@AGUPUBLICATIONS

Journal of Geophysical Research: Oceans

RESEARCH ARTICLE

10.1002/2016JC011667

Key Points:

- The meandering jet constitutes a major source of biological enrichment in the Alboran Sea
- The production varies seasonally depending on the intensity of the jet at the exit section of the Strait of Gibraltar
- Cross-frontal ageostrophic circulation and eddy pumping both support the production in summer-autumn

Correspondence to:

B. Mourre, bmourre@socib.es

Citation:

Oguz, T., B. Mourre, and J. Tintoré (2016), Upstream control of the frontal jet regulating plankton production in the Alboran Sea (Western Mediterranean), J. Geophys. Res. Oceans, 121, 7159–7175, doi:10.1002/ 2016JC011667.

Received 20 JAN 2016 Accepted 12 AUG 2016 Accepted article online 18 AUG 2016 Published online 30 SEP 2016

Upstream control of the frontal jet regulating plankton production in the Alboran Sea (Western Mediterranean)

Temel Oguz^{1,2}, Baptiste Mourre¹, and Joaquín Tintoré^{1,3}

¹SOCIB, Balearic Islands Coastal Observing and Forecasting System, Parc Bit, Palma de Mallorca, Spain, ²Institute of Marine Sciences, Middle East Technical University, Mersin, Turkey, ³IMEDEA (CSIC-UIB), Esporles, Spain

JGR

Abstract Using a coupled physical-biological model, we document that a ~30 km wide meandering jet constitutes a major source of biological enrichment in the Alboran Sea (Western Mediterranean) even in the absence of wind forcing and tidal dynamics. The level of enrichment is shown to vary markedly during the year depending on the upstream characteristics of the jet as it exits from the Gibraltar Strait. When its intensity is sufficiently low and characterized by weaker cross-frontal density gradients during winter-spring, the jet is weakly nonlinear and may not fulfill the necessary conditions for frontogenesis. It then remains weakly productive. In the case of stronger jet intensity (>1.1 Sv) accompanied by stronger cross-frontal density and velocity gradients within the Alboran Sea during summer-autumn, the frontal jet becomes strongly nonlinear and ageostrophic with large cross-frontal vorticity changes on the order of planetary vorticity. Under these conditions, upward vertical velocities in the range 10–50 m d⁻¹ supply nutrients into the euphotic layer more effectively and support high-level frontogenesis-induced phytoplankton production on the anti-cyclonic side of the main jet axis. The strong eddy pumping mechanism also provides a comparable level of plankton production within strongly nonlinear elongated cyclonic eddies along the outer periphery of the frontal jet. The plankton biomass is advected partially by the jet along its trajectory and dispersed within the basin by mesoscale eddies and meanders.

1. Introduction

The ways in which dynamic eddy-dominated circulation systems regulate nutrient transport and sustain productivity by various processes including eddy stirring and trapping, nutrient enrichment due to eddy-induced horizontal transports, eddy pumping, eddy-wind interactions, and ageostrophic cross-frontal circulation were examined by numerous modeling studies for idealized open ocean systems (see reviews by *Thomas et al.* [2008], *McGillicuddy* [2016], and *Mahadevan* [2016, and references therein]). Coastal and semienclosed seas, as impacted by multiple stressors, are exposed to particularly complex physical and biogeochemical processes and interactions at a wide range of spatial and temporal scales, which has limited our understanding of these systems so far. The present study elucidated specifically the roles of frontal-induced production in the Alboran Sea of the Western Mediterranean as an attempt to better understand the coupling between flow and plankton dynamics within coastal and semienclosed seas. This role has never been explored in details up to now, although frontal zones associated with buoyant jets and boundary currents have been recognized as biogeochemical hot spots in coastal, marginal, and semienclosed seas.

Frontal-induced production arises from the ageostrophic frontal dynamics. As described by *Mahadevan* [2016], the nonlinear interactions between the lateral velocity shear and buoyancy gradient sharpen the cross-frontal density gradient and cause collapse of the along-front geostrophic balance. The way in which it is restored requires developing an additional ageostrophic secondary circulation (ASC) across lateral density variations. The ASC upwells more dense deep waters toward the surface on the anticyclonic (light) side of the front near the crests of meanders (i.e., excursion of the frontal zone toward the more dense side) and subducts relatively dense surface waters toward deeper levels on the cyclonic (dense) side of the front near the troughs (i.e., excursions of the frontal zone toward the less dense side). The ASC is closed by the ageostrophic cross-front flow from the light side to the dense side near the surface and vice versa at deeper levels. This process restratifies the upper layer water column and thus reduces the cross-frontal density gradient to keep the flow in the geostrophic balance. The restratification process was shown to provide a

© 2016. American Geophysical Union. All Rights Reserved.

AGU Journal of Geophysical Research: Oceans



Figure 1. The location of the model domain (large rectangular box in blue color) within the Western Mediterranean Sea and its major morphological features such as the Western Alboran basin (1), the Eastern Alboran basin (2), the Algerian basin (3), the Alboran Ridge between the eastern and western basins (4), the Cape three Forcas along the south coast (5), and the Gibraltar Strait (6), Marbella (7), Almeria (8), and Oran (9). TRG denotes the meridional transect across the Gibraltar exit section. The bathymetry contours are plotted from 200 to 2000 m with the contour intervals of 200 m. While the large rectangular box shows the actual model domain, the small rectangular box (in red color) constitutes the Alboran Sea as the main region of interest in the present study.

positive contribution to the initiation of the spring bloom episode following the deep winter mixing of surface waters in high latitudes [*Mahadevan et al.*, 2012]. The biological implication of the ASC is to inject nutrients into the nutrient-starved photic layer at the anticyclonic side of the frontal zone and to subduct phytoplankton biomass at the dense side of the front [*Spall and Richards*, 2000; *Lévy et al.*, 2001; *Martin et al.*, 2001; *Lima et al.*, 2002; *Rivierea and Pondaven*, 2006; *Mahadevan et al.*, 2012].

The upper layer circulation system of the Alboran Sea (AS) possesses a well-defined meandering Atlantic Jet (AJ) maintained by the continuous supply of fresh Atlantic water mass on the order of 1 Sv (=10⁶ m³ s⁻¹) from the Gibraltar Strait (GS). It enters the sea as a narrow (~20 km) surface intensified buoyant jet within the uppermost 100–150 m. The incoming jet involves large lateral vorticity and buoyancy changes and attains highly nonlinear character up on exiting from the GS. It first interacts with the Western Alboran anticyclonic Gyre (WAG) and modifies its size and orientation. It then flows toward the Algerian basin either as a large meandering jet supporting an anticyclone called Eastern Alboran anticyclonic Gyre (EAG), or a weak-ly meandering mid-basin jet with several anticyclonic coastal eddies, or as a coastal boundary current along the African coast [*Renault et al.*, 2012].

In the AS, the long-term satellite data indicated higher chlorophyll concentrations along the AJ trajectory, particularly around the periphery of the WAG [see *Navarro et al.*, 2011, Figure 1; *Oguz et al.*, 2013, Figure 1; *Sanchez-Garrido et al.*, 2015, Figure 2b]. They were related predominantly to mesoscale and submesoscale frontal processes by diagnostic analysis of the available data [*Tintore et al.*, 1991; *Gomis et al.*, 2001; *Rodriguez et al.*, 2001] and in situ observations [*Ruiz et al.*, 2001; *García-Lafuente and Delgado*, 2004]. The three dimensional coupled physical-biological modeling study [*Oguz et al.*, 2014] expressed the enhanced production in terms of the nonlinear flow dynamics in the regions of large horizontal shear and strain rates along the AJ trajectory under winter mean climatological conditions, the steady barotropic transport, and water mass characteristics retained at the western open boundary, without lateral supply of nutrients and biogenic material from the GS. The present study modifies the previous one by allowing for temporally varying



Figure 2. Daily variations of the basin-averaged total heat flux (black color) and photosynthetically available radiation (red color) over the year. They were derived from the long-term averaged (1990–2009) heat flux data and filtered by the 7 days median filtering.

upstream characteristics of the jet intensity and water mass characteristics during the year, and thus simulated the annual structures of nutrient concentrations and plankton biomass within the AS in response to the temporal and spatial changes in the flow dynamics and biogeochemical characteristics.

