Structure and functioning of epipelagic mesozooplankton and response to dust events during the spring PEACETIME cruise in the Mediterranean Sea

Guillermo Feliu¹, Marc Pagano¹, Pamela Hidalgo², François Carlotti¹

¹ Aix-Marseille Univ, Univ Toulon, CNRS, IRD, MIO UM 110, Mediterranean Institute of Oceanography, Marseille, France
² Department of Oceanography and Millennium Institute of Oceanography, Faculty of Natural Science and Oceanography, University of Concepcion, P.O. Box 160 C, Concepción, Chile

Correspondence to: François Carlotti (francois.carlotti@mio.osupytheas.fr)

Abstract. The PEACETIME cruise (May-June 2017) was a basin scale study mainly dedicated to the study of different planktonic trophic regimes in the Algerian, Tyrrenian and Ionian basins and, in particular, focusing on areas impacted by Saharan dust deposition. This paper presents the structural and functioning patterns of the zooplankton component during this survey, including their responses to two major dust events in the Algerian and Tyrrenian basins. The mesozooplankton was sampled at 12 stations by combining nets with 2 mesh sizes (100 and 200 µm) mounted on a bongo frame for vertical hauls within the upper 300 meter layer. In this general post-bloom situation, total mesozooplankton showed reduced variations in abundance and biomass over the whole area, with a noticeable contribution of the small size fraction (< 500 µm) of up to 50 % in abundance and 25 % in biomass. The taxonomic structure was dominated by copepods, mainly cyclopoids and calanoids, and completed by appendicularians, ostracods and chaetognaths. Distinct zooplankton taxa assemblages in the three main regions were in agreement with recently proposed regional patterns for the Mediterranean Basin, although the assemblages found in the western Ionian stations presented a closer analogy with those of the Tyrrenian basin than with those of the Ionian basin., probably due to Atlantic water influence.

Zooplankton carbon demand, grazing pressure, respiration and excretion rates were estimated using allometric relationships to the mesozooplankton size-spectrum. On average, the daily zooplankton consumption potentially represents 15 % of the phytoplankton stock, almost the whole of the primary production, with a narrow range of variations, and its excretion contributes roughly one quarter of the N and P requirements of phytoplankton production. The small size fractions make a significant contribution to these mesozooplankton estimated fluxes.

Whereas in the Algerian basin (long station FAST), the initial impact on the pelagic ecosystem of a tracked dust deposition was studied, the survey of the southern Tyrrenian basin occurred almost a week after another dust event. The changes in mesozooplankton taxonomic structure appear to be a relevant indicator to study this response, with an initial phase with no real dominance of taxa, then a disturbed state of the community with strong dominance of certain herbivorous taxa and the appearance of carnivorous species, and finally a recovery state towards a more stable system with diversification of the...
community. To our knowledge, PEACETIME is the first in situ study allowing observation of mesozooplankton responses before and soon after natural Saharan dust depositions. The changes in rank-frequency diagrams of the zooplankton taxonomic structure are an interesting index to highlight short-term responses of zooplankton to episodic dust deposition events.

1 Introduction

The Mediterranean Sea is a semi-enclosed basin connected to the Atlantic Ocean and the Black Sea. It is composed of two major sub-basins, the Eastern and Western Mediterranean, connected by the Sicily strait (Skliris, 2014). The Mediterranean Sea can be considered as a model of the world’s oceans (Bethoux et al., 1999; Lejeusne et al., 2010) because of its characteristics, such as the unique thermohaline circulation pattern and the deep water formation process. In addition, it is considered to be oligotrophic with an excess of carbon, a deficiency of phosphorus relative to nitrogen (MERMEX Group, 2011) and a decreasing west-east gradient in chlorophyll-a (i.e. Siokou-Frangou et al., 2010).

For the last two hundred years, numerous investigations have documented the pelagic zooplankton community inhabiting the Mediterranean Sea (Saiz et al., 2014), including long-term time series (i.e. Fernández de Puelles et al., 2003; Mazocchi et al., 2007; Molinero et al., 2008; García-Comas et al., 2011; Berline et al., 2012) and a succession of oceanographic surveys covering wide transects at different time periods of the year (Kimor and Wood, 1975; Nowaczyk et al., 2011; Donoso et al., 2017). The regular monitoring of the zooplankton community is essential when considering the high sensitivity of the Mediterranean Sea to anthropogenic and climate disturbance (Sazzini et al., 2014). Some of those disturbances may alter the structure and functioning of the pelagic ecosystem, and this is critical considering that marine ecosystems are being altered by anthropogenic climate change at an unprecedented rate (Chust et al., 2017).

Dust deposition is a major source of micro- and macro-nutrients (Wagener et al., 2010) that can stimulate primary production (Ridame et al., 2014), accelerate carbon sedimentation and possibly aggregation of marine particles (i.e. Neuer et al., 2004; Ternon et al., 2010; Bressac et al., 2014). Large amounts of Saharan dust can be transported in the atmosphere throughout the western and eastern Mediterranean Sea and then deposited on the sea surface by wet or dry deposition. The PEACETIME oceanographic survey, carried out between May 10 and June 11 of 2017, was designed to study in situ the processes occurring in the Mediterranean Sea after atmospheric dust deposition and their impact on marine nutrient budget and fluxes, and on the biogeochemical functioning of the pelagic ecosystem. Thus, the survey strategy was designed to be flexible in order to be able to change the sampling area depending on atmospheric events (Guieu et al., 2020. in rev). Consequently, the survey sampling programme realised consisted in 14 oceanographic stations in the central and western parts of the Mediterranean Sea. The aims of the present contribution to the PEACETIME project are 1) to document the zooplankton abundance, biomass and size distribution along the survey transect, with special attention to small-sized zooplankton; 2) to analyze the relationship between zooplankton structure and environmental variability, including dust deposition; 3) to estimate the bottom-up (nutrient regeneration) and the top-down (grazing) impact of zooplankton on
phytoplankton stock and production by estimating its ingestion, respiration, ammonium and phosphate excretions using allometric models.

2 Material and methods

2.1 Study area and environmental variables

The PEACETIME cruise survey was conducted in May/June 2017 in the western Mediterranean Sea (Figure 1) on board R.V. Pourquoi pas?. Among the 12 stations studied, 10 were sampled once for zooplankton (the short stations ST1 to ST9, and the long station TYR), whereas two long stations ION and FAST, lasting 3 and 5 days respectively, were sampled three times. The station positions along the transect were planned before the cruise so as to sample the principal ecoregions (see Figure 4 in Guieu et al., submitted), with the exception of FAST, an opportunistic station to monitor a wet dust deposition event which occurred on June 5 a few hours after the first sampling date (Table 1). A quite important dust event occurred over a large area including the southern Tyrrhenian Sea starting on May 10 which could have impacted the samples at ST5, ST6 and TYR which were sampled on May 16, 19 and 22 respectively (pers. comm. C. Guieu).

Hydrological variables (temperature, density, salinity) were measured on vertical profiles using a CTD. Dissolved oxygen was measured using a SBE43 sensor and chlorophyll-a concentration was determined from Niskin bottle samples by HPLC following the protocol of Ras et al. (2008), and with Fluorescence sensor coupled with the CTD. The depth of the mixed layer (MLD) was computed using the density difference criterion \(\Delta \sigma = 0.03 \text{ kg} \cdot \text{m}^{-3}\) defined in de Boyer Montégut et al. (2004).

2.2 Zooplankton sampling and sample processing

A total of 16 zooplankton samples were collected at 12 stations (Table 1) using a Bongo frame (double net ring of 60 cm mouth diameter) equipped with 100 \(\mu\)m and 200 \(\mu\)m mesh size nets (noted \(N_{100}\) and \(N_{200}\) below) mounted with filtering cod-ends. At all sampling stations, the Bongo frame was towed from 300 m depth to the surface at a constant speed of 1 ms\(^{-1}\). The sampling was mostly performed during the morning, except for ST7, ST9 and TYR, and night tows were also performed for the long stations FAST and ION. The samples were preserved in 4% borax-buffered formalin immediately after the net was hauled back on to the deck.

The samples were processed using FlowCAM (Fluid Imaging Technologies Inc.) and ZOOSCAN (Gorsky et al., 2010). One of the goals of this study was to achieve the determination of the complete size structure of the zooplankton community by combining different plankton mesh size nets and analysis techniques (FlowCAM and ZOOSCAN) in order to optimize the observed size spectrum. The formalin preserved samples were rinsed with tap water to remove the formalin. For net \(N_{100}\), the sample was then split into 3 size fractions: < 200 \(\mu\)m (noted below \(N_{100F<200}\)), 200 \(\mu\)m – 1000 \(\mu\)m (noted below
N_{100}F_{200/1000}, and > 1000 \mu m (noted below N_{100}F_{>1000}). For net N_{200}, the sample was split into two size fractions: < 1000 \mu m (noted below N_{200}F_{<1000}) and > 1000 \mu m (noted below N_{200}F_{>1000}).

To determine the complete size spectrum, different combinations of size fractions from the two nets and analytical techniques were tested. Taking into account the two mesh sizes, (N_{100}, N_{200}), the limits of the size spectrum were defined from the fraction N_{100}F_{<200} for the lower limit and from the fraction N_{200}F_{>1000} for the upper limit. Considering that our FlowCAM does not detect particles larger than 1200 \mu m of ESD and our ZOOSCAN does not detect particles smaller than 300 \mu m of ESD, N_{100}F_{<200} was analyzed by FlowCAM and N_{200}F_{>1000} by ZOOSCAN. The intermediate size fractions N_{100}F_{200/1000} and N_{200}F_{<1000} were both analyzed with ZOOSCAN and FlowCAM. These analyses delivered abundance and biomass values for successive ESD size classes: <200 \mu m (noted C_{<200}); 200-300 \mu m (C_{200-300}); 300-500 \mu m (C_{300-500}); 500-1000 \mu m (C_{500-1000}); 1000-2000 \mu m (C_{1000-2000}); > 2000 \mu m (C_{2000-3000}). The challenge was to choose the best net-analysis technique combination for the intermediate size fractions (C_{200-300}, C_{300-500} and C_{2000-3000}). The abundance of each class for the two nets and the two treatments was statistically compared. Parts of the spectrum corresponding to fractions C_{200-300} and C_{300-500} from N_{100} measured with FlowCAM, and to the fractions C_{500-1000} from N_{200} measured with the ZOOSCAN have significantly higher abundances than other net-analysis technique combinations (T test, p<0.000). Consequently, we combined data for N_{100}F_{<200} and N_{100}F_{200-1000} measured with FlowCAM to compute ESD size classes <500 \mu m (Figure 2A) and data for N_{200}F_{<1000} and N_{200}F_{>1000} measured with ZOOSCAN to compute ESD size classes >500 \mu m (see Figure 2B). The combination of these data enabled us to compute the final size spectrum (Figure 2C), that was used to estimate abundance, biomass and metabolic rates for each ESD size class, and then for the whole sample (sum of all the size classes) and for the total mesozooplankton (sum of the size classes C_{200-300}, C_{300-500}, C_{500-1000} and C_{1000-2000}).

