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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

Biological Oceanography Laboratory, Facultad de Ciencias del Mar, Campus Universitario de Tafira, Las Palmas de Gran Canaria, Canary Islands, Spain

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.

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 2005*a*). 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

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* Corresponding author: shernandez@dbio.ulpgc.es

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 (Fig. 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 (Fig. 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 50°C 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.

Zooplankton was captured in oblique hauls with a Bongo net equipped with 200-μm 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 60°C for 24 h and later weighed, first allowing the sample to reach room temperature and avoiding humidity.

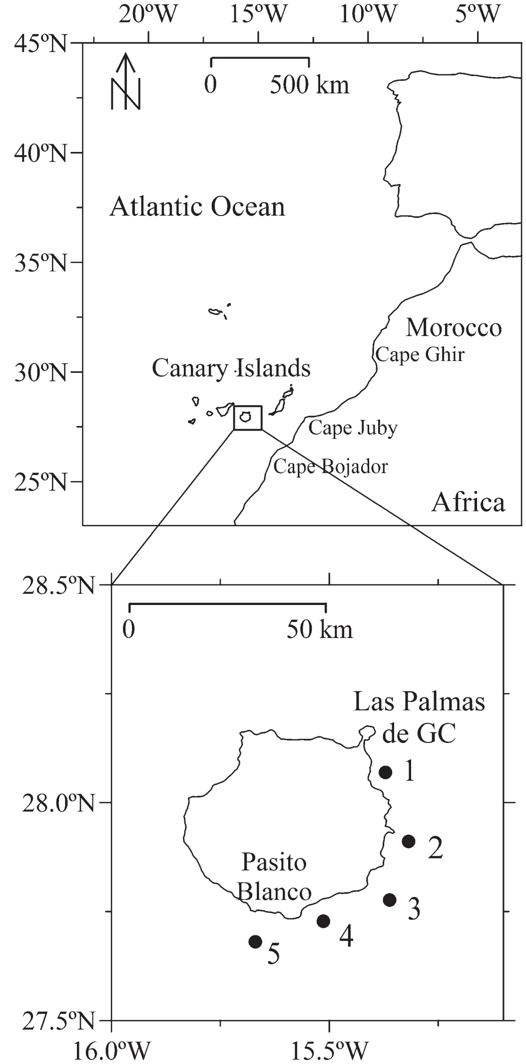

Fig. 1. Map of the study area showing the location of the five sampling stations over 100-m depth at the edge of the shelf break around Gran Canaria Island. The dust deposition devices were installed in the north (Las Palmas de Gran Canaria) and south of the island (Pasito Blanco).

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

$$\mathrm{P} = (\mathrm{B}_1 - \mathrm{B}_0) + \mathrm{M} \qquad (1)$$

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,

$$B_1 = B_0 + (B_0 \times g) - (B_0 \times m) \tag{2}$$

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 18°C, 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 (Fig. 2A), coinciding with temperature below 19°C, which indicate the suitable mixing conditions for the bloom (Hernández-León et al. 2004; Moyano et al. 2009). This bloom also coincided with the highest dust deposition during winter. This event occurred from the end of January to mid-April (Fig. 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 (Fig. 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 (Fig. 4). A significant positive correlation ($r^2 = 0.533$, $p < 0.05$) was also found between lunar illumination and mesozooplankton biomass.

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 (Fig. 5A,B). Using different maximum growth rates for every peak, we obtained a more realistic match between true and predicted biomass (Fig. 5C). In any case, good agreement was observed between the predicted and the measured mesozooplankton biomass in both cases (Table 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 1, upper panel) or different maximum growth rates for every peak (Table 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.

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 fig. 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 zooplankton bloom in March, while in the present work the increase in chlorophyll was observed at the end of January, coinciding with temperatures below 19°C, 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