The significance of the present study is to emphasize the importance of ageostrophic frontal dynamics and related plankton production along a buoyant jet trajectory within a semienclosed sea where the horizontal scale of fron-

tal processes is an order of magnitude smaller than open ocean frontal systems in oligotrophic subtropical waters [*Lévy et al.*, 2001; *Mahadevan and Tandon*, 2006] and in high-latitude subpolar waters [*Taylor and Ferrari*, 2011; *Mahadevan et al.*, 2012]. The present study also suggests the eddy pumping mechanism as an equally important biological enrichment process inside the strongly nonlinear cyclonic eddies with the Rossby number on the order of unity.

The subsequent section describes major features of the coupled physical-biological model invoked for the present study. It is followed by the presentation of flow characteristics at the GS exit section, the analysis of the physical characteristics of the annual frontal jet structure, and the description of the annual phytoplank-ton production characteristics supported by the frontogenesis and eddy pumping mechanisms. The paper concludes with an overview of the model findings and their contributions to our present level of understanding.

2. Model Description

2.1. Main Features of the Model

A five compartment biological model was embedded online into the Princeton Ocean Circulation Model (POM). The POM solves the three-dimensional Reynolds-averaged Navier-Stokes equations using the hydrostatic and Boussinesq approximations and the terrain-following vertical sigma coordinate system. The reader is referred to *Mellor* [2003] for a more complete description of the model features. In the present application, the horizontal advection terms in the biological equations were discretized by the fourth-order centered difference scheme [*Shchepetkin and McWilliams*, 2003]. Similarly, the horizontal pressure gradient terms in the momentum equations were solved by the fourth-order accurate scheme [*McCalpin*, 1994; *Mellor et al.*, 1998]. The vertical viscosity and diffusivity at each grid point were estimated by the 2.5 level Mellor-Yamada turbulence energy parameterization, whereas the horizontal viscosity was defined by the Smagorinsky parameterization. The horizontal diffusivity was set to half of the horizontal viscosity.

The biological model comprised the small and large phytoplankton size groups (P_s and P_L), zooplankton (Z), particulate organic nitrogen (D), and dissolved inorganic nitrogen (N) compartments [e.g., *Lima et al.*, 2002; *Rivierea and Pondaven*, 2006; *Oguz et al.*, 2013]. Please refer to Appendix A for a more detailed description of the biological model. The biological source-sink terms, their functional forms, and the definitions and values of the parameters are listed in Tables A1–A3, respectively.

2.2. Model Implementation to the Alboran Sea

The model domain covered the region from 6°W in the Gulf of Cadiz beyond the western exit of the GS to 1.6°E longitude in the western Algerian Basin and 39.0°N latitude at the Ibiza Channel of the Balearic Sea (Figure 1). It represented the westernmost part of the Western Mediterranean as shown by the larger rectangular box in Figure 1. The primary region of our interest, however, was limited to the region from the eastern exit of the GS to the Almeria-Oran cross section (the smaller rectangular box in Figure 1); the rest of the model domain served as the buffer zone to keep likely effects of open boundary conditions away from the main region of interest. The topography was retrieved from the 1 min global data base (http://topex. ucsd.edu/cgi-bin/get_data.cgi). It was interpolated to the model grid using the bilinear interpolation with some smoothing to reduce the pressure gradient error in the regions of steep topographic slopes. The topography was characterized by a general upward slope from 2000 m in the Algerian basin to about 500 m near the GS entrance region. Its eastern and western basins with maximum depths of 1800 and 1400 m, respectively, were separated by the Alboran Ridge and the Cape Three Forks at 3°W longitude along the south coast (Figure 1). These deep basins joined to narrow shelves of the Spanish and African coasts by steep topographic slopes.

The water column was represented by 25 sigma levels that were compressed toward the free surface and the bottom to better incorporate the boundary layer dynamics and the biological processes within the upper 100 m. The model domain was discretized by the horizontal grid dimensions of 0.04° (~ 3.1 km) in the zonal direction and 0.025° (~ 2.8 km) in the meridional direction. This grid size was adequate to resolve mesoscale features in the AS but may not be fine enough to represent submesoscale dynamics and details of the flow and biological characteristics along the GS. Nevertheless, the model incorporated the constriction region at the Tarifa Narrows and the eastern exit region of the GS reasonably well. The contributions of wind forcing and tidal and internal wave motions were excluded in order to better pinpoint the role of ASC in the plankton production characteristics. For their contributions on the local oceanographic characteristics, please refer to the recent works by *Peliz et al.* [2013], *Sannino et al.* [2014], and *Sanchez-Gorrido et al.* [2015].

Time step was set to 6 s for the barotropic (external) mode calculations of the circulation model and 180 s for the baroclinic (internal) mode as well as for the biological fields. The flow was initialized by the state of rest and horizontally uniform temperature, salinity, and nitrate profiles representative of the January-mean climatological conditions while the other state variables of the biological model were set to small values. Starting from such an idealized initial state, the model developed the physical and biological equilibrium states in response to the prescribed boundary conditions and the atmospheric forcing. The physical model equations were first integrated for 1 year and then together with the biological model equations for another 4 years. The first 2 years of the coupled model integration constituted the transient adjustment phase of the biochemical fields toward their quasi-equilibrium states. The solutions described in the subsequent sections were based on the fourth year of the coupled model integration.

2.3. Atmospheric Forcing

The circulation model was forced at the surface by the daily total climatological heat flux and shortwave radiation retrieved from the ERA40 Reanalysis data (Figure 2). Because of their weak spatial variability over the AS [*Criado-Aldeanueva et al.*, 2010], they were taken to be horizontally uniform, for simplicity. The Photosynthetically Available Radiation (PAR) was set to half of the shortwave radiation as a simplification to its more complex parameterization including its daily variations since this does not constitute a critical aspect for the present study. Both the PAR and the total heat flux data were smoothed by the Gaussian filter to



Figure 3. Annual variation of the upper layer transport at the eastern exit of the Gibraltar Strait computed from the fourth year model simulation. The vertical lines show three instants of the model year corresponding to the high (~1.3 Sv at day 1335; 15 September), intermediate (~1.0 Sv at day 1090; 10 January), and low (~0.7 Sv at day 1170; 30 March) transports. The data are sampled every 5 days for this plot.

exclude their high-frequency oscillations shorter than 1 week. The total heat flux forcing also included a restoring term by nudging the model computed sea surface temperature to its daily climatological value using the nudging parameter 80 W $m^{-2\circ}C^{-1}$. The nudging term, however, is of secondary importance. It introduces only a minor correction mainly affecting the summer temperature fields above the thermocline. The seasonal most intense cooling (around -150 W m^{-2}) took place during January and first half of February whereas the moderate cooling (between -50 and -150 W m^{-2}) occurred during October-November and second half of **AGU** Journal of Geophysical Research: Oceans



Figure 4. The meridional cross section of (a) density, (b) current speed, (c) nitrate concentration within the upper 100 m layer of the water column at the eastern exit of the Gibraltar Strait (the transect TRG in Figure 1) at day 1335, and (d) the zonal cross section of the current speed within the eastern part of the Gibraltar Strait (25–50 km) and the adjacent Alboran Sea (50–65 km), (e) the positions of the zonal cross section (marked by rectangles), the Tarifa Narrows region, and the cross-section TRG at the eastern exit of the GS.

February–first half of March. The most intense warming (>150 W m⁻²) was realized during May–August whereas September and April corresponded to the transitional moderate warming phases. The PAR varied annually from its maximum values ~150 W m⁻² during May–August to a minimum value ~50 W m⁻² during December–February.