For the FlowCAM analyses, the sample was concentrated in a given water volume. Then, an aliquot of each sample was analyzed using FlowCAM in auto-image mode. For the fraction N_{100}F_{<200}, a 4X magnification and 300 \mu m flow cell were used and the analysis was carried out up to 3000 counted particles. For the fraction N_{100}F_{200-1000} a 2X magnification and 800 \mu m flow cell were used and the analysis was carried out up to 1500 counted particles.

The digitalized images were analyzed using the VisualSpeadsheet® software and classified manually into taxonomic categories. Considered living organism groups for the FlowCAM were copepods, nauplii, crustaceans, appendicularians, gelatinous, chaetognaths and other diverse zooplankton groups (polychaeta, ostracods etc.). Non-organism particles were classified as detritus. Duplicates and bubbles were deleted.

To calculate the number of particles in the sample, the following equation was used.

\[ A = \frac{p_a \times V_c}{V_a \times V_s} \]

Where A is the abundance (ind m^{-3}); P_a is the number of particles in the analyzed aliquot; V_c is the given volume in the concentrated sample and V_a is the volume of the analyzed aliquot and V_s is the volume of sea water sampled by the zooplankton net (m^3).
For the ZOOSCAN analyses, the sample was homogenized and split using a Motoda box until a minimum of 1000 particles were obtained. Then, for the digitalization, the subsample was placed on the glass slide of the ZOOSCAN and the organisms were manually separated using a wooden spike to avoid overlapping. After scanning, the images were processed with the ZooProcess using the image analysis software Image J. Particles were classified automatically into taxonomic categories. Then the classification was manually verified to ensure that every outline is in the correct category. Considered living groups of organisms for the ZOOSCAN were copepods, nauplii, crustaceans, appendicularians, gelatinous, chaetognaths and diverse zooplankton (polychaeta, ostracods etc.). Non-organism particles were classified as detritus. Blurs and bubbles were deleted.

### 2.3 Normalized biomass size spectrum

The size spectra were computed for each station using combined FlowCAM and ZOOSCAN data, following Suthers et al. (2006). Firstly, the data were classified in size categories of 0.1 µm of ESD from 0.2 to 2.0 µm. Zooplankton biovolume (mm$^3$) was estimated for each category following the equation:

$$\text{Biovolume} = \frac{1}{6} \times \pi \times (\text{ESD})^3$$

With ESD expressed in mm. The X-axis of the normalized biomass sizespectrum (NBSS) was calculated by dividing the biovolume by the abundance of each category and transformed into Log10. For the Y-axis, the biovolume of each category was divided by the difference in biovolume between two consecutive categories and transformed into Log10. NBSS slope and intercept were determined using linear regression model.

### 2.4 Zooplankton carbon demand, respiration and excretion rates

The zooplankton carbon demand (ZCD in mg C m$^{-3}$ d$^{-1}$) was computed based on estimates of biomass from ZOOSCAN and FlowCAM samples and for estimates of growth rate:

$$\text{ZCD} = \text{Ration} \times B_{\text{zoo}}$$

where $B_{\text{zoo}}$ is the biomass of zooplankton in mgC m$^{-3}$, calculated using the area-weight relationships from Lehette and Hernández-León (2009) and converted to carbon assuming that carbon represent 40% of the total body dry weight (Omori and Ikeda, 1984). Ration (d$^{-1}$) is defined as the amount of food consumed per unit of biomass per day calculated as:

$$\text{Ration} = g_z + \frac{r}{A}$$

where $g_z$ is the growth rate, $r$ is the weight specific respiration and $A$ is assimilation efficiency. $g_z$ was calculated following Zhou et al. (2010):

$$g_z(w, T, Ca) = 0.033 \left( \frac{Ca}{Ca + 205e^{-0.125T}} \right) e^{0.09T}w^{-0.06}$$
as a function of sea water temperature (T, °C), food availability (Ca, mgC m⁻³), estimated from Chl-a, and weight of individuals (w, mg C). We consider here that food is phytoplankton following Calbet et al. (1996). Following Alcaraz et al. (2007) and Nival et al. (1975), values of r and A were 0.16 d⁻¹ and 0.7 respectively. ZCD was compared to the phytoplankton stock, converted to carbon assuming a C:Chl/a ratio of 50:1, and to primary production to estimate the potential clearance of phytoplankton by zooplankton.

Ammonium and phosphorus excretion and oxygen consumption rates were estimated using the multiple regression model by Ikeda et al. (1985) with carbon body weight and temperature as independent variables. Contribution to nutrient regeneration by zooplankton was estimated using the values of primary production and converted to nitrogen and phosphorus requirement using Redfield ratio. Respiration was converted to respiratory carbon lost assuming a respiratory quotient for zooplankton of 0.97 following Ikeda et al. (2000) and used as carbon requirement for zooplankton metabolism.

2.5 Data analysis

Principal component analysis (PCA) was used to explore spatial patterns of the environmental variables temperature, salinity, dissolved oxygen, using mean values of the layer 0-300 m depth, plus the estimated MLD. Averaged Chl-a values from fluorescence sensor coupled with CTD were also included in this analysis. The data were first normalized and then analyzed using Primer 6.0 software.

A taxonomic group-station matrix with the abundance values was created and then square-root transformed to estimate station similarity using Bray Curtis similarity. The similarity matrix was then ordinated using Nonmetric Multidimensional Scaling (NMDS). These analyses were performed using Primer 6.0 software.

Rank frequency diagrams (RFD) were created using the data from N₂₀₀ to see differences in taxonomic composition between the samples. Potential association between zooplankton data and spatial patterns of the environmental variables were tested using Spearman’s rank-correlations. T-test were used to compare mean values between zones. The 100 um sample of TYR station was discarded due to poor state of preservation of the sample.

3 Results

3.1 Spatial patterns of environmental variables

The Principle Component Analysis (PCA) on environmental data explains 90.3 % of the total variance in the first two axes and delivers three clusters of oceanographic areas plus two distinct stations (Figure 3). The first axis (62 % of the variance) is mostly influenced by temperature and dissolved oxygen, whereas the second axis (28.3 %) is mostly influenced by MLD, salinity and Chl-a.

The cluster of western stations in the Algerian Basin (AB) includes ST3, ST4, ST9, and FAST which are characterized by low temperature, salinity and MLD values. The cluster located in the Tyrhenian Basin (TB) comprises (ST5, ST6 and TYR
Zooplankton structure

Zooplankton abundance (Figure 4A) during PEACETIME ranges between 265 and 583 x 10^3 ind m^-2, with an average of 372 x 10^2 ± 84 x 10^3 ind m^-2, and biomass (Figure 4b) from 1160 to 2170 mgDW m^-2, with an average of 1707 ± 333 mgDW m^-2. The highest abundances are found in the PB transect and AB, and the highest biomass in the AB region. The averaged total biomass in PB is lower than in AB, due to the very low contribution of the size classes C_{1000-2000} and C_{2000-3000}, but size classes from C_{<200} to C_{500-1000} present higher biomass values than in AB. In TB, total biomass values decrease between ST4 and ST6, the latter presenting the lowest biomass value of the whole survey. Note that the biomass of TYR is obtained only for the size classes above 500 µm ESD, and the corresponding abundance is comparable to those obtained in ST5 and ST6 for these larger size classes. In IB, total biomass and abundance are lower than in AB and with low variability between stations. Detritus estimated for all analyzed classes by FlowCAM and ZOOSCAN represents between 14.6 to 39.1% of the total biomass. The C_{200-300} ESD size class has the highest averaged contribution (42.9 %) to the total zooplankton abundance, followed by C_{300-500} (28.5 %), C_{<200} (17.8 %), C_{500-1000} (8.9 %), C_{1000-2000} (1.7 %) and finally C_{>2000} (0.22 %). In terms of biomass, C_{500-1000} has the highest averaged contribution (25.3%), followed by C_{1000-2000} (23.8 %), C_{300-500} (21.3 %), C_{>2000} (15.5 %), C_{300-300} (11.9 %), and finally C_{<200} µm fraction (2.1 %). There is no correlation between total zooplankton abundance or biomass and integrated Chl-a, but C_{300-500} biomass is positively correlated with Chl-a (r=0.54, p= 0.024). Total abundance is negatively correlated with temperature (r= -0.55, p= 0.02).

Copepods are the most abundant taxonomic group in all stations (Figure 5), representing 40 to 79 % of the abundance and 32 to 85 % of the total biomass. Abundance of small zooplankton (<300 µm) is dominated by cyclopoid and calanoid copepods. In N_{200}, 51 taxonomic groups are found of which 34 are copepod genus. The adult stages of the copepod community are dominated by the genus *Para/Clausocalanus* spp.(28.7 %), *Oithona* spp. (13.7 %), *Corycaeus* spp. (6.2 %), *Oncaea* spp. (4.1 %) and undefined calanoid copepods (7.0 %). The most abundant non-copepod groups are appendicularians (5.1 %), ostracods (4.8 %) and chaetognaths (3.6 %). The highest contributions of copepods to abundance and biomass are found in PB, and then this proportion tends to decrease southwards where the abundance and biomass of the other groups such as chaetognaths and gelatinous zooplankton increase. The ratio between small (length <1 mm) and large (length > 1mm) copepods ranges from 2.8 to 8.3 (5.1 on average), with maximum mean values found in TB and minimum in IB.

