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Zooplankton diel vertical migration and contribution to deep active carbon flux in the NW Mediterranean

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ABSTRACT

The diel vertical migration (DVM) of zooplankton contributes to the biological pump transporting material from surface to deep waters. We examined the DVM of the zooplankton community in different size fractions (53–200 μm, 200–500 μm, 500–1000 μm, 1000–2000 μm and >2000 μm) during three cruises carried out in the open NW Mediterranean Sea. We assessed their metabolic rates from empirical published relationships and estimated the active fluxes of dissolved carbon to the mesopelagic zone driven by migrant zooplankton. Within the predominantly oligotrophic Mediterranean Sea, the NW region is one of the most productive ones, with a seasonal cycle characterized by a prominent spring bloom. The study area was visited at three different phases of the seasonal cycle: during the spring bloom, the post-bloom, and strongly stratified oligotrophic conditions. We found seasonal differences in DVM, less evident during the bloom. Changes in DVM intensity were related to the composition of the zooplanktonic assemblage, which also varied between cruises. Euphausiids appeared as the most active migrants in all seasons, and their life cycle conditioned the observed pattern. Immature stages, which are unable to perform large diel vertical movements, dominated during the bloom, in contrast to the higher relative importance of migrating adults in the other two sampling periods. The amount of dissolved carbon exported was determined by the migrant zooplankton biomass, being highest during the post-bloom (2.2 mmol C respired m^{-2} d^{-1}, and up to 3.1 mmol C exported m^{-2} d^{-1} when DOC release estimations are added). The active transport by diel migrants represented a substantial contribution to total carbon export to deep waters, especially under stratified oligotrophic conditions, revealing the importance of zooplankton in the biological pump operating in the study area.

1. Introduction

The Mediterranean has been traditionally described as an oligotrophic semi-enclosed sea (Siokou-Frangou et al., 2010). Nevertheless, in a comparative regional analysis based on satellite-derived chlorophyll-a (Chl-a) values D'Ortenzio and Ribera d'Alcalá (2009) identified seven different bioprovinces throughout the Mediterranean basin, with an increasing productivity gradient from East to West. The NW Mediterranean appears as the most productive area and its trophic regime is classified as "blooming" (D'Ortenzio and Ribera d'Alcalá, 2009), with an intense phytoplankton bloom occurring throughout the late winter and spring (Bosc et al., 2004). This open ocean bloom originates from deep convection (Lévy et al., 1998), a physical process that apart from here has only been detected in Greenland and in Labrador and Weddell Seas (Gascard, 1991). Given that the capacity of marine systems to sequester excess atmospheric carbon is related to their productivity (Siegenthaler and Sarmiento, 1993), the NW region is one of the areas with a higher biogeochemical activity within the Mediterranean Sea, attracting the attention of a large number of studies (Siokou-Frangou et al., 2010, and references therein). In this context, the project FAMOSO (FAte of the northwestern Mediterranean Open sea Spring blOom) aimed at investigating the fate of the carbon fixed during the aforementioned spring bloom, following its temporal evolution throughout different phases of the seasonal cycle. This project represents an integrative approach that combines physical, chemical and biological analyses, the latter encompassing several trophic levels, from primary producers to macrozooplankton.

The efficiency of the biological pump transferring carbon from the surface to deep waters can be reduced to a large extent due to the demineralization of sinking material in the upper layers (Buesseler et al., 2007). In such cases, the contribution of zooplankton to the biological pump would be mainly mediated by its capacity to perform diel vertical migrations (DVMs), releasing during the day, at depth, part of the material taken up at surface waters when migrating upward at nighttime (Longhurst and Harrison, 1989). Zooplankton DVM is generally thought as an antipredatory response (e.g. Frost and Bollens, 1992). This process is triggered by changes in light intensity, although

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there are some other factors (e.g., food concentration, abundance of predators, thermal or saline barriers) involved in its regulation (Hays, 2003; Pearre, 2003). The response to the different factors varies among taxa, which brings about a wide spectrum, both in the spatial and the temporal ranges, of DVM behavior within the zooplanktonic community (Irigoien et al., 2004). As a consequence, the total amount of migrant biomass (and therefore of material exported downward through DVM) is largely influenced by the taxonomic composition of the zooplanktonic assemblage.