2.4. Lateral Boundary Conditions

The free radiation conditions were specified for both the barotropic and baroclinic velocity components normal to the eastern and northern open boundaries that were placed sufficiently away from their direct influence on the AS circulation. The absence of inflow currents from these boundaries implied no impact of the Algerian and Balearic basin circulations on the Alboran Sea flow structure that was consistent with the



Figure 5. Horizontal distributions of density (kg m⁻³) at 25 m depth during (a) 15 September (day 1335) and (b) 10 January (day 1090). The bold black line represents the zero vorticity isoline, and the colored pattern shows the current speed of the jet stream (m s⁻¹). The straight line crossing zonally the western basin along 36.2° N latitude is the position of transect TR0.

Density



Figure 6. Vertical structures of density (kg m⁻³) along the transect TR0 during (a) 15 September (day 1335) and (b) 10 January (day 1090).

observations to a first order [*Millot and Taupier-Letage*, 2005]. In addition, the sponge layers of linearly increasing horizontal diffusivity were included along seven grid points (~20 km) nearest to the eastern and the northern open boundaries. Temperature, salinity, and biological fields along these open boundaries were computed from the model during the outflow conditions, and set to their values at the previous time step otherwise (which is consistent with the absence of inflow from the outside domain).

At the western open boundary, the daily varying temperature profiles were prescribed from the monthly climatological data, but the salinity profile was kept unchanged (at 36 psu within the upper 200 m) during the year due to its rather small range of variations. The zonal current velocity was prescribed in the form of two vertically uniform profiles above and below 200 m depth. They varied sinusoidally during the year to retain temporal variability of the observed layer transports and the barotropic transport [García-Lafuente et al., 2002]. Thus, the layer transports across the GS were developed not only in response to the prescribed current structure but also to an additional baroclinic contribution from the prescribed temperature and salinity structures at the western boundary. The water mass properties and transports were likely further modified along the GS by the hydraulic controls. The Atlantic water mass entering the AS was, however, always fresher than the ambient water mass of the AS. No biological fluxes were imposed along this boundary for simplicity, except retaining the initial nitrate profile at the western boundary.

3. Results

3.1. Flow Characteristics at the Gibraltar Exit Section

To begin with, it is appropriate to identify characteristics of the flow as it leaves the GS. The AJ intensity at the



Figure 7. Horizontal distributions of integrated phytoplankton biomass (mmol m^{-2}) over the 100 m water column during (a) 15 September (day 1335), (b) 10 January (day 1090), and (c) 30 March (day 1170) corresponding to the high, intermediate and low transport conditions of the AJ. Relative vorticity contours normalized by the planetary vorticity are embedded on the phytoplankton distributions. Their positive values are shown in red and negative values in green color. The black line represents the zero vorticity isoline separating the cyclonic-anticyclonic regions.

eastern exit section of the GS varied from its relatively high values up to 1.3 Sv in August-September to low values of 0.8 Sv in March-April (Figure 3). This setting was in agreement with the observed ranges of transports across the GS [García-Lafuente et al., 2002; Macias et al., 2008; Soto-Navarro et al., 2010], but it did not incorporate its anomalous occasional short-term changes (e.g., its reduction under exceptionally high atmospheric pressure rise in the Western Mediterranean with respect to that of the Eastern Atlantic).

Along the meridional cross-section TRG at the GS exit, maximum currents were confined roughly into 10 km wide deep central channel with magnitudes as high as 1.3 m s^{-1} at the surface decreasing to $\sim 0.3 \text{ m s}^{-1}$ at 100 m depth (Figure 4b). Defining the vertical component of the relative vorticity as $\zeta \approx -\partial u/\partial y$, the AJ acquired a strong negative relative vorticity on the southern side of the main jet axis (at 10-20 km zone of the transect) as opposed to the positive vorticity on the northern side (at 20-30 km range). They were comparable to the planetary vorticity and thus the jet was strongly nonlinear upon entering the AS. In the region of positive relative vorticity with strong upward motion, the isopycnals tilted upward as identified by rising of 27 kg m⁻³ isopycnal from 100 m depth near the south coast to near-surface on the north coast (Figure 4a). All these features were in fact related to hydraulic adjustment of the upper layer flow within the Tarifa Narrows upstream of the GS exit section where the width of the strait shrinks considerably with

respect to the exit sections on its both sides (Figure 4e). For example, taking the mean current speed as 1.0 m s^{-1} and the density difference as 0.5 kg m^{-3} for the upper 75 m layer, the value of the Froude number $F = u^2/g'h \approx 4$ exceeded unity, suggesting the supercritical flow condition fulfilled at the exit section. The hydraulic adjustment of the upper layer flow can be better illustrated by the zonal cross section of the current speed along the central part of the GS (Figure 4d). Within the Tarifa Narrow section of the strait (30–45 km range in Figure 4d and between the points C and E in Figure 4e) the upper layer flow was compressed by strong upward motion in response to its hydraulic adjustment that took place at the distance of 35 km along the transect (the point C). As a result, the current speed exceeded 1.0 m s⁻¹ at near-surface levels further eastward, indicating its buoyant jet character up on entering the AS. In Figure 4d, the GS eastern exit (the transect TRG in Figure 4e) was located within the supercritical zone roughly



Figure 8. Horizontal distributions of the vertical component of relative vorticity normalized by the planetary vorticity at the time of intense Atlantic Jet from 27 September (day 1347) to 17 October (day 1368). Their positive values are shown in red and negative values in green color. The black line represents the zero vorticity isoline separating the cyclonic-anticyclonic regions.

15 km away from the hydraulic control section, at the distance of 50 km. More detailed analysis of the hydraulic flow conditions is beyond the scope of the present work and will be reported separately in a future study. The flow structure, shown in Figure 4 for September, remained generally valid for the entire year. The core of the AJ was accompanied by nitrate concentrations less than 1.0 mmol m^{-3} within the upper 100 m layer with respect to higher concentrations closer to the coasts where the currents were weaker and advected nutrients less effectively as compared to the core of the jet (Figure 4c). In general terms, the nitrate distribution at the exit section agreed well with the observations [Macías et al., 2007].

3.2. Physical Characteristics of the Annual Frontal Jet Structure

The cross-frontal density structure of the AJ underwent strong summer-to-winter seasonal variations in response to temporal changes of the incoming Atlantic water mass properties. Figures 5a and 5b illustrated basin-wide density distributions for summer (mid-September) and winter (early January) at 25 m depth that was immediately below the surface layer affected by the surface warming/cooling characteristics over the year. In summer, the Atlantic water mass entered the western Alboran Sea within the density range 26.5–27.0 kg m⁻³(see Figure 4a), occupied the southern part of the basin, and built up strong frontal structure characterized by the density difference of \sim 1.0 kg m⁻³ with the more dense ambient waters on the northern side of the front (Figure 5a). This cross-frontal density difference weakened gradually toward east reducing to \sim 0.5 kg m⁻³ around the EAG. In addition, a narrow band of low density waters less than 26.5 kg m⁻³ along the south coast was related to the weaker coastal current emanating from the GS.

In winter, the density range of the Atlantic water mass entering the western AS was slightly higher (27.0–27.5 kg m⁻³). It filled the southern part of the western basin with \sim 27.2 kg m⁻³ density

whereas the rest of the sea acquired relatively higher densities (27.5–28.0 kg m⁻³) in response to the winter cooling. Accordingly, the cross-frontal density difference was smaller than the summer case and did not exceed 0.5 kg m⁻³ and even smaller in the eastern basin (Figure 5b). In addition to strong cross-frontal density differences along the AJ trajectory, the AS possessed a year-around meridional density difference between its south and north coasts.

