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

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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, Tyrrhenian 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 Tyrrhenian basins. The mesozooplankon 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 Tyrrhenian 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 Tyrrhenian 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

35   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

40   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; Mazzocchi et

45   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

50   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

55   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

60   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

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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 $\Delta\sigma_\theta = 0.03 \ kgr^{-3}$ 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 μm and 200 μm 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 $1ms^{-1}$. 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 onto 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 μm (noted below $N_{100}F_{<200}$), 200 μm $- 1000$ μm (noted below

3

$N_{100}F_{200/1000}$), and > 1000 µm (noted below $N_{100}F_{>1000}$). For net N_{200}, the sample was split into two size fractions:< 1000 µm

95 (noted below $N_{200}F_{<1000}$) and > 1000 µm (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 µm of ESD and our ZOOSCAN does not detect particles smaller than

100 300 µm 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 µm (noted $C_{<200}$); 200-300 µm ($C_{200-300}$); 300-500 µm ($C_{300-500}$); 500-1000 µm ($C_{500-1000}$); 1000-2000 µm ($C_{1000-2000}$); > 2000 µm ($C_{200-300}$). The challenge was to choose the best net-analysis technique combination for the intermediate size fractions ($C_{200-300}$, $C_{300-500}$ and $C_{500-1000}$). The abundance of each class for the

105 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 um (Figure 2A) and data for $N_{200}F_{<1000}$ and $N_{200}F_{>1000}$ measured with ZOOSCAN to compute ESD size classes >500 um (see Figure 2B). The

110 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 µm flow cell were

115 used and the analysis was carried out up to3000 counted particles. For the fraction $N_{100}F_{200-1000}$ a 2X magnification and 800 µm 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

120 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).

125 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 vignette is in the correct category. Considered living

130 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.

135 (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:

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

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

140 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:

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

where B_{zoo} is the biomass of zooplankton in mgC m^{-3}, calculated using the area-weight relationships from Lehette and

145 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:

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

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):

$$g_z(w, T, Ca) = 0.033 \left(\frac{Ca}{Ca + 205e^{-0.125T}} \right) e^{0.09T} w^{-0.06}$$

150   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.

155   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.

160   **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.

165   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 Multidimenstional Scaling (NMDS). These analyses were performed using Primer 6.0 software.

Rank frequency diagrams (RFD) were created using the data from N$_{200}$ to see differences in taxonomic composition between the samples. Potential association between zooplankton data and spatial patterns of the environmental variables were tested

170   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

175   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

180   low temperature, salinity and MLD values. The cluster located in the Tyrrhenian Basin (TB) comprises (ST5, ST6 and TYR

6

stations) is very close to the first group, but with lower chlorophyll-a concentrations and higher values of temperature and salinity. Eastern stations (ST7, ST8 and ION stations) located in the Ionian Basin (IB) are characterized by the temperature and salinity values and the lowest dissolved oxygen concentrations found during the survey. Stations 1 and 2 on the north-south transect (NS) do not cluster with any of the other stations due to deeper MLD and higher chlorophyll-a concentrations.

3.2 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 10^3 ± 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 $C_{>2000}$, 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 %), $C_{200-300}$ (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 copepodites. 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.
215   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
220   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 atST7 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
225   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

230   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
Tyrrhenian 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
235   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
240   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 1^{rst} and 2nd ranks during FAST1, but this order is reversed in FAST 3. 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
245   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

280   decrease in abundance with increasing mesh size (Turner, 2004;Pasternak et al., 2008;Riccardi, 2010; Makabe et al., 2012; Altukhovet 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*

285   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

290   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

295   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

300   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 Riandey 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,

305   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.

310   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

315   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

320   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

325   directly influenced by the main part of the MAW flowing through the Sardinia Channel. Ayata et al. (2018) also classified the Tyrrhenian 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).

330   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

335   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).

340   **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.

345 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

350 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 en 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

355 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 NH_3 and PO_4 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

360 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

365 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.

370 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

375 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

380 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

385 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 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

390 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

395 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

400 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

405 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.

410   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

415   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

420   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
425

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

430   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

435   (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.