Active fluxes of dissolved carbon due to migrant zooplankton respiration have been reported to represent a considerable percentage (as much as 50% in some cases) of total carbon exported (e.g. Al-Mutairi and Landry, 2001; Hannides et al., 2009; Hidaka et al., 2001; Kobari et al., 2013; Longhurst et al., 1990; Steinberg et al., 2000; Stukel et al., 2013; Yebra et al., 2005). The importance of the so-mediated fluxes is unanimously recognized, and the need of studies providing such data to better understand the ocean biogeochemical cycles has been already posed more than a decade ago (Marine Zooplankton Colloquium 2, 2001). Nevertheless, to our knowledge it has never been assessed in NW Mediterranean Sea, though previous studies in the area suggested that DVM plays an essential role in the vertical distribution of particulate matter (Stemmann et al., 2000). Here we estimate zooplankton DVM and associated respiratory carbon flux in the NW Mediterranean open sea bloom during three different seasonal periods corresponding to distinguished trophic situations (bloom, post-bloom and stratification). Our results contribute to the integrative view provided by the FAMOSO project and will be discussed in this framework to quantify the importance of the zooplankton DVM in ocean vertical fluxes.

2. Materials and methods

2.1. Study area and environmental conditions

The study area (Fig. 1) was sampled in 2009 covering three contrasting periods of the seasonal productive cycle in the open NW Mediterranean. Three oceanographic cruises were carried out on board the R/V 'Sarmiento de Gamboa': March 6 to 23, April 29 to May 14, and September 14 to 22. We sampled 13 stations during the March cruise, 18 stations during May, and 10 stations during September (Table 1). At each station, CTD casts were performed with a 24-bottle Niskin rosette equipped with sensors for temperature and conductivity, turbidity, oxygen and fluorescence (SBE 911 plus CTD). Calibration of the conductivity and oxygen sensors was performed with discrete salinity and oxygen samples.

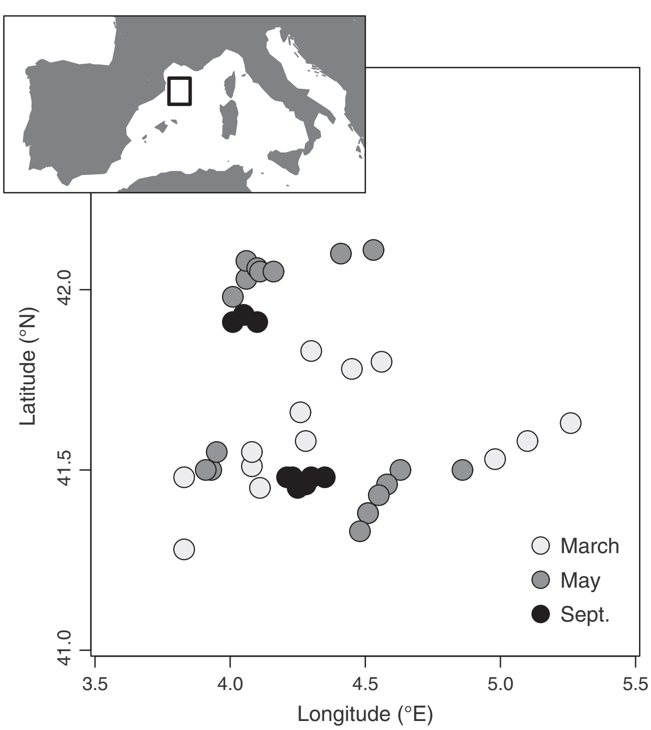

Fig. 1. Position of the stations sampled during the three cruises in the area indicated by a black rectangle in the inset map of the Mediterranean Sea.