The vertical density structures crossing the WAG along the zonal transect TR0 (see Figures 5a and 5b for its location) were displayed in Figures 6a and 6b. The summer transect (Figure 6a) revealed strong density variations within the upper 20 m in response to the summer heating but the upper layer water mass beneath



Figure 9. Horizontal distributions of depth-integrated nitrate concentration (mmol m⁻²) over the upper 100 m layer during (a) 15 September (day 1335), (b) 10 January (day 1090), and (c) 30 March (day 1170). The gray lines represent the surface density contours.

underwent marked density variations between the interior of WAG and the adjacent cyclonic basin; e.g., the density difference is as high as 1 kg m⁻³ at 25 m (26.5 versus 27.5 kg m⁻³) or 50 m depth (27 versus 28 kg m⁻³). The density transect for the winter case (Figure 6b) attained a similar vertical structure but with slightly weaker density stratification owing to the buoyancy-induced vertical mixing due to cooling. The seasonal variability took place mostly at depths above the 27.5 kg m⁻³ isopycnal (i.e., the upper 75-100 m layer). An important point to emphasize here was the strong ambient stratification of about 1.0 kg m^{-3} within the upper layer even in the absence of the restratification introduced by the ASC and/or eddying motion.

Figure 7 depicts snapshots of three different horizontal distributions of the vertical component of the relative vorticity at the surface for mid-September (summer), early January (winter), and end of March (spring) representing three different phases of the AJ shown in Figure 3. The summer case of high frontal jet intensity possessed strong relative vorticity (ζ) changes on the order of the planetary vorticity (f) across the narrow crossfrontal jet structure (Figure 7a) making the jet highly nonlinear. In the case of moderate jet intensity accompanied by moderate cross-frontal density gradients, sharp crossfrontal vorticity changes still prevailed and the AJ maintained its moderately nonlinear character (Figure 7b). The jet, however, became weakly nonlinear (with the Rossby number < 0.4) when the frontal jet intensity weakened further (Figure 7c). For all cases,

the jet possessed unstable features along the periphery of the WAG depending on the jet intensity; more pronounced instability features emerged in the case of stronger jet. Instabilities developed mainly along the inner side of the jet (i.e., within the interior of the WAG) whereas the outer flank of the jet remained stable. An example for their temporal evolution during September–October at the time of high AJ transport regime was shown by the snapshots of horizontal surface relative vorticity distributions in Figure 8. They indicated large structural variability of the western AS circulation on subinertial time scales that may be subject to further modifications under easterly/westerly wind forcing.

3.3. Annual Phytoplankton Production Characteristics

In response to the annual variation of the AJ intensity at the eastern exit of the GS, the annual structure of frontal-induced phytoplankton biomass distribution possessed a marked seasonal variability. Most dense biomass distribution over the year was realized within the western basin around the WAG in September–October (>60 mmol N m⁻²) at the time of high AJ transport around 1.2–1.3 Sv (Figure 7a). On the other hand, relatively low biomass (around 30–40 mmol N m⁻²) was maintained during January and March under the conditions of lower AJ transports (Figures 7b and 7c). For all cases, the integrated phytoplankton biomass along the AJ trajectory exceeded the rest of the basin by about 20–30 mmol N m⁻².



Figure 10. Surface chlorophyll distributions (mg m⁻³) displaying two different modes of the phytoplankton production along the Atlantic jet trajectory for (a) the monthly climatological January conditions and (b) October 2003. They are retrieved from the monthly composite Modis data sets.

The strong light limitation in January did not permit subsurface nutrients to be utilized effectively in the production mechanism both along the AJ trajectory and within the rest of the basin in winter months. Thus, majority of nutrients was piled up within lower part of the euphotic zone without being consumed in the phytoplankton growth process (Figure 9b). Highest nutrient accumulation coincided with the cyclonic vorticity regions to the east of the WAG as well as along the northern coastal zone. Even though it was not particularly effective due to relatively strong stratification of the upper 100 m, the cooling-induced vertical mixing contributed to nutrient enrichment all over the basin, but more effectively in cyclonic regions. But these nutrients were not able to be converted into phytoplankton biomass due to the relatively strong light limitation. Nevertheless, the winter plankton production

was benefited by the ambient stratification that reduced the turbulent flux of phytoplankton cells out of the euphotic zone. We note that a similar winter production can only be realized by restratification of the upper layer water column due to frontal instabilities and/or eddy-driven slumping of isopycnals in high-latitude open ocean ecosystems [*Taylor and Ferrari*, 2011; *Mahadevan et al.*, 2012]. On the other hand, higher PAR availability allowed for slightly stronger production in spring (Figure 7c) on the basis of rich availability of nutrients (Figure 9c) and weakening light limitation even in the case of weaker AJ intensity.

The conditions during summer were reversed. Contrary to the nutrient limitation at near-surface levels, accumulation of rich nutrient stocks within lower part of the euphotic zone from the previous winter and



Figure 11. The positions of transects TR1 and TR3 crossing the cyclonic eddies C0, C1, C3, C4 and the anticyclonic eddies AC1, AC3, AC4 during 15 September (day 1335). The contours shown in the green and purple colors denote the negative and positive values of the normalized surface relative vorticity, respectively. The contour interval is 0.2.

recycling of nutrients afterward when combined with higher and deeper light exposure toward deeper levels converted most of nutrients into organic form as evident by lower integrated nutrient concentration (Figure 9a) and twice higher integrated phytoplankton biomass (Figure 7a) with respect to the winter case. This mechanism at the basin scale was further complemented at the frontal scale by more dominant frontogenesis-induced production within the euphotic zone. Thus, the AS provided stronger overall production during summer instead of the classical late winter-early spring one.

Although the present study does not include all the processes that drive the chlorophyll distributions, the different production characteristics provided by the model may be partly supported by the climatological monthly composite chlorophyll



Figure 12. Vertical structures of (a) density (kg m⁻³) and current speed (m s⁻¹) in white lines, (b) phytoplankton biomass (mmol N m⁻³) and nitrate concentrations (mmol N m⁻³) in black lines, (c) relative vorticity (normalized by the planetary vorticity) and the vertical velocity (m d⁻¹) contours with the negative and positive values in purple and green color, respectively, during 15 September (day 1335) along the transect TR1 (see Figure 11 for its position). The distance in km's is directed from the southern end to the northern end of the transect. The arrows show the regions of main upward-downward motions.

concentrations. In general, the satellitebased climatological surface chlorophyll concentrations acquired relatively low chlorophyll values of approximately 0.5 mg m⁻³ during summer (June-September) followed by a gentle increase up to 0.8 mg m⁻³ during autumn (from September to December), slightly higher values (>0.9 mg m⁻³) during February–April and decreasing afterward to the low summer values within the western AS [Macías et al., 2007]. The model supported similar annual variations of the surface phytoplankton biomass, but the integrated biomass was highest during summer months due to the contributions of small phytoplankton development above the seasonal thermocline and large phytoplankton development below with respect to lower biomass of mainly large group in winter. The January monthly climatological chlorophyll distribution (Figure 10a) shows slightly higher concentrations along the northern and eastern flanks of the WAG in partial agreement with the integrated phytoplankton biomass depicted in Figure 7b. The high chlorophyll zone along the northern coast and its eastward extension should presumably be caused by the coastal upwelling mechanism generated by the persistent westerly winds of the region, which have not been considered in this study. On the contrary, the model strong and patchy production conditions of the western basin during late summer (Figure 7a) were not supported by the monthly climatological data for these months. One of the reasons is that the temporal average smooths out the patchiness of the instantaneous fields in the climatological distribu-

tions. Instead of illustrating the climatology, Figure 10b then shows a particular case when patchiness is observed in October 2003.

