a los migradores (Capítulos 3.3; 3.4). En las aguas eutróficas de la zona del afloramiento, la productividad fitoplanctónica es incrementada y el fitoplancton grande así como el zooplancton se desarrolla, favoreciendo los migradores y el desvío de energía y materia a través de la vía macrobiana (Hernández-León, 2009), aumentando el flujo activo de carbono (Capítulos 3.3; 3.4). Por el contrario, en aguas oligotróficas la materia y la energía producidas se canaliza a través del microzooplancton hacia la vía microbiana, reduciendo la cantidad de carbono disponible para la comunidad migratoria y el flujo activo de carbono (capítulo 3.3; 3.4). Esta explicación es posible puesto que >60% de la producción primaria en la

región de Canarias, así como en otras áreas oligotróficas, se puede atribuir a las células picoplanctónicas (<2µm, Arístegui *et al.*, 2001), las cuales están por debajo del tamaño de detección o de predilección como fuente de alimento para los copépodos (Calbet y Landry, 1999). Los organismos no pigmentados constituyen una porción grande (35-80%) de la dieta del zooplancton en aguas oligotróficas (Hernández-León *et al.*, 2001, 2002, 2004; capítulos 3.2; 3.3; 3.4), lo cual se corresponde con los resultados de otros autores que trabajan en las aguas oligotróficas (Dam *et al.*, 1995; Gaudy *et al.*, 2003).

Así, la disponibilidad de comida para los migradores puede ser otra causa de la alta variabilidad del flujo activo de carbono, dependiendo de la productividad y de la estructura de la red trófica de las áreas estudiadas y probablemente de la composición taxonómica.

El transporte de carbono hacia aguas profundas en las aguas subtropicales no termina con el hundimiento del carbono orgánico producido en las capas más superficiales. De hecho, el proceso es mucho más complejo, y parte de la producción se desvía a la zona mesopelágica debido a la actividad depredadora de los migradores sobre el zooplancton epipelágico (Capítulos 3.2; 3.3; 3.4; 3.5). Los cálculos basados en la desaparición de la biomasa zooplanctónica epipelágica durante el ciclo lunar indica valores de flujo activo debido a la depredación del 63% del flujo gravitacional (Hernández-León *et al.*, 2002; Capítulo 3.5). El consumo estimado y el subsiguiente transporte de biomasa zooplanctónica epipelágica por los migradores después de cada luna llena es del orden del promedio de la exportación gravitacional y es un flujo de carbono hacia la zona mesopelágica no considerado, que puede desempeñar un papel fundamental en la eficacia de la bomba biológica. Las consecuencias biogeoquímicas del ciclo lunar sobre la bomba biológica en el océano deben ser consideradas seriamente. Por otra parte, la influencia del ciclo lunar podría explicar también la periodicidad de 30 días en el flujo gravitacional (Khripounoff *et al.*, 1998) así como el desfase entre la producción primaria y el flujo exportado de partículas en el océano (Michaels *et al.*,1994; Karl *et al.*, 1996).

Por lo tanto, el modelo desarrollado (Capítulo 3.1) vincula por primera vez los movimientos verticales de biomasa, los procesos metabólicos y los flujos activos de carbono. La influencia de la luz sobre la distribución vertical del zooplancton fue reproducida con éxito y las hipótesis empleadas con este fin apoyan el efecto de la fauna interzonal sobre epizooplancton durante el ciclo lunar observado (Hernández-León, 1998; Hernández-León *et al.*, 2001, 2002; Capítulo 3.5). De hecho, estas hipótesis podrían también explicar la influencia de la luz del sol y de la luna sobre las migraciones verticales (Casper y Thorp, 2007; Van Haren, 2007; Hernández-León *et al.*, 2010) así como la distribución de los migradores durante acontecimientos tales como eclipses (Sherman y Honey, 1970; Tarling *et al.*, 1999; Strömberg *et al.*, 2002; Economou *et al.*,2008).