The NMDS analysis (Figure 6) on the mesozooplanktonic taxa abundances based on N_{200} delivers a distribution pattern for the stations rather similar to that of the PCA on environmental variables. ST1 and ST2 on the north south transect are the most dissimilar stations due to the higher abundance of copepods, especially *Para/Clausocalanus*. at ST1, which is twice as
high as at ST2, and between 5 to 13 times higher than the rest of the transect (Figures 6A and 5). Similarly, *Centropages* spp. abundance is 10 times higher at ST1 and ST2 than in other stations of the survey. In contrast, abundances of *Oithona* spp. and *Corycaeus* spp., are respectively 6 and 10 times lower at ST1 and ST2 than at other stations. The zooplankton community in AB is slightly different from those in TB and IB due to appendicularians and unidentified calanoid copepods being more abundant in AB and to *Haloptilus* spp. being more abundant in TB and IB. Within TB and IB, the three sampling dates (ION1, ION2, ION3) at ION station form a unique cluster, whereas, ST7 and 8 are grouped with the TB station in another cluster. This differentiation of ST7 and 8 from the ION sampling dates in the NMDS analysis is mainly due to higher relative abundance of small copepods (Figure 5), and specifically to several taxa such as *Mesocalanus* spp. (more abundant), *Pontellidae* spp. and ostracoda (less abundant), *Clytemnestra* spp. (absent in ION) and *Pontellidae* spp. (absent at ST7 and 8). NBSS is calculated for each station as shown in Figure 7 taking ION1 as an example. During the PEACETIME survey, the NBSS slopes (Figure 8) range between -0.60 and 1.27, with an average value of -0.80. The most negative slopes are found in PB, whereas the IB region has the fewest negative slopes. At the long stations FAST and ION, strong variations in slope values appear depending on the sampling time, with steeper slopes in the samples collected during the day time indicating higher contributions of small zooplankton compared to large ones, and potentially linked to daily migration of larger forms deeper than 300 m.

### 3.3 Zooplankton community changes at long stations

The RFDs for stations TYR, ST5, ST6, ION and FAST are presented separately in Figures 9A to 9D, and grouped in Figures 9E and 9F. As only one sample was done at TYR station, nine days after a large dust deposition event in the Southern Tyrrenian Sea, RFDs of ST5 and ST6 also sampled in TB (six and twelve days after the dust event, respectively) are added for comparison (Figures 9A and 9B). At all three TB stations, RFDs are characterized by high dominance of herbivorous zooplankton *Para/Clausocalanus* spp. and *Oithona* spp. in 1st and 2nd position with a strong drop in abundance for the following ranked taxa (undefined calanoid copepods or *Corycaeus*). Appendicularians drop from the 4th position at ST5 and TYR to the 10th position at ST6. The shapes of RFDs change more between ST5 and TYR than between TYR and ST6. In ION station RFD shapes are similar at both sampling dates (ION1 and ION3) with the community dominated by *Para/Clausocalanus* spp. (Figure 9C). *Corycaeus* spp. changes from the 2nd position to the 4th, calanoid copepods from 3rd to 6th and *Oithona* spp. from 4th to 2nd. Appendicularians occupy a very similar position in both RFDs (6th and 7th rank at ION1 and ION3 respectively). At FAST station, the taxonomic composition is dominated by copepods (Figure 9D), but the rank order of the most dominant species changes between the two sampling dates (FAST1 and FAST3). *Oithona* spp. and *Para/Clausocalanus* spp. have the 1st and 2nd ranks during FAST1, but this order is reversed in FAST3. The 3rd place on both days are occupied by calanoid copepods. Appendicularians present one of the most significant changes, with their rank dropping from 4th to 14th between the two dates. It is remarkable that the RFDs change from a convex shape at FAST1 to a more concave one at FAST2, influenced by the high dominance of *Para/Clausocalanus* at the first rank (Figure 9D). The comparison of the standardized RFDs for all the stations (Figure 9E) highlights that the greatest change in shape is visible at
FAST, whereas it stays moderate in ION and negligible in TB. Figure 9F is similar to Figure 9E, but without ION, to visualize changes in zooplankton community composition at different time lags after a dust event, and will be commented on in more detail in the Discussion section.

3.4 Estimated zooplankton carbon demand, grazing pressure, respiration and excretion rates

Zooplankton carbon demand ZCD (Figure 10) varies between 145.9 and 280.1 mgC m\(^{-2}\) d\(^{-1}\) at ST6 and FAST1 respectively. Assuming phytoplankton as the major food source, zooplankton consumption potentially represents 15\% of the phytoplankton stock on average per day and 97\% of the primary production (see Table 2). ZCD follows the zooplankton biomass pattern with higher values in AB and lower values in TB, and does not increase with primary production (\(r= -0.18, p>0.05\)). The average respiration (mean: 83.1 mgC m\(^{-2}\) d\(^{-1}\) and range between 62.9 and 112.2 mgC m\(^{-2}\) d\(^{-1}\) ) corresponds to 36.4\% of the integrated primary production. Almost half of this zooplankton respiration is due to organisms smaller than 500 µm of ESD. Mean ammonium excretion is 12.3 mg NH4 m\(^{-2}\) d\(^{-1}\) (range between 9.1 and 17.7 mg NH4 m\(^{-2}\) d\(^{-1}\) ), and mean phosphate excretion 1.7 mg PO4 m\(^{-2}\) d\(^{-1}\) (range between 1.3 to 2.3 PO4 m\(^{-2}\) d\(^{-1}\) ). The potential contributions of excreted nitrogen and phosphorus to primary production are respectively 31.5\% (range between 19.9 to 42.6\% ) and 26.3\% (range between 19.9 to 42.6\% ). Zooplankton size classes smaller than 500 µm of ESD contribute 45\% and 47\% of the total ammonium and phosphate excretion respectively. The detailed data is shown in Table 2.

4 Discussion

4.1 Methodological concerns and the importance of the small zooplankton fraction

This methodology combining two nets (N\(_{100}\) and N\(_{200}\)) and two sample treatments (FlowCAM and ZOOSCAN) enables us to deliver a more accurate mesozooplankton community size spectrum (200-2000 µm), whereas size classes C\(_{<200}\) and C\(_{>2000}\) at the edges of the spectrum range remain under-sampled and require other equipment for proper sampling (respectively bottles and larger mesh size net). The length:width ratio of mesozooplankton organisms is quite variable, from 1 for the nearly round-shaped organisms such as nauplii or cladoceran, to more than 10 for long organisms such as chaetognaths (Pearre, 1982) or some copepods such as Macrosetella gracilis (Böttger-Schnack, 1989), with an average value between 3 and 4 for copepods (Mauchline, 1998). If we consider that organisms with a length:width ratio of 6 caught by the 200 µm mesh size will present an ESD of at least 490 µm, it is consistent that this net quite correctly samples organisms having an ESD above 500 µm ESD. For these organisms (> 500 µm ESD), ZOOSCAN is the most appropriate tool to deliver the size spectrum. Similarly, the 100 µm mesh size net allows small organisms of width just below 100 µm to pass through, but most of them might have an ESD up to 200 µm because for these smaller sizes, the length:width ratio is mostly below 4 (Mauchline, 1998). Due to the threshold of ZOOSCAN at 300 µm ESD, FlowCAM is the best tool to process organisms in the fraction below 500 µm.
Several authors have already highlighted the limitation of the 200 µm mesh size to catch small zooplankton individuals: comparisons of different zooplankton mesh size nets comprised between 60 and 330 µm have systematically shown a decrease in abundance with increasing mesh size (Turner, 2004; Pasternak et al., 2008; Riccardi, 2010; Makabe et al., 2012; Altukhov et al., 2015). When the goal of the study is to achieve a full understanding of the complete mesozooplankton community structure and functioning, the size selectivity of the sampling nets is an important issue: clearly, a large fraction of organisms of ESD between 200 and 500 µm is undersampled using a single 200 µm mesh size net. Pasternak et al. (2008) reported that a 220 µm mesh can lose up to 98% of the abundance of *Oithona* spp. and 80% of copepodite stages of *Calanus* spp. Riccardi (2010) found that a classical 200 µm net catches only 11% of the abundance and 54% of the biomass compared to a 80 µm mesh size, leading also to differences in observed species composition in the Venice lagoon. During the PEACETIME survey, the small size classes (C$_{200-300}$ and C$_{300-500}$) of mesozooplankton have been optimally sampled using a 100 µm mesh size net (N$_{100}$). Consequently, these size classes represent very large percentages of the total abundance (respectively 52.3 and 34.8 %) and a significant contribution to the total biomass (respectively 14.5 and 25.9 %). These reliable estimations have direct consequences for the estimated fluxes (see below).

### 4.2 Differences in abundance, biomass and zooplankton community structure in relation to regional environmental characteristics

A review of the most relevant information available on zooplankton biomass and abundance in different regions of the Mediterranean Sea (Table 3) shows a wide range of variation that can be attributed to location, sampling seasons and/or sampling methods (mesh size net, depth of the tow, etc), and in general, the values during PEACETIME survey are in the same order of magnitude, although most of other studies were performed with a 200 µm mesh size net and often over a shallower surface layer. However, during this post-bloom period, no clear regional patterns in abundance and biomass were found, unlike other descriptions showing a north-south and west-east decrease in zooplankton stocks (Dolan et al., 2002, Siokou-Frangou, 2004). In PB, Donoso et al. (2017) and Nival et al. (1975) highlighted a strong variability which is consistent with the strong gradient found between ST1 and ST2 during PEACETIME (see Figure 4). In AB, abundance and biomass values obtained during the survey are similar to those recorded in late spring by Nowaczyk et al. (2011), whereas Rianidey et al. (2005) found lower abundance and higher biomass values. However, the latter study focused on high resolution of a mesoscale eddy highlighting an important fine-scale variability of abundance and biomass values. For TB, the data are difficult to compare due to different sampling conditions (net mesh size), depth of tow and sampling season. In IB, all biomass presented in Table 3 are in the same order, but abundances found by Mazzocchi et al. (2003, 2014) are three times lower than those observed during PEACETIME, probably due to a high contribution of C$_{<200}$ and C$_{200-300}$ obtained with N$_{100}$ (see Figure 4). In general, the better sampling of small size classes with N$_{100}$ should lead to higher abundance values. However, the comparison of data in Table 3 shows that regional and temporal variability of these values partially masked this benefits.
In PEACETIME, clear regional differences are found both in terms of environmental variables and zooplankton taxonomic composition. ST1 and ST2 are clearly differentiated from all others with deeper MLD, higher chlorophyll-a concentrations and a zooplankton community dominated by typical herbivorous copepods of PB (*Centropages*, *Para/Clausocalanus*, *Acartia*, etc), as mentioned by Gaudy et al. (2003) and Donoso et al. (2017), and characterized by a scarcity of thaliaceans which normally occur in ephemeral and aperiodical patches (Deibel and Paffenhöfer, 2009). AB and TB are very closely related to each other in terms of hydrological features and chlorophyll-a, but slightly differentiated in salinity and zooplankton taxonomy. In AB, 17 days separated the sampling of ST3 and ST4 with that of ST9 and FAST, but despite this time gap, they are very close in terms of hydrological features, chlorophyll-a level and zooplankton community structure. IB is clearly differentiated from these groups in terms of environmental parameters (see Figure 3) due to higher salinity and lower chlorophyll-a, but in terms of zooplankton community the western Ionian stations (ST7 and ST8) present more analogy with TB than with the ION station (see Figure 6). During PEACETIME, the station ION appears clearly separated from ST7 and ST8 located further westwards by a north-south jet (ADCP and MVP observations, Berline et al., in preparation), which might correspond to the Mid-Mediterranean Jet (Malanotte-Rizzoli et al., 2014, their Figure 5). The location of ST7 and ST8 within anticyclonic structures of the portion of the Modified Atlantic Water (MAW) flowing through the Sicily Channel, could explain their similarity with TB stations in terms of zooplankton assemblages, as TB is directly influenced by the main part of the MAW flowing through the Sardinia Channel. Ayata et al. (2018) also classified the Tyrhenian Sea as heterogeneous due to complex circulation patterns including transient hydrodynamic structures in the south, which could also explain the similarity of ST7 and ST8 with TB stations in terms of zooplankton assemblages during PEACETIME. This visited area of the IB during PEACETIME certainly represents a transition area between the eastern and western Mediterranean basins (Siokou-Frangou et al., 2010; Mazzocchi et al., 2003).