3.4. Mechanisms of Plankton Production by Frontogenesis and Eddy Pumping

In Figures 12 and 13, we further delineated plankton production characteristics driven by the frontogenesis and the eddy pumping mechanisms along the transects TR1 and TR3 (see Figure 11 for their positions) for the conditions of high jet intensity in September (at day 1335). We however note that the transects provide only a simplified view of the nutrient enrichment and plankton production due to the depiction of these three-dimensional processes only in two dimensions. As a common feature along these transects, the frontal jet had a width of 30–40 km and maximum speed of 1.0 m s⁻¹ near the surface along its central axis. The anticyclonic side of the jet attained a relatively low density water mass in the range 26.5–27.5 kg m⁻³ within the upper 100 m. A well-defined subsurface front below a thin stratified surface layer (<20 m) separated this low-density water mass from more dense (27.5–28.0 kg m⁻³) water mass located on the other side of the main jet axis. The transects showed localized high phytoplankton patches (~1.0 mmol N m⁻³)



Figure 13. Vertical structures of (a) density (kg m⁻³)and current speed (m s⁻¹) in white lines, (b) phytoplankton biomass (mmol N m⁻³) and nitrate concentrations (mmol N m⁻³) in black lines, (c) relative vorticity (normalized by the planetary vorticity) and the vertical velocity (m d⁻¹) contours with the negative and positive values in purple and green color, respectively, during 15 September (day 1335) along the transect TR3 (see Figure 11 for its position). The distance in km's is directed from the southern end to the northern end of the transect. The arrows show the regions of main upward-downward motions.

along the AJ trajectory superposed on the background level of phytoplankton biomass distribution around 0.5 mmol N m⁻³ within the upper 60 m layer.

The transect TR1 crossed the cyclonic eddies C0 and C1 and the anticyclonic eddy AC1 at northwestern part of the WAG. The cyclonic eddy C1 that was located close to the northwestern coast immediately outside of the frontal jet zone (centered at 55 ± 5 km from the beginning of the transect) was characterized by the upward vertical velocities up to $30-40 \text{ m d}^{-1}$ that gave rise to relatively high phytoplankton biomass around 1.5 mmol N ${\rm m}^{-3}$ within the upper 50 m layer (Figure 12). The upward rise of nitrate concentrations and relatively high phytoplankton biomass up to about 0.7 mmol N m⁻³ also occurred on the anticyclonic side of the front (centered at 40 ± 5 km) as a part of the frontogenesis process. The strength of the upwelling motion by these two processes was highlighted by the upward rise of 1.0 mmol N m^{-3} nitrate isoline up to 50 m depth in this region. The associated net upward nitrate flux roughly amounts to 30 mmol $m^{-2} d^{-1}$. The upwelling motion and phytoplankton production was accompanied by a cross-frontal transport of phytoplank-

ton biomass about 0.5 mmol m⁻² s⁻¹, and a downwelling motion on the cyclonic side of the front (centered at 45–50 km) as well as along the isopycnals toward the center of the AC1 (within 25–40 km zone along the transect) on the order of 20 mmol m⁻² d⁻¹. The core of phytoplankton biomass was maintained within near-surface levels of the water column without any clear signal of subduction toward deeper levels. The frontal zone on the other side of the AC1 that was adjacent to the cyclonic eddy C0 also supported frontogenesis-induced phytoplankton biomass formation of 0.75 mmol N m⁻³ in response to upward vertical velocity of about 10 m d⁻¹ on the anticyclonic side of the front (within 20–25 km zone along the transect) and the corresponding downward motion of comparable magnitude on the cyclonic side of the front (within 10–15 km zone along the transect). A schematic representation of these upward/downward motions was depicted in Figures 12a and 13a.

Similar features were also developed along the transect TR3 on the southern side of the WAG. The frontal jet and the dipole eddy system AC3 and C3 showed high upward velocities up to 60 m d⁻¹ on the anticyclonic side of the front (at 110 km from the beginning of the transect) (Figure 13). It elevated the nitracline up to 50 m depth and produced phytoplankton biomass around 0.8 mmol N m⁻³ whereas another patch adjacent to it was developed even at lower upwelling velocities at cyclonic side of the jet (at 130 km from the beginning of the transect) by means of the eddy pumping mechanism due to the favorable position of the nitracline in the water column. Similar level of production also took place within the southwestern side of the AC3 (within 85–90 km zone) adjacent to a weak downwelling zone (at 85 km). The vertical and lateral nitrate fluxes were of the same order as those quantified for transect TR1. On the other hand, although the anticyclonic eddy AC4 attained large upwelling velocities up to 50 m d⁻¹ (within 45–55 km zone), deeper

position of the nitracline below 100 m was unable to support phytoplankton production as efficient as in the AC3. For additional details on the plankton dynamics related to the frontogenesis process, we refer to *Oguz et al.* [2014].

4. Discussion and Concluding Remarks

Using a coupled physical-biological model, the present study elaborated our conceptual understanding of the frontogenesis-induced plankton production in the AS. It represented a strongly stratified ambient water column throughout the year characterized by density differences higher than 1.0 kg m⁻³ within the upper 100 m. Strong stratification limited nutrient enrichment of surface waters to some extent due to the winter mixing. But, at the same time, it did not strongly rely on an additional restratification of the water column by the ASC to promote winter-early spring primary production as in the weakly stratified open ocean cases. Thus, because the nutricline is closer to the euphotic zone, even a moderately strong ASC can promote enhanced plankton production in the AS.

One of the main findings of the present study was to document that the meandering AJ constituted the major source of biological enrichment even in the case of a limited lateral supply of nutrients from the GS in the absence of tidal dynamics. The level of enrichment varied seasonally during the year depending on the upstream characteristics of AJ. When it entered from the GS with stronger intensity (>1.1 Sv) within the density range of 26.5–27.0 kg m⁻³ during summer-autumn, the frontal jet around the periphery of the WAG was characterized by strong cross-frontal density difference (~1.0 kg m⁻³) within the upper 100–150 m layer. Its large anticyclonic to cyclonic cross-frontal vorticity changes on the order of planetary vorticity made the jet strongly nonlinear and ageostrophic. The frontal jet system was accompanied by the cyclonic and anticyclonic eddy pairs that were located on two sides of the main jet axis along the periphery of the WAG. Unstable features of the jet were developed mainly along inner flank of the jet. The meandering structure involved anticyclonic eddies near the crests of meanders (i.e., inward excursions of the frontal zone toward the less dense side). Contrary to the open ocean frontal jets in which strong unstable meandering flow development was the necessary condition for maintaining strong nonlinearity of the jet, the frontal jet has already acquired strong vorticity as it entered the AS in the present case.

A general tendency of upward motion on the cyclonic northern side of the basin resulted in a general upward trend of isopycnals toward north in the western basin. Subsequently, upward rise of subsurface nutrients made the eddy and frontal-induced nutrient enrichment of the near-surface levels more effective on the northern side. Therefore, an upwelling motion with the same intensity within a cyclonic eddy in the southern basin provided weaker plankton production.

A narrow zone on the anticyclonic side of the main jet axis involved upward vertical velocities in the range 10–50 m d⁻¹ where nutrients are supplied into the euphotic layer and support high-level phytoplankton production as a part of the frontogenesis-driven ageostrophic cross-frontal circulation. On the other hand, the eddy pumping mechanism within strongly nonlinear cyclonic eddies on denser side of the frontal jet also provided equally strong upwelling velocities and subsequently plankton production. The present form of the eddy pumping mechanism therefore differed from its open ocean counterparts that were characterized by weaker upward velocities around 1–3 m d⁻¹ [*McGillicuddy*, 2016]. These two upwelling sites were separated by a narrow downwelling zone on the cyclonic side of the main jet axis where phytoplankton cells partly subducted along isopycnal surfaces. The subduction, however, was limited to shallow depths within the upper 100 m. Parts of nutrient concentrations and phytoplankton biomass produced within these localized eddies were advected along the frontal jet trajectory as well as by the eddying motion and thus giving rise to considerable patchiness within the basin. Plankton production supported by the dipole eddy structures along the frontal jet was an elaboration of the traditional frontogenesis-driven production documented to date.