Chl-a concentration was estimated at some selected stations and depths. Here, between 50 and 200 mL water samples were filtered through GF/F filters, which were stored at −20 °C for several hours and subsequently introduced into 90% acetone for 24 h extraction in the dark. The fluorescence was read in a 10 AU Turner Designs fluorometer and converted to Chl-a after a calibration with pure Chl-a (Sigma-Aldrich). These Chl-a estimates were compared to the corresponding CTD fluorescence values ($n = 68$; $R^2 = 0.97$). We applied this relationship to assess Chl-a concentration for the upper 100 m at each station.

2.2. Zooplankton sampling

Sampling was carried out alternating day- and nighttime. The smaller size fraction (53–200 μm) was collected with a double CalVET net (53 μm mesh size, 25 cm Ø), and small mesozooplankton (200–1000 μm) with three WP2 nets (200 μm mesh, 40 cm Ø) mounted

Table 1
List of the zooplankton stations during the three FAMOSO cruises. The third column indicates whether the stations were diurnal (D) or nocturnal (N).

Station	Date	D/N	Sampling time (GMT)	Latitude (N)	Longitude (E)
F1.1	14/03/2009	N	1:30	41°32	4°59
F1.2	14/03/2009	D	12:30	41°35	5°06
F1.3	14/03/2009	N	22:54	41°38	5°16
F1.4 [a]	15/03/2009	D	15:00	41°29	3°50
F1.5 [a]	17/03/2009	D	14:03	41°17	3°50
F1.6	18/03/2009	N	0:42	41°27	4°07
F1.7	18/03/2009	D	11:30	41°31	4°05
F1.8	18/03/2009	N	21:54	41°33	4°05
F1.9	19/03/2009	D	14:36	41°35	4°17
F1.10	19/03/2009	N	21:12	41°40	4°16
F1.11	21/03/2009	D	13:42	41°50	4°18
F1.12	21/03/2009	N	21:36	41°47	4°27
F1.13	22/03/2009	D	16:12	41°48	4°34
F2.1 [a,b]	30/04/2009	D	9:04	41°30	4°52
F2.2	03/05/2009	D	10:53	41°30	3°56
F2.3	04/05/2009	N	0:41	41°30	3°55
F2.4	04/05/2009	D	10:48	41°33	3°57
F2.5	06/05/2009	N	21:45	42°06	4°25
F2.6	07/05/2009	D	9:48	42°07	4°32
F2.7	07/05/2009	N	21:55	41°59	4°01
F2.8	08/05/2009	D	10:23	42°02	4°04
F2.9	08/05/2009	N	20:55	42°05	4°04
F2.10	09/05/2009	D	10:16	42°04	4°06
F2.11	09/05/2009	N	20:51	42°03	4°07
F2.12	10/05/2009	D	10:25	42°03	4°10
F2.13	10/05/2009	N	21:03	41°30	4°38
F2.14	11/05/2009	D	10:26	41°28	4°35
F2.15	11/05/2009	N	21:00	41°26	4°33
F2.16	12/05/2009	D	11:16	41°23	4°31
F2.17	12/05/2009	N	22:14	41°23	4°31
F2.18	13/05/2009	D	11:52	41°20	4°29
F3.1	15/09/2009	N	20:20	41°29	4°21
F3.2	16/09/2009	D	9:50	41°29	4°18
F3.3	16/09/2009	N	19:58	41°28	4°17
F3.4	17/09/2009	D	12:38	41°27	4°15
F3.5	17/09/2009	N	20:13	41°29	4°14
F3.6	18/09/2009	D	13:21	41°29	4°13
F3.7	18/09/2009	N	20:50	41°55	4°01
F3.8	19/09/2009	D	13:05	41°56	4°03
F3.9	19/09/2009	N	20:45	41°56	4°03
F3.10	20/09/2009	D	11:06	41°55	4°06

[a] Bongo net not deployed.
[b] CalVET net not deployed.