These regional differences highlighted both in terms of environmental characteristics and zooplankton taxa assemblages are in agreement with the regionalization of the Mediterranean basin by Ayata et al. (2018) based on historical biogeochemical, biological and physical data of the epipelagic zone. For instance, ST1 of PEACETIME characterized by high Chl-a, high zooplankton abundance and dominance of small copepods is clearly located in the ‘consensual Ligurian Sea Region’ sensu Ayata et al. (2018) identified as the most productive of the Mediterranean due to intense deep convection events. Among AB stations, stations 3, 4 and 9 are clearly in the ‘consensual Algerian region’ (Ayata et al., 2018), whereas station FAST corresponds to the ‘western Algerian heterogeneous region’. Among the IB stations, the separation of stations 7 and 8 from the ION stations in terms of zooplankton communities and, to a lesser extent, of environmental variables, also correspond to the distinction between the ‘consensual North Ionian’ region and the western part of the ‘Ionian Sea region’, considered as a heterogeneous region (Ayata et al., 2018).

### 4.3 Estimated zooplankton-mediated fluxes during the PEACETIME survey

By using allometric relationships relating zooplankton grazing and metabolic rates to size structure, zooplankton impacts (top-down vs. bottom-up) on primary production have been investigated. ZCD estimations show that zooplankton required...
15% of the daily phytoplankton stock, with narrow variations over the whole area (between 9.5 to 19.3), which are twice lower than the values estimated by Donoso et al. (2017) during the spring bloom in the North-Western Mediterranean Sea. However, estimated grazing rates are in the order of the estimated primary production, which corresponds to the highest range of the values summarized by Siokou-Frangou et al. (2010) for the whole Mediterranean Sea (from 14 to 100%). Just estimating ZCD on the basis of mesozooplankton alone certainly leads to overestimation of its top-down impact on phytoplankton. In the Mediterranean Sea, the primary production is consumed by a “multivorous web” including microbial and zooplankton components (Siokou-Frangou et al., 2010). Mesozooplankton simultaneously grazes on phytoplankton and heterotrophic prey, such as heterotrophic dinoflagellates (Sherr and Sherr, 2007) or ciliates (Dolan et al., 2002), and might be quite flexible in its feeding strategy depending on composition and size of prey as well as on environmental variables such as turbulence (Kleppel, 1993; Yang et al., 2010). On one hand, a large part of the primary production can be consumed by ciliates (Dolan and Marrasé et al., 1995) but on the other hand, mesozooplankton can consume almost the entire ciliate production (Pitta et al., 2001; Pérez et al., 1997; Zervoudaki et al., 2007) potentially explaining the wide variations of standing stock of ciliates over the Mediterranean Sea (Dolan et al., 1999; Pitta et al., 2001; Dolan et al., 2002). The generally described east-west pattern of decreasing grazing impact (Siokou-Frangou et al., 2010) could not be observed during this study as only one station (ION station) was typical of the Eastern Mediterranean Sea.

Estimated NH₃ and PO₄ excretion rates by mesozooplankton during PEACETIME are consistent with the few observations collected in the Mediterranean Sea (Alcaraz, 1988; Alcaraz et al., 1994; Gaudy et al., 2003) and with those obtained at similar latitudes (see review in Hernández-León at al., 2008). From our estimation, zooplankton excretion would contribute respectively to 21 - 44% and 17 - 38% of the N and P requirements for phytoplankton production. In the NWMS, Alcaraz et al. (1994) estimated a zooplankton nitrogen excretion contribution to primary production > 40%, whereas Gaudy et al. (2003) reported 31 - 32% and 10 - 100% N and P contributions. This impact on phytoplankton production can be even greater in proximity to the DCM where zooplankton tends to aggregate fuelling regenerated production (Saiz and Alcaraz, 1990) and enhancing bacterial production (Christaki et al., 1998). Zooplankton grazing impact and nutrient contribution to primary production are higher in the western basin than in the Ionian Sea, mainly linked to variations of zooplankton biomass. Mean carbon released through zooplankton respiration represents 36% of the primary production during PEACETIME, which is higher than previous measurements in NWMS (by Alcaraz, 1988 and Gaudy et al., 2003) from onboard incubation experiments on zooplankton collected by a 200 µm mesh size net.

Metabolic estimations clearly show that the size fractions < 500 µm (optimally captured with the 100 µm mesh size net) make a significant contribution to the whole mesozooplankton estimated fluxes: 14.9% of the ZCD is due to organisms <300 µm, and this size class contributes 21% and 20% of the total ammonium and phosphate excretion respectively.

### 4.4 Impact of dust deposition on the zooplankton community

In the past years, responses to Saharan dust inputs in marine systems have been mostly studied in microcosm and mesocosm experiments, but more rarely observed in situ. Most studied responses to dust are focused on the microbial biota and are
generally marked by an increase in metabolic rates rather than by standing stock changes (probably due to trophic transfer along the food-web) (Ternon et al., 2011; Guieu et al., 2014; Ridame et al., 2014; Herut et al., 2016). In mesocosms, changes in zooplankton stocks are strongly dependent of the initial conditions, and cannot really reflect what could occur in natural waters within the Mediterranean “multivorous planktonic food-web” (Siokou-Frangou et al., 2010). Pitta et al. (2017) found an increase in mesozooplankton biomass 9 days after the beginning of a mesocosm experiment, probably as a result of an earlier increase of prey (flagellates, ciliates and dinoflagellates). Tsagaraki et al. (2017) described an increase in productivity after an artificial dust deposition that was transferred to higher trophic levels by the classical food web, resulting in an increase of copepod egg production 5 days after the beginning of the experiment. Very few in situ studies have documented mesozooplankton responses to Saharan dust. Abundance increase was observed by Thingstad et al. (2005) in the Eastern Mediterranean Sea, and by Hernández-León et al. (2004) in Atlantic waters close to the Canary Islands one week after the deposition. In this latter area, Franchy-León et al. (2013) detected increases of zooplankton grazing and zooplankton biomass after another event. Thus, the PEACETIME survey dedicated to the tracking of such events was an opportunity to observe real in situ responses.

At station FAST (an opportunistic station after a Saharan dust deposition event), an increase in nitrate (from 50 nM to 120 nM) and phosphate concentrations (from 8 nM to 16 nM) occurred in the mixed layer (pers. comm. C. Guieu), which led to an increase primary production from FAST1 to FAST3, but with no visible changes in phytoplankton biomass or species composition (see Table 2). For zooplankton, the total abundance slightly decreases but the community composition presents obvious changes, mainly a decrease of appendicularians and an increase of Para/Clausocalanus spp. and of carnivorous taxa (Candacia spp., chaetognaths, siphonophores) (see Figure 9D). The sharp decrease of appendicularian abundance (four-fold decrease) and rank position (see Figure 9D) could potentially be linked either to food limitation or to predation. Size and species composition of the phytoplankton community in FAST did not show any change after the dust (pers. comm. J. Uitz), but there were potential increases in food competition with Para/Clausocalanus spp. (Lombard et al., 2010) and/or in predation by chaetognaths and siphonophores (Purcell et al., 2005). Although total zooplankton biomass remains relatively stable at FAST, the contribution of the size classes C_{500-1000} and C_{1000-2000} increase relative to the smaller size classes (see Figure 4B) inducing variations on the NBSS slope from -0.76 to -0.63 (see Figure 8). This 15% increase in biomass is mainly due to large migrating taxa such as copepods Eucalanus spp., Rhincalanus spp. and Candacia spp., chaetognaths and siphonophores. The daily observation of sediment traps at 200 and 500 meters over five days between FAST1 and FAST3 (pers. comm. C. Guieu) shows a relative increase of swimmers collected at 500 m versus those collected at 200 m, also suggesting increasing numbers of migrants. An obvious planktonic transition occurred during this period but it is difficult to conclude which of the bottom-up (changes in primary producers) or top-down (increase of carnivorous migrants) effects was dominant. The change in the RFDs (Figure 9D), from a convex shape at FAST1, indicating a more stable system with no dominance of the first taxonomic groups, to a more concave shape at FAST3 influenced by the high dominance of Para/Clausocalanus at the first rank, could reflect a disturbance effect (sensu Pinca and Dallot, 1997) of the dust deposition on the zooplankton community.
A synoptic analysis of the RFDs linked to the dust events observed in the Tyrrhenian basin and at FAST station offers a basis for proposing a conceptual model of a virtual time series of zooplankton community responses after a dust deposition event (Figure 9F): the first sampling occurs before the event (FAST1), and several other samplings are realized with time-lag of five days (FAST3), six days (ST5), nine days (TYR) and twelve days (ST6) after the event. FAST1 represents an initial steady state (state 1) with no dominance in the first taxa ranks, meanwhile FAST3 and ST5 represent a disturbed state of the community (state 2) with strong dominance of the first taxa and the collapse of the following ones. TYR and ST6 represent the beginning of recovery towards a stable system (state 3) with the move up of the second rank. State 1 before the dust event is characterized by oligothropic conditions with low nutrients, low phytoplankton concentration dominated by small-size cells and their typical zooplankton grazers (e.g. appendicularians and thaliaceans), leading to a convex RFD shape (like FAST1 Figure 9F) reflecting a mature community (sensu Frontier, 1976). State 2 is characterized by a nutrient input linked to the dust event stimulating larger phytoplankton cells and their herbivorous grazers (copepods) and attracting carnivorous migrants leading to a more concave RFD shape (like FAST3, ST5 and TYR Figure 9F) typical of a disturbed community (sensu Frontier, 1976). State 3 is characterized by the diversification of herbivorous taxa leading to changes in RFD towards a convex shape (like ST6 Figure 9F).