The frontal strength weakened in winter-early spring due primarily to weaker AJ intensity (<1.0 Sv). The AJ then supported a relatively weak production around the WAG, confined mostly along its northern part and its limited extension to the eastern basin. In fact, a general reduction in phytoplankton biomass along with the jet intensity toward the eastern basin throughout the year points out the dependence of phytoplankton production on the jet intensity. Although nutrient enrichment was supported by the buoyancy-induced

mixing, the winter production within the basin was limited by low light intensity. In spring, the frontogenesis-induced production along the AJ was weakened. The northwestern zone extending from the GS exit to the Marbella (known as the Estepona upwelling zone) remained productive all year around due to the presence of a permanent cyclonic eddy between the coast and the jet.

In the absence of tidal and wind forcing, the present study provided only the first-order dynamics of the annual plankton production of the AS. Undoubtedly, the tidal and wind forcing are expected to modify the plankton production characteristics by introducing additional temporal and spatial variability in the ecosystem properties. It was shown recently by *Sanchez-Garrido et al.* [2015] that tidal forcing may account for 40% increase of phytoplankton biomass and primary productivity in the basin with respect to the nontidal case. The major contribution of the tidal dynamics was to pump nutrient-rich subsurface waters into the upper layer along the GS. The bulk of nutrients were then transported into the AS and made available for plankton production within the western basin as also noted by *Huertas et al.* [2009] and *Macias et al.* [2010]. An important implication of their study was therefore a need to parameterize the tidally induced nutrient transport through the GS in the models that did not resolve tides. The internal tides within the AS, however, were found to play a negligible role on the plankton production characteristics [*Sanchez-Garrido et al.*, 2015].

The studies on the open ocean frontal systems (e.g., the Subpolar Fronts of the Japan/East Sea and the North Atlantic Ocean) showed that downfront winds intensify the frontal-induced ageostrophic circulation and likely support stronger production in the regions of frontal jets and mesoscale-submesoscale features whereas upfront winds set unfavorable conditions [e.g., *Thomas and Lee*, 2005; *Mahadevan and Tandon*, 2006; *Capet et al.*, 2008; *Yoshikawa et al.*, 2012]. Wind events were found to be particularly effective in the case of high-frequency wind forcing [*Mahadevan et al.*, 2008; *Lévy et al.*, 2009]. The importance of wind-driven upwelling events by westerly winds on plankton production along the northern coastal waters was documented by *Reul et al.* [2005], *Macías et al.* [2007], and *Sanchez-Garrido et al.* [2015]. This topic is the subject of a forthcoming study similar to the one documented recently for the Catalano-Balearic Sea coastal boundary current system [*Oguz et al.*, 2015].

To conclude, an important finding of this work is to demonstrate a year-around persistency of relatively high plankton biomass produced simultaneously on both anticyclonic and cyclonic sides of the main axis of the frontal jet, although it is subject to some seasonal variability and may be additionally affected by transient effects of adverse wind forcing. Its persistency implies a continual bottom-up resource supply to higher trophic levels to sustain fishery not only on coastal sites as often reported, but also within the basin interior and along the AJ trajectory [*Ruiz et al.*, 2013].

Appendix A: Description of the Biological Model Equations

(

The NP2ZD-type biological model comprised the small and large phytoplankton size groups (P_s and P_L), zooplankton (Z), particulate organic nitrogen (D), and dissolved inorganic nitrogen (N) compartments, as an extension of our former four compartment NPZD model of the Alboran Sea [*Oguz et al.*, 2014]. The rate of change of their biomass or concentrations were expressed in the flux form by

$$\frac{\partial (X \cdot H)}{\partial t} + \nabla (\vec{u} \cdot (X \cdot H)) = F_X + H \cdot B_X, \tag{A1}$$

Table A1. Source-Sink Terms of the Biological Model	
Equations for the Source-Sink Terms	Equation No.
$B_{PS} = PP_S - G_{PS} - m_{PS} \cdot P_S$	(A2a)
$B_{PL} = PP_L - G_{PL} - m_{PL} \cdot P_L$	(A2b)
$B_Z = \gamma \cdot (G_{PS} + G_{PL} + G_D) - \mu_z \cdot Z - m_Z \cdot Z^2$	(A2c)
$B_D = (1 - \gamma) \cdot (G_{PS} + G_{PL}) - \gamma \cdot G_D + m_{PS} \cdot P_S + m_{PL} \cdot P_L + \beta \cdot m_Z \cdot Z^2$	(A2d)
$-\varepsilon \cdot D - \frac{\partial(w_D D)}{\partial z}$	
$B_N = -PP_S - PP_L + \mu_Z \cdot Z + \varepsilon \cdot D$	(A2e)

where X denote each of the state variables, **u** is the three-dimensional fluid velocity, $H = h + \eta$ the total water depth with h defining the bottom topography and η the surface elevation, F_X denotes the sum of horizontal and vertical diffusion terms represented similar to those in the circulation model, and B_X denotes the biological source-sink terms described in Tables A1 and A2. The list of

Definition	Functional Form	Equation No.
Temperature limitation for small phytoplankton	$f_{S}(T) = 1.0$	(A3a)
Temperature limitation for large phytoplankton	$f_L(T) = Q_{10}^{(T_a - T)/T_b}$	(A3b)
Nutrient uptake for small phytoplankton	$f_{S}(N) = \frac{N}{K_{NS} + N} \exp(-\kappa_{S} \cdot N)$	(A3c)
Nutrient uptake for large phytoplankton	$f_L(N) = \frac{N}{K_{NM} + N}$	(A3d)
Light limitation for small phytoplankton	$f_{S}(I) = [1 - \exp(-I/I_{oS})]$	(A3e)
Light limitation for large phytoplankton		(A3f)
	$f_L(I) = [1 - \exp(-I/I_{oL})] \exp(-\alpha_L I)$	
Vertical structure of PAR depending on its attenuation coefficients	$I(z) = I_{s} \exp \left[-k_{w} \cdot z + k_{b} \int_{z}^{0} (P_{s} + P_{l} + D) \cdot dz \right]$	(A3g)
Phytoplankton growth	$PP_{PX} = r_{PX} \cdot f_X(T) \cdot f_X(N) \cdot f_X(I) \cdot P_X$	(A3h)
Zooplankton grazing on small phytoplankton	$G_{PX} = r_Z \cdot Z \frac{a_1 P_X}{K_Z + a_1 P_S + a_2 P_I + a_3 D}$	(A3i)
Zooplankton grazing on large phytoplankton	$G_{PL} = r_Z \cdot Z \frac{a_2 P_L}{K_Z + a_1 P_S + a_2 P_L + a_3 D}$	(A3j)
Zooplankton grazing on detritus	$G_D = r_z \cdot Z \frac{a_3 D}{K_z + a_2 P + a_2 P + a_2 D}$	(A3k)
Food capture efficiency expressed by the ratio of the food contribution of a particular food item and the total food contribution	$a_i = \frac{b_i X_i}{\sum_k b_k X_k}$	(A3I)
Concentration dependent detritus sinking velocity	$W_D = W_{Dmax} \frac{D}{K_D + D}$	(A3m)

parameters and their values were given in Table A3. The parameters were optimized by a series of sensitivity experiments based on their values used in our previous model studies for the same region [*Oguz et al.*, 2013, 2014].