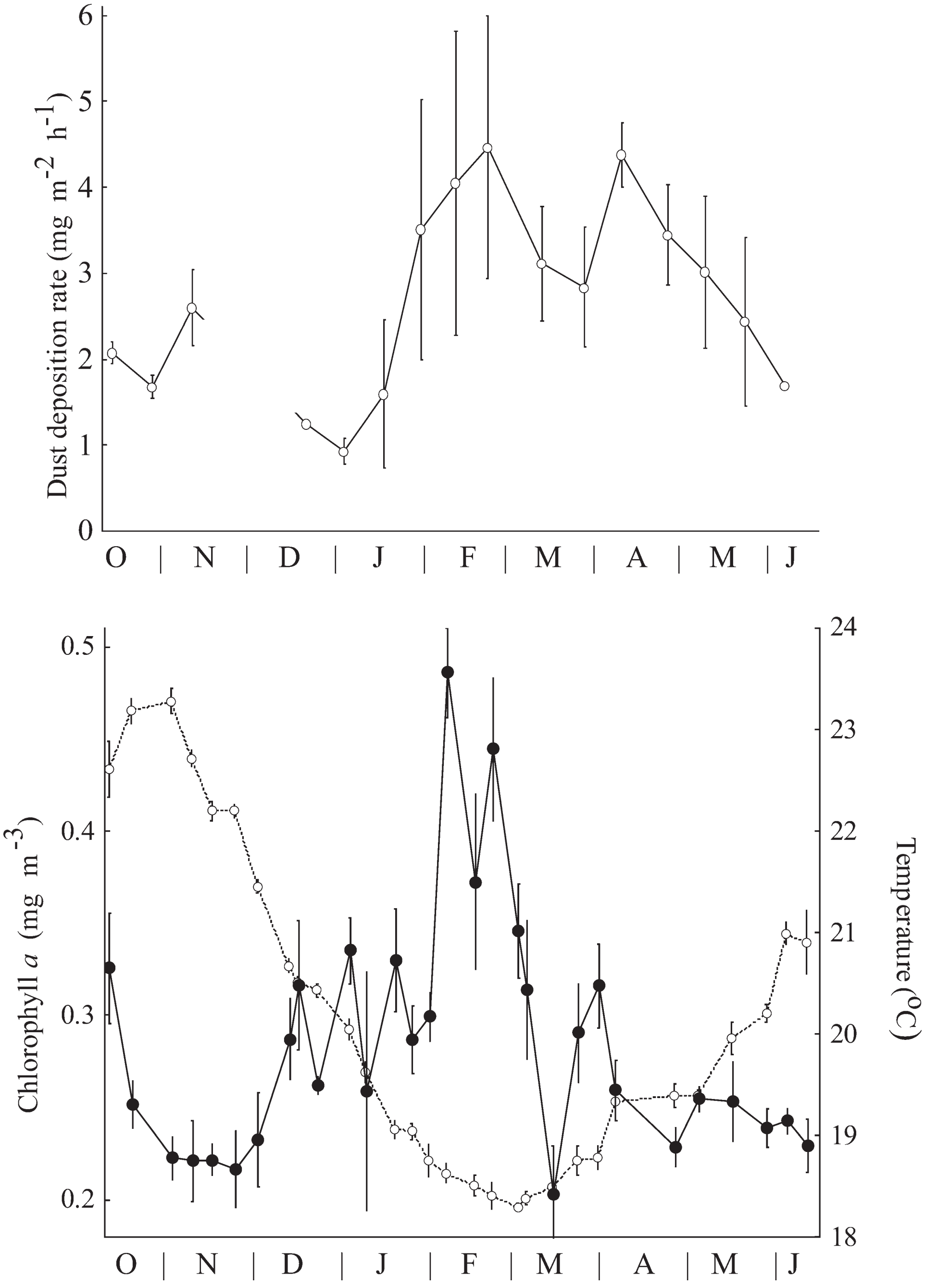

Fig. 2. (A) Dust deposition rates from October 2005 to June 2006, and (B) time series of temperature and chlorophyll in the mixed layer. Vertical bars represent standard error. Observe the increase in chlorophyll coinciding with the increase in dust deposition rates.

complex and still not fully understood. 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 (Figs. 3, 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