5 Conclusion

To our knowledge, PEACETIME was the first study in the Mediterranean Sea that managed to collect zooplankton samples before and soon after natural Saharan dust deposition events and to highlight in situ zooplankton responses in terms of community composition and size structure. Our study suggests that a complete understanding of the mesozooplankton community response to a single massive dust event would require continuous observation over two to three weeks, from an initial state just before the event to a complete process of zooplankton community succession after the event. To identify such a succession, the rank-frequency diagrams of the zooplankton taxonomic structure appears to be a more practical and sensitive index than observable changes in stock (abundance and biomass) or in metabolic rates, and should be further tested. This approach requires a complete overview of mesozooplankton size spectrum and community composition which was achieved in our study by combining data from two mesh size nets (100 and 200 µm) and two analytical techniques (FlowCAM and ZOOSCAN). In our study, this strategy also enabled us to show the importance of small forms (< 500 µm of ESD) both in terms of stocks and fluxes.

Acknowledgments

This study is a contribution to the PEACETIME project (http://peacetime-project.org), a joint initiative of the MERMEX and ChArMEx components supported by CNRS-INSU, IFREMER, CEA, and Météo-France as part of the programme MISTRALS coordinated by INSU. The PEACETIME cruise (https://doi.org/10.17600/17000300) was managed by C. Guieu
(LOV) and Karine Desboeufs (LISA). We thank the PEACETIME project coordinators and scientists on board, especially Nagib Bhairy and Cécile Guieu who did the zooplankton sampling. Thanks to E. Maranon and M. Perez-Lorenzo for the PP data and to Julia Uitz, Céline Dimier and the SAPIGH analytical service at the Institut de la Mer de Villefranche (IMEV) for onboard sampling and HPLC analysis. Thanks to Cécile Guieu, Elvira Pullido, France Van Wambake, and Julia Uitz for critical reading and advice on a first version of the draft, and to Michael Paul for correcting the language. G. Feliú was supported by a Becas-Chile PhD scholarship (CONICYT Government of Chile).

Data availability

All data and metadata will be made available at the French INSU/CNRS LEFE CYBER database (scientific coordinator: Hervé Claustre; data manager, webmaster: Catherine Schmechtig). INSU/CNRSLEFE CYBER (2020)

Authors contribution

GF, MP and FC wrote the paper with contributions by PH. GF participated in the sample treatment. GF, FC, MP and PH participated in the data analysis

Competing interests

The authors declare that they have no conflict of interest

References

Alcaraz, M.: Summer zooplankton metabolism and its relations to primary production in the Western Mediterranean, edited by: Minas, J. H. and Nival, P., Océanographie pêlagique méditerranéenne, Oceanol. Acta SP 9, 185–191, 1988.

Alcaraz, M., Calbet, A., Estrada, M., Marrasé, C., Saiz, E., and Trepat, I.: Physical control of zooplankton communities in the Catalan Sea, Prog. Oceanogr., 74, 294–312, doi:10.1016/j.pocean.2007.04.003, 2007.

Alcaraz, M., Saiz, E., and Estrada, M.: Excretion of ammonia by zooplankton and its potential contribution to nitrogen requirements for primary production in the Catalan Sea (NW Mediterranean), Mar. Biol., 119, 69–76, doi:10.1007/BF00350108, 1994.

Alcaraz, M., Saiz, E., Fernandez, J. A., Trepat, I., Figueiras, F., Calbet, A., and Bautista, B.: Antarctic zooplankton metabolism: carbon requirements and ammonium excretion of salps and crustacean zooplankton in the vicinity of the Bransfield strait during January 1994, J. Mar. Syst., 17, 347–359, 1998.

Altukhov, D., Siokou, I., Pantazi, M., Stefanova, K., Timofte, F., Gubanova, A., Nikishina, A. and Arashkevich, E.: Intercomparison of five nets used for mesozooplankton sampling. Mediterranean Marine Science, 16(3): 550-561, doi: http://dx.doi.org/10.12681/mms.1100, 2015.
Ayata, S. D., Irisson, J. O., Aubert, A., Berline, L., Dutay, J. C., Mayot, N., Nieblas, A., D’Ortenzio, F., Palmiéri, J., Reygondeau, G., Rossi, V. and Guieu C.: Regionalisation of the Mediterranean basin, a MERMEX synthesis. Prog. Oceanogr., 163, 7-20, https://doi.org/10.1016/j.pocean.2017.09.016, 2018.

Berline, L., Siokou-Frangou, I., Marasović, I., Vidjak, O., Fernández de Puelles, M. L., Mazzocchi, M. G., Assimakopoulou, G., Zervoudaki, S., Fonda-Umani, S., Conversi, A., García-Comas, C., Ibanez, F., Gasparini, S., Stemmann, L. and Gorsky, G.: Intercomparison of six Mediterranean zooplankton time series, Prog. Oceanogr., 97–100, 76–91, doi:10.1016/j.pocean.2011.11.011, 2012.

Bethoux, J. P., Gentili, B., Morin, P., Nicolas, E., Pierre, C. and Ruiz-Pino, D.: The Mediterranean Sea: A miniature ocean for climatic and environmental studies and a key for the climatic functioning of the North Atlantic, Prog. Oceanogr., 44, 131–146, doi.org/10.1016/S0079-6611(99)00023-3, 1999.

Böttger-Schnack, R.: Body length of female Macrosetella gracilis (Copepoda: Harpacticoida) from various depth zones in the Red Sea. Mar. Ecol. Prog. Ser., 52, 33–37, 1989.

Bressac, M., Guieu, C., Doxaran, D., Bourrin, F., Leblond, N., Desboeufs, K. and Ridame, C.: Quantification of the lithogenic carbon pump following a simulated dust deposition event in large mesocosm, Biogeosciences, 11: 1007–1020 | doi: 10.5194/bg-11-1007-2014, 2014.

Calbet, A., Alcaraz, M., Saiz, E., Estrada, M. and Trepat, I.: Planktonic herbivorous food webs in the catalan Sea (NW Mediterranean): temporal variability and comparison of indices of phyto-zooplankton coupling based on state variables and rate processes, J. Plankton Res., 18(12), 2329–2347, doi:10.1093/plankt/18.12.2329, 1996.

Champalbert, G.: Characteristics of zooplankton standing stock and communities in the western Mediterranean: relation to hydrology, Sci. Mar., 60(Suppl. 2), 97–113, 1996.

Christaki, U., Dolan, J. R., Pelegri, S. and Rassoulzadegan, F.: Consumption of picoplankton-size particles by marine ciliates: Effects of physiological state of the ciliate and particle quality, Limnol. Oceanogr., 43(3), 458–464, doi:10.4319/lo.1998.43.3.0458, 1998.

Chust, G., Vogt, M., Benedetti, F., Nakov, T., Villéger, S., Aubert, A., Vallina, S. M., Righetti, D., Not, F., Biard, T., Bittner, L., Benoiston, A. S., Guidi, L., Villarino, E., Gaborit, C., Cornils, A., Buttay, L., Irisson, J. O., Chiarello, M., Vallin, A. L., Blanco-Bercial, L., Basconi, L. and Ayata, S. D.: Mare incognitum: A glimpse into future plankton diversity and ecology research, Front. Mar. Sci., 4:68, doi:10.3389/fmars.2017.00068, 2017.

de Boyer Montegut, C., Madec, G., Fischer, A. S., Lazar, A., and Iudicone, D.: Mixed layer depth over the global ocean: An examination of profile data and a profile-based climatology, J. Geophys. Res., 109, C12003, doi:10.1029/2004JC002378, 2004.

Deibel, D and Paffenhöfer, G. A.: Predictability of patches of neritic salps and doliolids (Tunicata, Thaliacea) , J. Plankton Res., 31, 1571–1579, doi.org/10.1093/plankt/fbp091, 2009.

Dolan, J. R. and Marrasé, C.: Planktonic ciliate distribution relative to a deep chlorophyll maximum: Catalan Sea, N.W. Mediterranean, June 1993, Deep. Res. Part I, 42(11–12), 1965–1987, doi:10.1016/0967-0637(95)00092-5, 1995.
Dolan, J. R., Vidussi, F. and Claustre, H.: Planktonic ciliates in the Mediterranean Sea: Longitudinal trends, Deep. Res. Part I Oceanogr. Res. Pap., 46(12), 2025–2039, doi:10.1016/S0967-0637(99)00043-6, 1999.

Dolan, J. R., Claustre, H., Carlotti, F., Plounevez, S. and Moutin, T.: Microzooplankton diversity: Relationships of tintinnid ciliates with resources, competitors and predators from the Atlantic Coast of Morocco to the Eastern Mediterranean, Deep. Res. Part I Oceanogr. Res. Pap., 49(7), 1217–1232, doi:10.1016/S0967-0637(02)00021-3, 2002.

Donoso, K., Carlotti, F., Pagano, M., Hunt, B. P. V., Escribano, R. and Berline, L.: Zooplankton community response to the winter 2013 deep convection process in the NW Mediterranean Sea, J. Geophys. Res. Ocean., 122(3), 2319–2338, doi:10.1002/2016JC012176, 2017.

Durrieu de Madron, X., Guieu, C., Sempéré, R., Conan, P., Cossa, D., D’Ortenzio, F., Estournel, C., Gazeau, F., Rabouille, C., Stemmann, L., Bonnet, S., Diaz, F., Koubbi, P., Radakovitch, O., Babin, M., Baklouti, M., Bancon-Montigny, C., Belviso, S., Bensoussan, N., Bonsang, B., Bouloubassi, I., Brunet, C., Cadiou, J. F., Carlotti, F., Chami, M., Charmasson, S., Charrière, B., Dachs, J., Doxaran, D., Dutay, J. C., Elbaz-Poulichet, F., Eléaume, M., Eyrolles, F., Fernandez, C., Fowler, S., Francour, P., Gaertner, J. C., Galzin, R., Gasparini, S., Ghiglione, J. F., Gonzalez, J. L., Goyet, C., Guidi, L., Guizien, K., Heimbürger, L. E., Jacquet, S. H. M., Jeffrey, W. H., JouX, F., Le Hir, P., Leblanc, K., Lefèvre, D., Lejeune, C., Lemé, R., Loïé-Pilot, M. D., Mallet, M., Méjanelle, L., Mélin, F., Mellon, C., Mérigot, B., Merle, P. L., Migon, C., Miller, W. L., Mortier, L., Mostajir, B., Mousseau, L., Moutin, T., Para, J., Pérez, T., Petrenko, A., Poggiale, J. C., Prieur, L., Pujo-Pay, M., Pulido-Villena, Rainmbault, P., Rees, A. P., Ridame, C., Rontani, J. F., Ruiz Pino, D., Sicre, M. A., Taillandier, V., Tamburini, C., Tanaka, T., Taupier-Letage, I., Tedetti, M., Testor, P., Thébault, H., Thouvenin, B., Touratier, F., Tronczynski, J., Ulses, C., Van Wambkeke, F., Vantrepotte, V., Vaz, S. and Verney, R.: Marine ecosystems’ responses to climatic and anthropogenic forcings in the Mediterranean, Prog. Oceanogr., 91(2), 97–166, doi:10.1016/j.pocean.2011.02.003, 2011.