According to equations (A2a) and (A2b) (Table A1), temporal changes of phytoplankton biomass depended up on the biomass growth, the zooplankton grazing, and the mortality that also included the respiratory losses. The biomass growth (equation (A3h)) was controlled by temperature, light, and nutrient availability (equations (A3a)–(A3g)). Weaker nutrient uptake of small phytoplankton group at high concentrations favored the growth of large phytoplankton group under nutrient enrichment of the euphotic layer (equation (A3c) versus equation (A3d)). Its growth was also made more favorable under relatively low light and

Parameter	Value
Maximum growth rate for small phytoplankton	$r_{PS} = 1.3 day^{-1}$
Maximum growth rate for small phytoplankton	$r_{PL} = 1.6 day^{-1}$
Mortality rate for small phytoplankton	$m_{PS} = 0.06 day^{-1}$
Mortality rate for large phytoplankton	$m_{PL} = 0.06 \text{ day}^{-1}$
Mortality rate for large zooplankton	$m_z = 0.30 \text{ day}^{-1}$
Zooplankton excretion rate	$\mu_Z = 0.07 \text{ day}^{-1}$
Zooplankton grazing assimilation efficiency	$\gamma = 0.75$
Detritus remineralization rate	$\varepsilon = 0.1 \text{ day}^{-1}$
Recycling efficiency of zooplankton loss	$\beta = 0.75$
Q10 parameter for temperature limitation	Q ₁₀ = 2
Temperature parameters controlling growth intensity of the large phytoplankton	$T_{a} = 18^{\circ}C, T_{b} = 6^{\circ}C$
Parameter defining the decline of PAR	$\alpha_{\rm L} = 0.002 \ ({\rm W} {\rm m}^{-2})^{-1}$
Limiting PAR value for the small phytoplankton	$I_{0S} = 37.5 \text{ W m}^{-2}$
Limiting PAR value for the large phytoplankton	$I_{0L} = 25.0 \text{ W m}^{-2}$
Limiting nutrient concentration for the small phytoplankton nutrient uptake	$\kappa_{\rm S} = 0.3 \; ({\rm mmol} \; {\rm m}^{-3})^{-1}$
Half saturation constant for the nitrate uptake of small phytoplankton	$K_{NS} = 0.3 \text{ mmol N m}^{-3}$
Half saturation constant for the nitrate uptake of large phytoplankton	$K_{NL} = 0.5 \text{ mmol N m}^{-3}$
Light extinction coefficient for pure water	$k_w = 0.05 m^{-1}$
Light extinction coefficient due to turbidity	$k_{b} = 0.03 \text{ mmol N}^{-1} \text{ m}^{2}$
Surface value of PAR	$50 < I_s < 150 \text{ W m}^{-2}$
Maximum zooplankton grazing rate	$r_{Z} = 0.5 \text{ day}^{-1}$
Half saturation constant of zooplankton grazing	$K_{Z} = 0.5 \text{ mmol m}^{-3}$
Half saturation constant of detritus sinking	$K_{\rm D} = 0.2 \text{ mmol m}^{-3}$
Maximum detritus sinking velocity	$w_{Dmax} = 8.0 \text{ m d}^{-1}$
Small phytoplankton feeding efficiency	b ₁ = 1.0
Large phytoplankton feeding efficiency	b ₂ = 1.0
Detritus feeding efficiency	$b_3 = 0.5$

temperature conditions of the late autumn-winter-early spring phase by introducing temperature and light limitations for T > 18°C and PAR > 75 W m⁻², respectively (equations (A3b) and (A3f)). The small phytoplankton group prevailed mainly within the surface mixed layer under high light and temperature and low nutrient conditions of the late spring-summer-early autumn phase.

The zooplankton biomass changes in equation (A2c) were controlled by the zooplankton grazing on phytoplankton and detritus (equations (A3i)–(A3k)) minus excretion and quadratic predation loss. The food preference coefficients specified in the grazing functions were made spatially and temporally variable by expressing their initially prescribed constant values (b_i) in terms of individual food items normalized by the total food availability (equation (A3I)). In equation (A2d), unassimilated parts of the zooplankton grazing and zooplankton and phytoplankton mortalities constituted the sources of detritus material which was reduced due to its consumption by zooplankton, remineralization, and sinking. The sinking velocity was made concentration-dependent (equation (A3m)) indicating faster sinking of detritus at its higher concentrations due to their likely aggregations. Seventy-five percent of the zooplankton mortality was recycled within the water column ($\beta = 0.75$) whereas the rest constituted permanent losses at higher trophic levels. According to equation (A2e), nitrate concentration was consumed by its uptake during phytoplankton growth, and recycled due to zooplankton excretion and remineralization of the particulate organic material. When the equations (A2a)–(A2e) were summed over the upper layer water column and over the model domain, the total biomass was conserved except the losses to higher predators and detritus sinking to deep waters and exchanges across the open boundaries. The total loss was, however, compensated by vertical supply of nutrients from subsurface levels.

Acknowledgments

We are grateful to the two anonymous reviewers for their constructive remarks on the manuscript. This paper is a contribution to Medclic (the Mediterranean in one click) program, a collaboration between "la Caixa" Foundation and SOCIB. Both the data and input files necessary to reproduce the experiments described in the present paper are available from the authors upon request (oguz@ims. metu.edu.tr). The data are archived at the Balearic Islands Coastal Observing and Forecasting System (SOCIB) data center.

References

Capet, X., J. C. McWilliams, M. J. Molemaker, and A. F. Shchepetkin (2008), Mesoscale to submesoscale transition in the California Current System. Part II: Frontal processes, J. Phys. Oceanogr., 38, 44–64.

Criado-Aldeanueva, F., F. J. Soto-Navarro, and J. Garcia-Lafuente (2010), Seasonal and interannual variability of surface heat and freshwater fluxes in the Mediterranean Sea: Budgets and exchange through the Strait of Gibraltar, Int. J. Climatol., 32, 286–302, doi:10.1002/joc.2268. García-Lafuente, J., and J. Delgado (2004), Meandering path of a drifter around the Western Alboran Gyre, J. Phys. Oceanogr., 34, 685–692.

García-Lafuente, J., J. Delgado, J. M. Vargas, M. Vargas, F. Plaza, and T. Sarhan (2002), Low frequency variability of the exchanged flows through the Strait of Gibraltar during CANIGO, Deep Sea Res., Part II, 49, 4051–4067.

Gomis, D., S. Ruiz, and M. A. Pedder (2001), Diagnostic analysis of the 3D ageostrophic circulation from a multivariate spatial interpolation of CTD and ADCP data, *Deep Sea Res., Part I, 48, 269–295.*

Huertas, I. E., A. F. Rios, J. Garcia-Lafuente, A. Makaoui, S. Rodriguez-Galvez, A. Sanchez-Roman, A. Orbi, J. Ruiz, and F. F. Perez (2009),

Anthropogenic and natural CO₂ exchange through the Strait of Gibraltar, *Biogeosciences*, *6*(4), 647–662, doi:10.5194/bg6-647-2009. Lévy, M., P. Klein, and A.-M. Tréguier (2001), Impacts of sub-mesoscale physics on phytoplankton production and subduction, *J. Mar. Res.*, *59*, 535–565.

Lévy, M., P. Klein, and M. B. Jelloul (2009), New production stimulated by high-frequency winds in a turbulent mesoscale eddy field, Geophys. Res. Lett., 36, L16603, doi:10.1029/2009GL039490.

Lima, I. D., D. B. Olson, and S. C. Doney (2002), Intrinsic dynamics and stability properties of size-structured pelagic ecosystem models, J. Plankton Res., 24, 533–556.

Macías, D., A. P. Martin, J. García-Lafuente, C. M. García, A. Yool, M. Bruno, A. Vázquez-Escobar, A. Izquierdo, D. V. Sein, and F. Echevarría (2007), Mixing and biogeochemical effects induced by tides on the Atlantic–Mediterranean flow in the Strait of Gibraltar. An analysis through a physical–biological coupled model, *Prog. Oceanogr.*, 74, 252–272.

Macias, D., M. Bruno, F. Echevarria, A. Vazquez, and C. M. Garcia (2008), Meteorologically-induced mesoscale variability of the northwestern Alborán Sea (southern Spain) and related biological patterns, *Estuarine Coastal Shelf Sci.*, 78, 250–266.

Macias, D., E. Ramirez-Romero, and C. M. Garcia (2010), Effect of nutrient input frequency on the structure and dynamics of the marine pelagic community: A modeling approach, J. Mar. Res., 68, 119–151.