Así, los resultados sugieren un papel fundamental del zooplancton epipelágico y de los migradores en la bomba biológica y dan una idea sobre el destino de un *bloom*. Debido a la importancia de los migradores micronectónicos sobre el flujo activo (Hidaka *et al.*, 2001) es importante evaluar la biomasa, la alimentación, y el metabolismo de esta comunidad, que de hecho es una laguna en nuestro conocimiento del océano. En todo caso, el flujo activo vinculado al ciclo lunar descrito para las aguas oligotróficas subtropicales (Capítulo 3.5) representa un flujo de carbono importante y no estimado hacia la zona mesopelágica que merece una investigación adicional. El hallazgo de los movimientos de migradores entre 800 y 1300 m de profundidad siguiendo el ciclo lunar (Van Haren, 2007) también no da una idea sobre el funcionamiento de la escalera de migración (Vinogradov, 1970) con sus importantes consecuencias para el transporte del carbono hacia el océano profundo.

Finalmente, los datos recogidos en este trabajo pueden utilizarse para demostrar la robustez del modelo propuesto en el capítulo 3.1. Los resultados preliminares obtenidos de simulaciones iniciales (Figura 5.2 y Tabla 5.2) mostraron encajar adecuadamente con perfiles *in situ*. Los flujos integrados (Tabla 5.2) obtenidos con el modelo mostraron varias diferencias comparados con los datos *in situ*, por lo tanto requerirían análisis adicional. Este trabajo

representa una contribución de aproximadamente un 70% de la información disponible para el área de Canarias y un 20% del volumen total de datos publicados sobre los flujos activos de carbono atribuidos a los migradores a escala global. El uso de toda esta información conjuntamente con el modelo citado anteriormente mejorará nuestro conocimiento sobre la importancia del flujo activo en el océano.

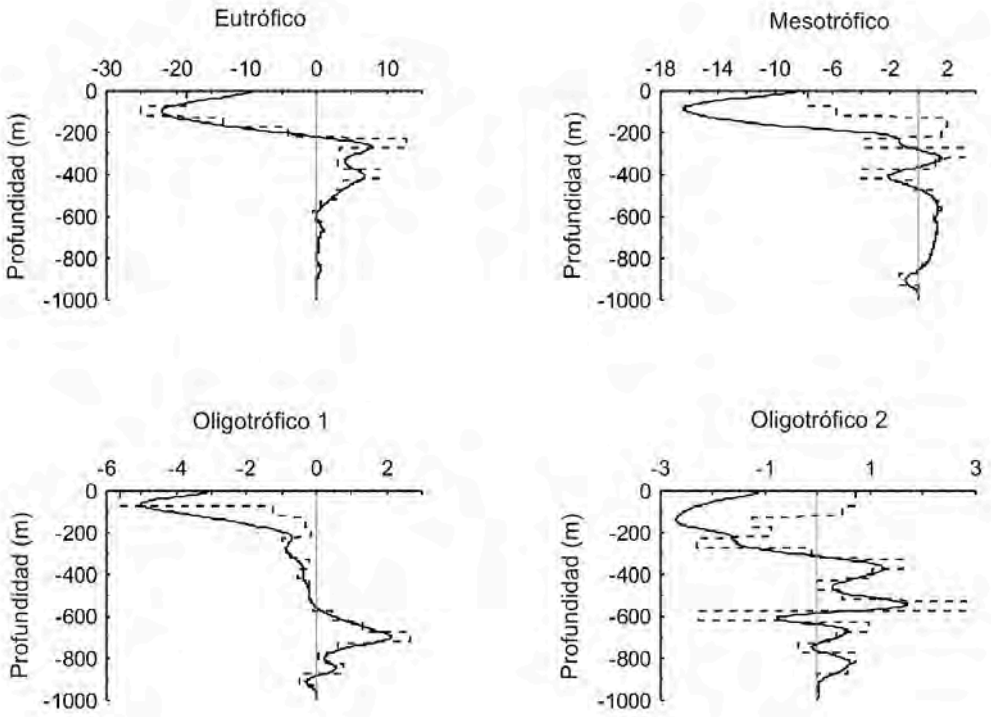

Figura 5.2. Comparación de valores día-menos-noche entre la biomasa zooplanctónica proveniente de simulaciones (línea continua) y los valores *in situ* (línea discontinua) para diferentes condiciones tróficas.

Tabla 5.2. Comparación entre valores simulados y valores *in situ* para diferentes condiciones tróficas. Biomasa migradora (MB) en mmolC·m^{-2}, Flujo respiratorio (RF) en mmolC·m^{-2}·d^{-1}.