Fernández de Puelles, M.L., Grás, D., Hernández-León, S.: Annual Cycle of Zooplankton Biomass, Abundance and Species Composition in the Neritic Area of the Balearic Sea, Western Mediterranean, Mar. Ecol., 24, 123–139, doi:10.1046/j.1439-0485.2003.03816.x, 2003.

Fernández De Puelles, M. L., Pinot, J. M. and Valencia, J.: Seasonal and interannual variability of zooplankton community in waters off Mallorca island (Balearic Sea, Western Mediterranean): 1994-1999, Oceanol. Acta, 26, 673–686, doi:10.1016/j.oceacta.2003.07.001, 2003.

Fonda Umani, S., and De Olazábal, A.: Tuscan Northern Tyrrhenian net zooplankton Autumn 1986, Rapp. Comm. int. Mer Médit, 31, 235, 1988.

Franchy, G., Ojeda, A., López-Cancio, J. and Hernández-León, S.: Plankton community response to Saharan dust fertilization in subtropical waters off the Canary Islands, Biogeosciences Discuss., 10(11), 17275–17307, doi:10.5194/bg-2020-126, 2020.
García-Comas, C., Stemmann, L., Ibanez, F., Berline, L., Mazzocchi, M. G., Gasparini, S., Picheral, M. and Gorsky, G.: Zooplankton long-term changes in the NW Mediterranean Sea: Decadal periodicity forced by winter hydrographic conditions related to large-scale atmospheric changes?, J. Mar. Syst., 87(3–4), 216–226, doi:10.1016/j.jmarsys.2011.04.003, 2011.

Gaudy, R., Youssara, F., Diaz, F. and Raimbault, P.: Biomass, metabolism and nutrition of zooplankton in the Gulf of Lions (NW Mediterranean), Oceanol. Acta, 26, 357–372, doi:10.1016/S0399-1784(03)00016-1, 2003.

Gorsky, G., Ohman, M. D., Picheral, M., Gasparini, S., Stemmann, L., Romagnan, J.-B., Cawood, A., Pesant, S., Garcia-Comas, C. and Prejger, F.: Digital zooplankton image analysis using the ZooScan integrated system, J. Plankton Res., 32, 285–303, doi:10.1093/plankt/fbp124, 2010.

Guieu, C., Ridame, C., Pulido-Villena, E., Bressac, M., Desboeufs, K. and Dulac, F.: Impact of dust deposition on carbon budget: a tentative assessment from a mesocosm approach, Biogeosciences, 11(19), 5621–5635, doi:10.5194/bg-11-5621-2014, 2014.

Hernández-León, S., Almeida, C., Becognée, P., Yebra, L., and Arístegui, J.: Zooplankton biomass and indices of grazing and metabolism during a late winter bloom in subtropical waters, Mar. Biol., 145, 1191–1200, 2004.

Hernandez-Leon, S., Fraga, C. and Ikeda, T.: A global estimation of mesozooplankton ammonium excretion in the open ocean, J. Plankton Res., 30, 577–585,https://doi.org/10.1093/plankt/fbn021, 2008.

Herut, B., Rahav, E., Tsagaraki, T. M., Giannakourou, A., Tsiola, A., Psarra, S., Lagaria, A., Papageorgiou, N., Mihalopoulos, N., Theodosi, C. N., Violaki, K., Stathopoulou, E., Scoullos, M., Krom, M. D., Stockdale, A., Shi, Z., Berman-Frank, I., Meador, T. B., Tanaka, T. and Paraskevi, P.: The potential impact of Saharan dust and polluted aerosols on microbial populations in the East Mediterranean Sea, an overview of a mesocosm experimental approach, Front. Mar. Sci., 3, 226, doi:10.3389/fmars.2016.00226, 2016.

Ikeda, T.: Metabolic rates of epipelagic marine zooplankton as a function of body mass and temperature, Mar. Biol., 85, 1–11, doi:10.1007/BF00396409, 1985.

Ikeda, T., Torres, J. J., Hernández-León, S. and Geiger, S. P.: Metabolism, in Zooplankton Methodology Manual, Academic Press, 455–532, 2000

Kirim, B. and Wood, E. J. F.: A plankton study in the eastern Mediterranean Sea, Mar. Biol., 29, 321–333, doi:10.1007/BF00388852, 1975.

Kleppel, G. S.: On the diets of calanoid copepods, Mar. Ecol. Prog. Ser., 99, 183–195, doi:10.3354/meps099183, 1993.

Kovalev, A., Mazzocchi, M.G., Kideys, A.E., Toklu, B. and Skryabin, V.A., Seasonal Changes in the Composition and abundance of zooplankton in the seas of the Mediterranean basin, Turk J Zool., 27, 205–219, 2003.

Lehette, P. and Hernández-León, S.: Zooplankton biomass estimation from digitized images: a comparison between subtropical and Antarctic organisms, Limnol. Oceanogr. Methods, 7, 304–308, doi:10.4319/lom.2009.7.304, 2009.
Lejeusne, C., Chevaldonné, P., Pergent-Martini, C., Boudouresque, C. F. and Pérez, T.: Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea, Trends Ecol. Evol., 25(4), 250–260, doi:10.1016/j.tree.2009.10.009, 2010.

Lombard, F., Eloire, D., Gobet, A., Stemmann, L., Dolan, J. R., Sciandra, A. and Gorsky, G.: Experimental and modeling evidence of appendicularian-ciliate interactions, Limnol. Oceanogr., 55(1), 77–90, doi:10.4319/lo.2010.55.1.0077, 2010.

Makabe, R., Tanimura, A. and Fukuchi, M.: Comparison of mesh size effects on mesozooplankton collection efficiency in the Southern Ocean, J. Plankton Res., 34, 432–436, doi:10.1093/plankt/fbs014, 2012.

Mauchline, J.: The biology of calanoid copepods, Advances in marine biology, 710 pp, 1998.

Mazzocchi, M. G., Christou, E. D., Capua, I., Di Capua, I., Aguzzi,L., and Boldrin, A.: Spring mesozooplankton communities in the epipelagic Ionian Sea in relation to the Eastern Mediterranean Transient, J. Geophys. Res., 108, 8114, doi:10.1029/2002JC001640, 2003.

Mazzocchi, M. G., Nervegna, D., D’Elia, G., Di Capua, I., Aguzzi,L., and Boldrin, A.: Spring mesozooplankton communities in the epipelagic Ionian Sea in relation to the Eastern Mediterranean Transient, J. Geophys. Res., 108, 8114, doi:10.1029/2002JC001640, 2003.

Mazzocchi, M. G., Christou, E. D., Capua, I., Di, Fernández de Puelles, M. L., Fonda-Umani, S., Molinero, J. C., Nival, P. and Siokou-Frangou, I.: Temporal variability of Centropages typicus in the Mediterranean Sea over seasonal-to-decadal scales, Prog. Oceanogr., 72, 214–232, doi:10.1016/j.pocean.2007.01.004, 2007

Mazzocchi, M.G., Licandro, P., Dubroca, L., Di Capua, I. and Saggiomo, V.: Zooplankton associations in a Mediterranean long-term time-series, J Plankton Res., 33, 1163–1161, doi:10.1093/plankt/fbr017, 2011.

Mazzocchi, M. G., Siokou, I., Tirelli, V., Bandelj, V., Fernandez de Puelles, M. L., Ak Örek, Y., de Olazabal, A., Guanova, A., Kress, N., Protopapa, M., Solidoro, C., Taglialatela, S. and Terbiyik Kurt, T.: Regional and seasonal characteristics of epipelagic mesozooplankton in the Mediterranean Sea based on an artificial neural network analysis, J. Mar. Syst., 135, 64–80, doi:10.1016/j.jmarsys.2013.04.009, 2014.

Molinero, J. C., Ibañez, F., Souissi, S., Buecher, E., Dallot, S., and Nival, P.: Climate control on the long-term anomalous changes of zooplankton communities in the North western Mediterranean, Global Change Biology, 14, 11–26, doi:10.1111/j.1365-2486.2007.01469.x, 2008.

Neuer, S., Torres-Padrón, M. E., Gelado-Caballero, M. D., Rueda, M. J., Hernández-Brito, J. J., Davenport, R., and Wefer, G.: Dust deposition pulses to the eastern subtropical North Atlantic gyre: Does ocean’s biogeochemistry respond?, Global Biogeochem. Cy., 18, GB4020, https://doi.org/10.1029/2004GB002228, 2004.
Nival, P., Nival, S., and Thiriot, A.: Influence des conditions hivernales sur les productions phyto-et zooplanctoniques en Méditerranée Nord-Occidentale. V. Biomasse et production zooplanctonique - relations phyto-zooplancton, Mar. Biol., 31, 249–270, doi:10.1007/BF00387153, 1975.

Nowaczyk, A., Carlotti, F., Thibault-Botha, D. and Pagano, M.: Distribution of epipelagic metazooplankton across the Mediterranean Sea during the summer BOUM cruise, Biogeosciences, 8, 2159–2177, doi:10.5194/bg-8-2159-2011, 2011.

Omet, M. and Ikeda, T.: Methods in marine zooplankton ecology, John Wiley, New York, 332pp, 1984.

Pasternak, A., Arashkevich, E., Reigstad, M., Wassmann, P. and Falk-Petersen, S.: Dividing mesozooplankton into upper and lower size groups: Applications to the grazing impact in the Marginal Ice Zone of the Barents Sea, Deep. Res. Part II Top. Stud. Oceanogr., 55, 2245–2256, doi:10.1016/j.dsr2.2008.05.002, 2008.

Pearse, S.: Feeding by Chaetognatha: Aspects of inter and intra specific predation, Mar. Ecol. Prog. Ser., 7, 33–45, 1982.

Pérez, M., Dolan, J., and Fukai, E.: Planktonic oligotrich ciliates in the NW Mediterranean: growth rates and consumption by copepods, Mar. Ecol. Prog. Ser., 155, 89–101, 1997.

Pinca, S. and Dallot, S.: Zooplankton community structure in the Western Mediterranean sea related to mesoscale hydrodynamics, Hydrobiologia, 356(1–3), 127–142, doi:10.1023/A:1003151609682, 1997.