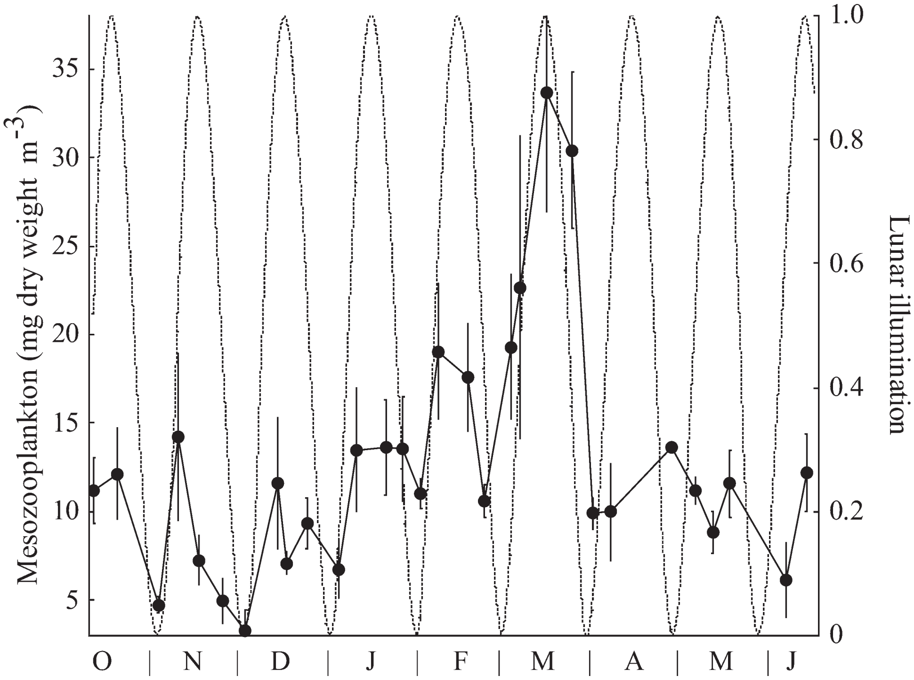

Fig. 3. Time series of mesozooplankton biomass and lunar illumination (dashed line) from October 2005 to June 2006. Vertical bars represent standard error. Lunar illumination is scaled relative to maximum brightness. Observe the lunar cycle in mesozooplankton biomass as the mixing develops through winter (from December to March).

simulate the bloom (Table 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 fig. 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 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

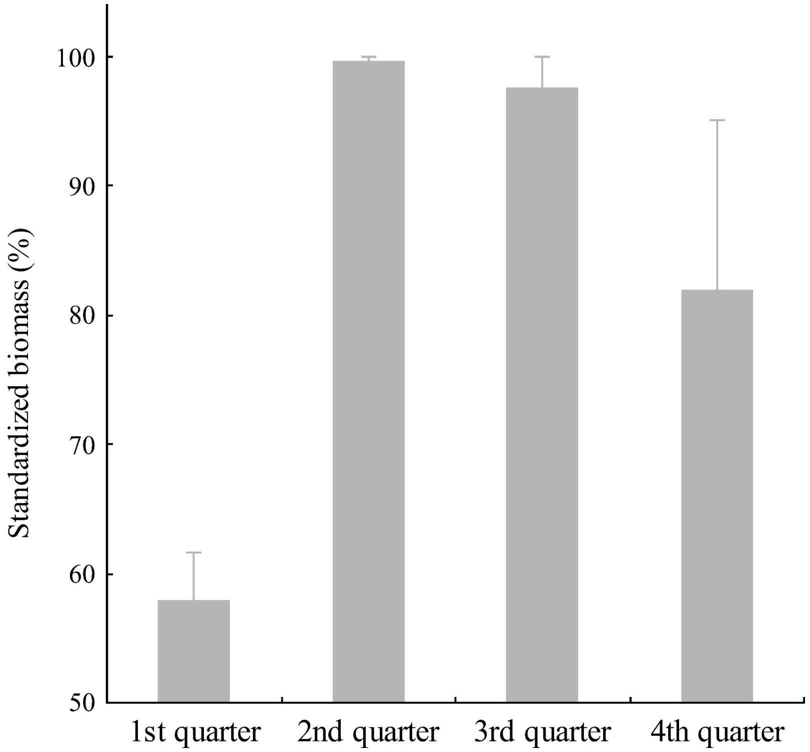

Fig. 4. Standardized biomass (maximum value of biomass in each lunar cycle converted to 100%) during the late winter bloom in the Canary Island waters.