Mahadevan, A. (2016), Physics on primary productivity of plankton, Annu. Rev. Mar. Sci., 8, 17.1–17.24.

Mahadevan, A., and A. Tandon (2006), An analysis of mechanisms for submesoscale vertical motion at ocean fronts, *Ocean Model.*, 14(3–4), 241–256.

Mahadevan, A, L. N. Thomas, and A. Tandon (2008), Comment on "Eddy/wind interactions stimulate extraordinary mid-ocean plankton blooms," *Science*, 320, 448.

Mahadevan, A., E. D'Asaro, C. Lee, and M. J. Perry (2012), Eddy-driven stratification initiates North Atlantic Spring phytoplankton blooms, Science, 337, 54–58.

Martin, A. P., K. J. Richards, and M. J. R. Fasham (2001), Phytoplankton production and community structure in an unstable frontal region, J. Mar. Syst., 28(1–2), 65–89, doi:10.1016/S0924-7963(00)00084-1.

McCalpin, J. D. (1994), A comparison of second-order and fourth-order pressure gradient algorithms in a sigma coordinate ocean model, Int. J. Numer. Methods Fluids, 18, 361–383.

McGillicuddy, D. J. Jr. (2016), Mechanisms of physical-biological-biogeochemical interaction at the oceanic mesoscale, Annu. Rev. Mar. Sci., 8, 13.1–13.36.

Mellor, G. L. (2003), Users Guide for a Three-Dimensional, Primitive Equation, Numerical Ocean Model (June 2003 version), 53 pp., Program in Atmos. and Ocean. Sci., Princeton Univ., Princeton, N. J.

Mellor, G. L., L. Y. Oey, and T. Ezer (1998), Sigma coordinate pressure gradient errors and the seamount problem, J. Atmos. Oceanic Technol., 15(5), 1122–1131.

Millot, C., and I. Taupier-Letage (2005), Circulation in the Mediterranean Sea, in *The Mediterranean Sea*, *Handb. Environ. Chem.*, vol. 5, edited by A. Saliot, Part K, pp. 29–66, Springer, Berlin Heidelberg, doi:10.1007/b107143.

Navarro, G., Á. Vázquez, D. Macías, M. Bruno, and J. Ruiz (2011), Understanding the patterns of biological response to physical forcing in the Alborán Sea (western Mediterranean), *Geophys. Res. Lett.*, 38, L23606, doi:10.1029/2011GL049708.

Oguz, T., D. Macias, L. Renault, J. Ruiz, J. Tintore (2013), Controls of plankton production by pelagic fish predation and resource availability in the Alboran and Balearic Seas, *Prog. Oceanogr.*, 112 113–, 1–14.

- Oguz, T., D. Macias, J. Garcia-Lafuente, A. Pascual, and J. Tintore (2014), Fueling plankton production by a meandering frontal jet: A case study for the Alboran Sea (Western Mediterranean), *PLoS One*, *9*(11), e111482, doi:10.1371/journal.pone.0111482.
- Oguz, T., D. Macias, and J. Tintore (2015), Ageostrophic frontal processes controlling phytoplankton production in the Catalano-Balearic Sea (Western Mediterranean), *PLoS One*, *10*(6), e0129045, doi:10.1371/journal.pone.0129045.

Peliz, A., D. Boutov, and A. Teles-Machado (2013), The Alboran Sea mesoscale in a long term high resolution simulation: Statistical analysis, Ocean Model., 72, 32–52.

Renault, L., T. Oguz, A. Pascual, G. Vizoso, and J. Tintore (2012), Surface circulation in the Alborán Sea (Western Mediterranean) inferred from remotely sensed data, J. Geophys. Res., 117, C08009, doi:10.1029/2011JC007659.

Reul, A., V. Rodriguez, F. Jimenez-Gomez, J. Blanco, B. Bautista, T. Sarhan, F. Guerrero, J. Ruiz, and J. Garcia-Lafuente (2005), Variability in the spatio-temporal distribution and size-structure of phytoplankton across an upwelling area in the NW-Alboran Sea (W-Mediterranean), *Cont. Shelf Res.*, 25(5–6), 589–608, doi:10.1016/j.csr.2004.09.016.

Rivierea, P., and P. Pondaven (2006), Phytoplankton size class competitions at submesoscale in a frontal oceanic region, J. Mar. Syst., 60, 345–364.

Rodriguez, J., et al. (2001), Mesoscale vertical motion and the size structure of phytoplankton in the ocean, Nature, 410, 360–363.

Ruiz, J., et al. (2001), Surface distribution of chlorophyll, particles and gelbstorff in the Atlantic Jet of the Alboran Sea: From mesoscale to subinertial scales of variability, J. Mar. Syst., 29, 277–292, doi:10.1016/S0924-7963(01)00020-3.

Ruiz, J., D. Macias, M. M. Rincon, A. Pascual, I. A. Catalan, and G. Navarro (2013), Recruiting at the edge: Kinetic energy inhibits anchovy populations in the Western Mediterranean, *PLoS One*, 8(2), e55523, doi:10.1371/journal.pone.0055523.

- Sanchez-Garrido, J. C., C. Naranjo, D. Macias, J. Garia-Lafuente, and T. Oguz (2015), Modeling the impact of tidal flows on the biological productivity of the Alboran Sea, J. Geophys. Res., 120, 7329–7345, doi:10.1002/2015JC010885.
- Sannino, G., J. C. Sánchez Garrido, L. Liberti, and L. Pratt (2014), Exchange flow through the Strait of Gibraltar as simulated by a *σ*coordinate hydrostatic model and a z-coordinate nonhydrostatic model, in *The Mediterranean Sea: Temporal Variability and Spatial Patterns, Geophys. Monogr.*, vol. 202, edited by G. L. E. Borzelli, M. Gacic, P. Lionello, and P. Malanotte-Rizzoli, pp. 25–50, AGU, Washington, D. C.

Shchepetkin, A. F., and McWilliams, J. C. (2003), A method for computing horizontal pressure-gradient force in an oceanic model with a non-aligned vertical coordinate, J. Geophys. Res., 108(C3), 3090, doi:10.1029/2001JC001047.

Soto-Navarro, J., F. Criado-Aldeanueva, J. García-Lafuente, and A. Sánchez-Román (2010), Estimation of the Atlantic inflow through the Strait of Gibraltar from climatological and in situ data, J. Geophys. Res., 115, C10023, doi:10.1029/2010JC006302.

Spall, S. A., and K. J. Richards (2000), A numerical model of mesoscale frontal instabilities and plankton dynamics. I. Model formulation and initial experiments, *Deep Sea Res. Part I*, 47, 1261–1301.

Taylor, J. R., and R. Ferrari (2011), Ocean fronts trigger high latitude phytoplankton blooms, *Geophys. Res. Lett.*, 38, L23601, doi:10.1029/2011GL049312.

Thomas, L. N., and C. M. Lee (2005), Intensification of ocean fronts by down-front winds, J. Phys. Oceanogr., 35, 1086–1102.

Thomas, L. N., A. Tandon, and A. Mahadevan (2008), Submesoscale processes and dynamics, in *Ocean Modeling in an Eddying Regime, Geophys. Monogr.*, vol. 177, edited by M. W. Hecht and H. Hasumi, pp. 17–38, AGU, Washington, D. C.

Tintore, J., D. Gomis, S. Alonso, and G. Parrilla (1991), Mesoscale dynamics and vertical motion in the Alboran Sea, J. Phys. Oceanogr., 21, 811–823.

Yoshikawa, Y., C. M. Lee, and L. N. Thomas (2012), The Subpolar Front of the Japan/East Sea. Part III: Competing roles of frontal dynamics and atmospheric forcing in driving ageostrophic vertical circulation and subduction, J. Phys. Oceanogr., 42, 991–1011.