Pitta, P., Giannakourou, A., and Christaki, U.: Planktonic ciliates in the oligotrophic Mediterranean Sea: longitudinal trends of standing stocks, distributions and analysis of food vacuole contents, Aquat. Microb. Ecol., 24, 297–311, 2001.

Pitta, P., Kanakidou, M., Mihalopoulos, N., Christodoulaki, S., Dimitriou, P. D., Frangoulis, C., Giannakourou, A., Kagiorgi, M., Lagaria, A., Nikolaou, P., Papageorgiou, N., Psarra, S., Santi, I., Tsapakis, M., Tsiola, A., Violaki, K. and Petihakis, G.: Saharan Dust Deposition Effects on the Microbial Food Web in the Eastern Mediterranean: A Study Based on a Mesocosm Experiment, Front. Mar. Sci., 4, 124–142, doi:10.3389/fmars.2017.00117, 2017.

Purcell, J.E., Sturdevant, M.V. and Galt, C.P.: A review of appendicularians as prey of invertebrate and fish predators, in: Gorsky, G., Youngbluth, M.J., Deibel, D. (Eds.). Response of marine ecosystems to global change: ecological impact of appendicularians, Éditions Scientifiques, Paris, 359-435, 2005.

Ras, J., Clausre, H., and Uitz, J.: Spatial variability of phytoplankton pigment distributions in the Subtropical South Pacific Ocean: comparison between in situ and predicted data, Biogeosciences, 5, 353–369, https://doi.org/10.5194/bg-5-353-2008, 2008.
Saiz, E. and Alcaraz, M.: Pigment gut contents of copepods and deep phytoplankton maximum in the Western Mediterranean, J. Plankton Res., 12, 665–672, 1990.

Saiz, E., Sabatés, A., and Gili, J-M.: The Zooplankton. In: Goffredo, S. and Dubinsky, Z. (Eds.). The Mediterranean Sea: Its history and present challenges, Springer Science, Dordrecht, 183-212, 2014.

Sazzini, M., Sarno, S and Luiselli, D.: The Mediterranean human population: An anthropological genetics perspective. In: Goffredo, S. and Dubinsky, Z. (Eds.). The Mediterranean Sea: Its history and present challenges, Springer Science, Dordrecht, 29–48, 2014.

Sherr, E. and Sherr, B.: Heterotrophic dinoflagellates: a significant component of microzooplankton biomass and major grazers of diatoms in the sea, Mar. Ecol. Prog. Ser., 352, 187–197, doi:10.3354/meps07161, 2007.

Siokou-Frangou, I.: Epipelagic mesozooplankton and copepod grazing along an east-west transect in the Mediterranean Sea, Rapports de la Commission Internationale pour l’Exploration Scientifique de la Mer Méditerranée, 37, 439, 2004.

Siokou-Frangou, I., Christaki, U., Mazzocchi, M. G., Montresor, M., Ribera d’Alcalá, M., Vaqué, D. and Zingone, A.: Plankton in the open Mediterranean Sea: a review, Biogeosciences, 7, 1543–1586, doi:10.5194/bg-7-1543-2010, 2010.

Skliris, R.: Past, present and future patterns of the thermohaline circulation and characteristic water masses of the Mediterranean Sea. In: Goffredo, S. and Dubinsky, Z. (Eds.). The Mediterranean Sea: Its history and present challenges, Springer Science, Dordrecht, 29–48, 2014.

Suthers, I., Taggart, C., Rissik, D. and Baird, M.: Day and night ichthyoplankton assemblages and zooplankton biomass size spectrum in a deep ocean island wake, Mar. Ecol. Prog. Ser., 322, 225–238, doi:10.3354/meps322225, 2006.

Ternon, E., Guieu, C., Loïe-Pilot, M.-D., Leblond, N., Bosc, E., Gasser, B., Miquel, J-C. and Martín, J.: The impact of Saharan dust on the particulate export in the water column of the North Western Mediterranean Sea, Biogeosciences, 7(3), 809–826, doi:10.5194/bg-7-809-2010, 2010.

Ternon, E., Guieu, C., Ridame, C., L'Helguen, S. and Catala, P.: Longitudinal variability of the biogeochemical role of Mediterranean aerosols in the Mediterranean Sea, Biogeosciences, 8(5), 1067–1080, doi:10.5194/bg-8-1067-2011, 2011.

Thingstad, T. F., Krom, M. D., Mantoura, R. F. C., Flaten, G. A. F., Groom, S., Herut, B., Kress, N., Law, C. S., Pasternak, A., Pitta, A., Psarra, S., Rassoulzadegan, F., Tanaka, T., Tsellepides, A., Wassman, P., Woodeard, E. M. S., Wexels Riser, C., Zodiatis, G. and Zohary, T.: Nature of phosphorus limitation in the ultraoligotrophic Eastern Mediterranean, Science, 309, 1068–1071, 2005.

Tsagaraki, T. M., Herut, B., Rahav, E., Berman Frank, I. R., Tsiola, A., Tsapakis, M., Giannakourou, A., Gogou, A., Panagiopoulos, C., Violaki, K., Psarra, S., Lagaria, A., Christou, E. D., Papageorgiou, N., Zervoudaki, S., de Puelles, M. L. F., Nikoloudakis, N., Meador, T. B., Tanaka, T., Pedrotti, M. L., Krom, M. D. and Pitta, P.: Atmospheric deposition effects on plankton communities in the Eastern Mediterranean: A mesocosm experimental approach, Front. Mar. Sci., 4, 210, doi:10.3389/fmars.2017.00210, 2017.
Turner, J. T.: The importance of small planktonic copepods and their roles in pelagic marine food webs, Zool. Stud., 43, 255-266, 2004.

Vives, F.: Los copépodos planctónicos del mar Tirreno en septiembre y octubre de 1963, Investigación Pesquera, 31, 539–583, 1967.

Wagener, T., Guieu, C. and Leblond, N.: Effects of dust deposition on iron cycle in the surface Mediterranean Sea: results from a mesocosm seeding experiment, Biogeosciences, 7, 3769–3781, doi:10.5194/bg-7-3769-2010, 2010.

Yang, E. J., Ju, S. J. and Choi, J. K.: Feeding activity of the copepod *Acartia hongi* on phytoplankton and micro-zooplankton in Gyeonggi Bay, Yellow Sea, Estuar. Coast. Shelf Sci., 88, 292–301, doi:10.1016/j.ecss.2010.04.005, 2010.

Zervoudaki, S., Christou, E.D., Nielsen, T.G., Siokou-Frangou, I., Assimakopoulou, G., Giannakourou, A., Maar, M., Pagou, K., Krasakopoulou, E., Christaki, U. and Moraitou-Apostolopoulou, M.: The importance of small-sized copepods in a frontal area of the Aegean Sea, J. Plankton Res., 4, 317-338, doi.org/10.1093/plankt/fbm018, 2007.

Zhou, M., Carlotti, F., and Zhu, Y, A size-spectrum zooplankton closure model for ecosystem modelling, J. Plankton Res., 32, 1147–1165, doi:10.1093/plankt/fbq054, 2010.
Figure 1: Map with the sampling points during PEACETIME cruise 2017. The colours of the points indicate the different regions considered in the course of the study. Green dots: Provencal basin (PB); Dark blue dots: Algerian Basin (AB); Light blue dots: Tyrrhenian Sea (TB); Red dots: Ionians Basin (IB).
Figure 2: Size spectrum of ST ION1 as an example obtained by: A) FlowCAM (N\textsubscript{100}), B) ZOOSCAN (N\textsubscript{200}) and C) combination of FlowCAM (N\textsubscript{100} counting only zooplankton smaller than 500 µm of ESD) and ZOOSCAN (N\textsubscript{200} counting only zooplankton bigger than 500 µm of ESD)
Figure 3: Principal Component Analysis (PCA) ordination of five environmental indicators: Mixed/layer Depth (MLD), Integrated values of Chl-a concentration, mean values on the upper 0/300 m of temperature, salinity and dissolved oxygen. (A) Plots of the stations and (B) variables on the first factorial plan. AB: Algerian Basin, PB: Provencal Basin, TB: Tyrrhenian Basin, IB: Ionian Basin.
Figure 4: Values of zooplankton abundance (A) and biomass (B) cumulated by ESD size classes along different stations of the PEACETIME cruise. Integrated Chl-a concentrations (green line). (*)Stations sampled during the night.(**) At station TYR, only the abundance and biomass values above 500 µm obtained with the 200 µm mesh size net are presented.
Figure 5: spatial variation of taxonomic groups (stock bars) and small (length< 1 mm)/large (length> 1 mm) copepod ratio (dashed line). (*)Stations sampled during the night.
Figure 6: NMDS analysis of the zooplankton taxa for the whole stations (A) and with exclusion of st 1 and st2 (B): plot of the stations and the taxa correlated at >0.65 with the axes. Colour of the stations represents the eco-regions identified by the PCA on the environmental analysis (see Fig. 2). This analysis was performed on the zooplankton collected with the data from N200. PB: Provencal Basin, AB= Algerian Basin, TB =Tyrrhenian Basin, IB = Ionian Basin.
Figure 7: Example of a Normalized biomass size spectrum (NBSS) and slope of STION1.
Figure 8: NBSS slope for all stations during PEACETIME survey.
Figure 9: Rank frequency diagram on long station TYR (A), ST5 and 6 (B) ION (C) FAST (D) and Log standardized frequency for all stations (E) and station influenced by dust deposition (F). Ac: Acartia spp.; Cal: Calanoid copepods; Cala: Calanus spp.; Cent: Centropages spp.; Cor: Corycaeus spp.; Euc: Eucalanus spp.; Halop: Haloptilus spp.; Luci: Lucicutia spp.; Mecy: Mecynocera spp.; On: Oncaea spp.; Ot: Oithona spp.; P/Cla: Para/Clausocalanus spp.; Pleu: Pleuromamma spp.; Pont: Pontellidae; Tem: Temora spp.; App: Appendicularia; Cha: Chaetognatha; Dec: Decapods; Hydro: Hydrozoans; Ich: Ichtyoplankton; Ost: Ostracods; Poly: Polychaeta; Pte: Pteropods; Siph: Siphonophores; Thal: Thaliaceans.
Figure 10. Changes in Zooplankton carbon demand (black bars), primary production (green bars) and daily grazing impact from zooplankton to primary production (straight line). (*)Stations sampled during the night.
Table 1. Sampled stations during the PEACETIME survey: geographical information, date and time of zooplankton net sampling. AB: Algerian Basin; PB: Provencal Basin; TB: Tyrrhenian Basin; IB: Ionian Basin.