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 2005*a*) 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 2005*a*). 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 (2005*b*) in their review of respiration in the ocean found an average biomass of mesopelagic mesozooplankton of 33.4 mmol C m^{-2} ($\pm$ 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

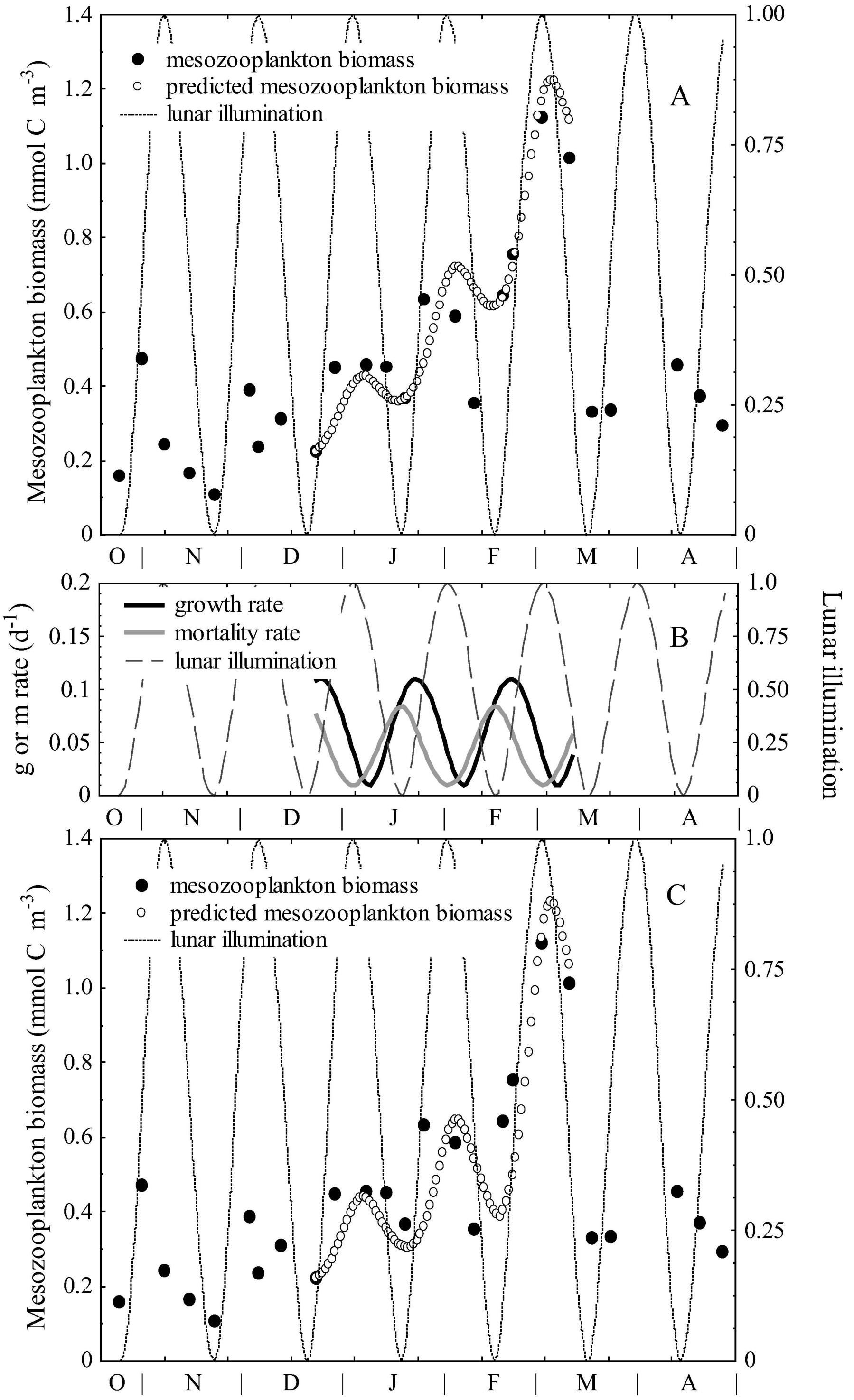

Fig. 5. (A) True (filled circles) and predicted (open circles) mesozooplankton biomass ($r = 0.902$, $p < 0.001$) according to the lunar illumination (dashed line). (B) Growth and mortality rates used to simulate the biomass in (A). Maximum growth rate was set within waxing moon ($g = 0.11\ d^{-1}$) and maximum mortality rate was set within new moon ($m = 0.08\ d^{-1}$). 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.

Table 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

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} 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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