	Eutrófico		Mesotrófico		Oligotrófico 1		Oligotrófico 2	
	Simulado	*In situ*	Simulado	*In situ*	Simulado	*In situ*	Simulado	*In situ*
MB	250.7	254.5	157.1	55.6	55.7	50.1	40.9	47.9
RF	7.1	4.1	2.1	0.7	9.5	0.3	0.22	0.33

VII·6 CONCLUSIONES

Las conclusiones principales de esta tesis son:

1. El modelo desarrollado reproduce tanto el comportamiento migratorio, en términos de velocidad y amplitud migratoria, como, el flujo activo de carbono del zooplancton grande. Este modelo se puede utilizar como herramienta predictiva para las aguas oligotróficas.

2. Las hipótesis forzantes empleadas soportan el efecto de la fauna interzonal sobre el epizooplancton durante el ciclo lunar y se pueden emplear para estudiar el impacto significativo de este ciclo en el flujo activo de carbono.

3. El *bloom* tardío de invierno es mucho más complejo que divulgado previamente. La red trófica pelágica en las aguas subtropicales es gobernada por la interacción entre los recursos y los consumidores. Esta interacción tiene consecuencias tanto en la dieta de los organismos migradores como sobre el flujo activo de carbono.

4. El pulso productivo de finales de invierno aumentó el flujo activo de carbono exportado debido a la migración verticale. Este aumento, nos da una idea del destino de una parte de la materia orgánica producida anualmente en el océano subtropical. Esta exportación activa de carbono durante el *bloom* de finales de invierno se ha cuantificado por primera vez en este trabajo.

5. El complejo sistema hidrológico al sur del Archipiélago Canario afecta el flujo activo de carbono. La alta variabilidad latitudinal y longitudinal observada en el flujo activo de carbono se relaciona con la productividad local, la estructura de la red trófica, y la presencia de estructuras mesoscalares.

6. El flujo activo de carbono debido a los migradores verticales responde coherentemente a las condiciones estacionales con flujos más altos

durante la primavera que durante el otoño. Las diferencias estacionales observadas afectaron tanto la biomasa epipelágica zooplanctónica como la biomasa migradora. Este es el primer estudio que muestra el vínculo entre la productividad estacional del afloramiento y el flujo activo de carbono debido a los migradores verticales.

7. El flujo activo de carbono en el área meso-eutrófica era más alto comparado con el área oligotrófica confirmando de nuevo la influencia de la productividad local. Esta productividad local aumentó el flujo activo de carbono y determinó el transporte y el destino de una parte de la materia orgánica producida anualmente en la zona de estudio.

8. El uso de ecuaciones metabólicas demostró ser útil para determinar el origen del carbono activamente exportado por la comunidad migradora. El balance metabólico también demostró una adaptación de la dieta de la comunidad migradora a la estructura planctónica epipelágica. La cantidad de carbono exportado activamente hacia el océano profundo esta vinculado a la estructura planctónica de las capas superficiales.

9. Durante el ciclo lunar, la comunidad de los migradores fue responsable de un incremento significativo del flujo activo de carbono hacia la capa mesopelágica. Este aumento cíclico del flujo activo de carbono es del orden del promedio del flujo gravitacional y no ha sido cuantificado hasta este estudio. Así, el ciclo lunar puede desempeñar un papel fundamental y recurrente en la eficacia de la bomba biológica.

VII·7 LÍNEAS FUTURAS DE INVESTIGACIÓN

Los resultados obtenidos en esta tesis aumentaron nuestro conocimiento sobre el flujo activo de carbono debido al ciclo diario de los migradores verticales en el giro subtropical del Atlántico nordeste y se podrían utilizar como referencia para futuros estudios.

En este trabajo destaca la alta variabilidad del flujo activo de carbono. La evolución, la productividad y las relaciones tróficas entre la comunidad epiplanctónica y los migradores verticales merece más investigación para determinar el origen de la variabilidad del flujo activo de carbono.

Un estudio a largo plazo del flujo activo de carbono debido a los migradores verticales (incluyendo el micronecton) se debe considerar para cuantificar la variabilidad anual así como la influencia del ciclo lunar sobre la cantidad de carbono transportada anualmente a la capa mesopelágica.

La cantidad de datos recogidos *in situ* en las diversas áreas muestreadas y condiciones hidrológicas se podrían utilizar para mejorar la robustez del modelo y además, para realizar un análisis de sensibilidad de cada uno los parámetros del modelo.

Finalmente, el modelo propuesto se podría implementar y debería incluir la influencia de la luna. También, la posible incorporación de este modelo de migración a un modelo regional (sistema de modelado regional del océano, ROM) debería estudiarse.

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