| Station ID | Area | lat (N) | long (E) | Date (DD/MM/YYYY) | Time (HH:MM) |
|------------|------|---------|----------|-------------------|--------------|
| St1        | PB   | 41°53,51| 6°20,00  | 12/05/2017        | 11:30        |
| St2        | PB   | 40°30,37| 6°43,79  | 13/05/2017        | 9:30         |
| St3        | AB   | 39°8,00 | 7°41,01  | 14/05/2017        | 9:15         |
| St4        | AB   | 37°58,99| 7°58,61  | 15/05/2017        | 9:15         |
| St5        | TB   | 38°57,19| 11°1,40  | 16/05/2017        | 7:05         |
| TYR        | TB   | 39°20,39| 12°35,57 | 19/05/2017        | 23:00        |
| St6        | TB   | 38°48,46| 14°29,98 | 22/05/2017        | 10:15        |
| St7        | IB   | 36°39,49| 18°9,29  | 24/05/2017        | 2:00         |
| ION1       | IB   | 35°29,38| 19°46,51 | 26/05/2017        | 21:59        |
| ION2       | IB   | 35°29,38| 19°46,51 | 27/05/2017        | 8:50         |
| ION3       | IB   | 35°29,38| 19°46,51 | 28/05/2017        | 8:45         |
| St8        | IB   | 36°12,62| 16°37,86 | 30/05/2017        | 9:05         |
| St9        | AB   | 38°8,08 | 5°50,45  | 01/06/2007        | 23:00        |
| FAST1      | AB   | 37°56,81| 2°54,99  | 04/06/2007        | 22:15        |
| FAST2      | AB   | 37°56,81| 2°54,99  | 06/06/2007        | 9:50         |
| FAST3      | AB   | 37°56,81| 2°54,99  | 08/06/2007        | 23:45        |
Table 2. Estimated grazing, respiration and excretion rates of zooplankton based on allometric models (see methods) and their impact on the phytoplankton stock and production along the PEACETIME survey transect.

|                      | Provencal basin | Algerian basin | Tyrrenian Basin | Ionian Basin |
|----------------------|-----------------|----------------|-----------------|--------------|
|                      | st1  | st2  | fast1 | fast2 | fast3 | st9  | st3  | st4  | st5  | st6  | st8  | st7  | ion1 | ion2 | ion3 |
| **Grazing impact**   |      |      |       |       |       |      |      |      |      |      |      |      |      |      |      |
| Phytoplankton stock  | 1749 | 1632 | 1554  | 1691  | 1412  | 1805 | 1161 | 1458 | 1526 | 933  | 1582 | 1212 | 1376 | 1587 | 1587 |
| Primary Production   | 295  | 155  | 229   | 184   | 297   | 303  | 165  | 225  | 197  | 190  | 289  | 187  | 266  | 279  | 304  |
| ZCD (mgC m\(^{-2}\)d\(^{-1}\)) | 280  | 155  | 274   | 263   | 249   | 228  | 224  | 278  | 202  | 145  | 195  | 205  | 204  | 244  | 177  |
| Grazing impact on Phyto. stock (%) | 16.0 | 9.5  | 17.7  | 15.6  | 17.7  | 12.7 | 19.3 | 19.1 | 13.3 | 15.6 | 12.4 | 17.0 | 14.8 | 15.4 | 11.2 |
| Grazing impact on PP (%)   | 94.8 | 99.9 | 119.7 | 143.3 | 83.9  | 75.4 | 135.6| 123.7| 102.5| 76.7 | 67.6 | 109.7| 76.5 | 87.6 | 58.3 |

| **Respiration**       |      |      |       |       |       |      |      |      |      |      |      |      |      |      |      |
| Respiration           | 112.2| 64.3 | 95.3  | 90.1  | 86.2  | 81.3 | 83.8 | 100.2| 78.7 | 62.9 | 75.6 | 77.0 | 72.4 | 94.7 | 71.6 |
| % of Primary production respired by zooplankton | 38.0 | 41.4 | 41.5  | 49.0  | 29.0  | 26.8 | 50.6 | 44.5 | 39.8 | 33.1 | 26.1 | 41.0 | 27.1 | 33.9 | 23.5 |

| **NH\(_4\)** zooplankton contribution |      |      |       |       |       |      |      |      |      |      |      |      |      |      |      |
| Excretion              | 17.7 | 9.2  | 13.6  | 12.9  | 12.3  | 16.2 | 12.0 | 14.3 | 11.3 | 9.1  | 10.9 | 11.0 | 10.4 | 13.6 | 10.3 |
| Phyttoplankton needs   | 50.2 | 26.4 | 39.0  | 31.3  | 50.6  | 51.6 | 28.2 | 38.3 | 33.6 | 32.4 | 49.2 | 31.9 | 45.3 | 47.4 | 51.8 |
| N demand (%)           | 32.2 | 35.9 | 37.3  | 43.5  | 25.2  | 23.2 | 43.8 | 38.6 | 34.5 | 28.8 | 22.5 | 35.8 | 23.1 | 29.2 | 20.7 |

| **PO\(_4\)** zooplankton contribution |      |      |       |       |       |      |      |      |      |      |      |      |      |      |      |
| Excretion              | 2.3  | 1.3  | 2.0   | 1.9   | 1.8   | 1.7  | 1.8  | 2.1  | 1.6  | 1.3  | 1.6  | 1.5  | 2.0  | 1.5  |      |
| Phyttoplankton needs   | 8.6  | 4.5  | 6.7   | 5.3   | 8.6   | 8.8  | 4.8  | 6.5  | 5.7  | 5.5  | 8.4  | 5.4  | 7.7  | 8.1  | 8.8  |
| P demand (%)           | 27.5 | 30.5 | 32.4  | 37.9  | 22.0  | 20.0 | 37.8 | 33.5 | 29.3 | 24.1 | 18.9 | 30.4 | 19.9 | 24.4 | 17.2 |
Table 3: Comparison of zooplankton biomass and abundance in different regions of the Mediterranean Sea. ** wet weight

| Area                              | Sampling period  | Net mesh size (µm) | Layer (m) | Biomass (mg m\(^{-3}\)) | Abundance (ind m\(^{-3}\)) | Reference                        |
|-----------------------------------|------------------|-------------------|-----------|--------------------------|----------------------------|----------------------------------|
| NWMS - Provencal and Ligurian Seas| Feb 2013         | 120               | 0-250     | 12.3 (1.9-42.3)          | 608 (21-2548)              | Donoso et al. (2017)             |
| NWMS - Provencal and Ligurian Seas| Apr 2013         | 120               | 0-250     | 64.5 (13.9-197.8)        | 3668 (850-7205)            | Donoso et al. (2017)             |
| NWMS - Gulf of Lions shelf        | Mar/Apr 1998     | 80-200            | 0-200     | 9.56 ± 4.73              | 608 (21-2548)              | Gaudy et al. (2003)              |
| NWMS - Gulf of Lions shelf        | Jan 1999         | 80-200            | 0-200     | 4.73 ± 2.53              | 10 - 210                  | Gaudy et al. (2003)              |
| NWMS - Provencal sea              | Mar 1969         | 200               | 0-200     | 0.4 - 53                 | 10 - 210                  | Nival et al. (1975)              |
| NWMS - Provencal sea              | Apr 1969         | 200               | 0-200     | 10 - 210                 | 10 - 210                  | Nival et al. (1975)              |
| NWMS - Provencal sea              | Spring 2008      | 200               | 0-200     | 13.15 ± 2.5              | 1731                      | Mazzocchi et al. (2014)          |
| NWMS - Provencal sea              | May/Jun 2017     | 100-200           | 0-300     | 5.5 ± 2.1                | 1638 ± 433                | this study                       |
| SWMS - Algerian sea               | Jul-Aug 1997     | 200               | 0-200     | 8.2 (2.1-34.5)           | 370 (36-844)              | Riandey et al. (2005)            |
| SWMS- Algero Provencal sea        | Jun/Jul 2008     | 200               | 0-200     | 5.4                      | 1561 ± 205                | Nowaczyk et al. 2011            |
| SWMS- Algerian sea                | May/Jun 2017     | 100-200           | 0-300     | 6.6 ± 0.6                | 1254 ± 191                | This study                       |
| Tyrrenian Sea                     | Autumn 1986      | 200               | 0-50      | 3.6 - 32                 |                            | Fonda Umani and de Olazábal (1988) |
| Coastal Tyrrenian sea             | 1984-2006        | 200               | 0-50      | 1708                     |                            | Mazzocchi et al. (2011) Cited in Champalbert, (1996) |
| Tyrrenian sea                     | Sep/Oct 1963     | 60-300            | 0-700     | 0.15-0.3                 |                            | Nowaczyk et al. 2011 Cited in Kovalev et al. (2003) |
| Tyrrenian sea                     | Jun/Jul 2008     | 200               | 0-200     | 3.2                      | 1250                      | Nowaczyk et al. 2011 Cited in Kovalev et al. (2003) |
| Tyrrenian sea                     | Jun 1968         | Not specify       | 0-200     | 5.8**                    | 1250                      | Nowaczyk et al. 2011 Cited in Kovalev et al. (2003) |
| Tyrrenian sea                     | May/Jun 2017     | 100-200           | 0-300     | 4.8 ± 1.1                | 1398 ± 108                | Nowaczyk et al. 2011 Cited in Kovalev et al. (2003) |
| Ionian sea                        | Apr/May 1999     | 200               | 0-100     | 6.0 ± 0.8 (eastern)      | 219                      | Mazzocchi et al. (2003)          |
| Ionian sea                        | Apr/May 1999     | 200               | 0-100     | 8.2 to 13.4 (western)    | 219                      | Mazzocchi et al. (2003)          |
| Ionian sea                        | Spring 1992      | 200               | 0-300     | 219                      | 219                      | Mazzocchi et al. (2003)          |
| Ionian sea                        | Spring 1999      | 200               | 0-300     | 193                      | 193                      | Mazzocchi et al. (2003)          |
| Ionian sea                        | Spring 2008      | 200               | 0-200     | 2.73                     | 213                      | Mazzocchi et al. (2014)          |
| Ionian sea                        | Autumn 2008      | 200               | 0-200     | 3.25                     | 338                      | Mazzocchi et al. (2014)          |
| Ionian sea                        | Jun/Jul 2008     | 200               | 0-200     | 8                       | 1181 ± 630               | Nowaczyk et al. 2011 Cited in Kovalev et al. (2003) |
| Ionian sea                        | May/Jun 2017     | 100-200           | 0-300     | 5.1 ± 0.5                | 1003± 76                 | Nowaczyk et al. 2011 Cited in Kovalev et al. (2003) |