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Data availability

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

Authors contribution

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

Competing interests

455 The authors declare that they have no conflict of interest

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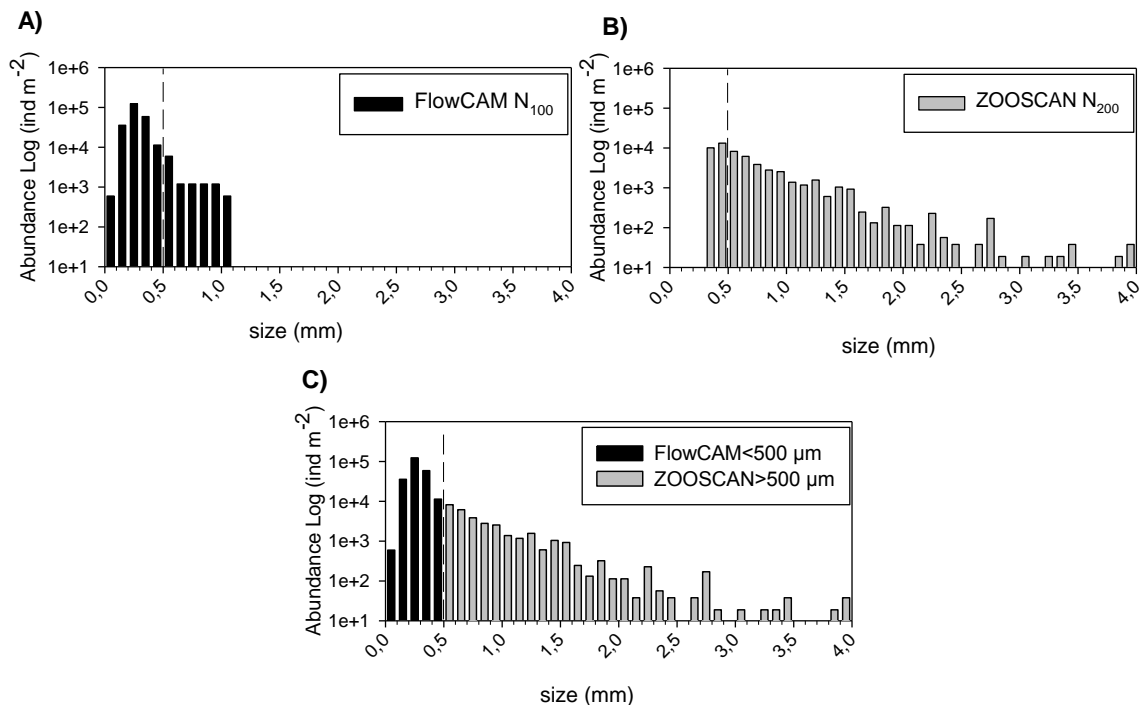
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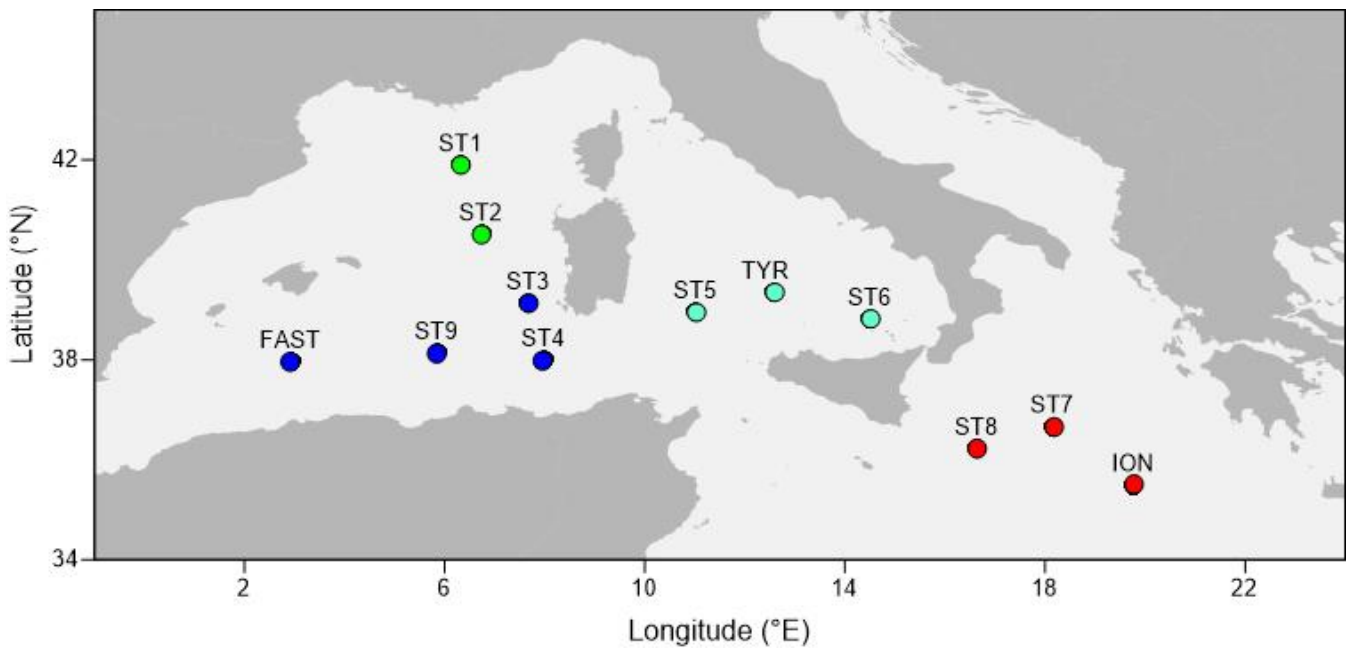
Figure 1: Map with the sampling points during PEACETIME cruise 2017. The colours of the points indicate the different regions considered in the course of the study. Green dots: Provencal basin (PB); Dark blue dots: Algerian Basin (AB); Light blue dots: Tyrrhenian Sea (TB); Red dotes: Ionians Basin (IB).

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Figure 2: Size spectrum of ST ION1 as an example obtained by: A) FlowCAM (N_{100}), B) ZOOSCAN (N_{200}) and C) combination of FlowCAM (N_{100} counting only zooplankton smaller than 500 μm of ESD) and ZOOSCAN (N_{200} counting only zooplankton bigger than 500 μm of ESD)

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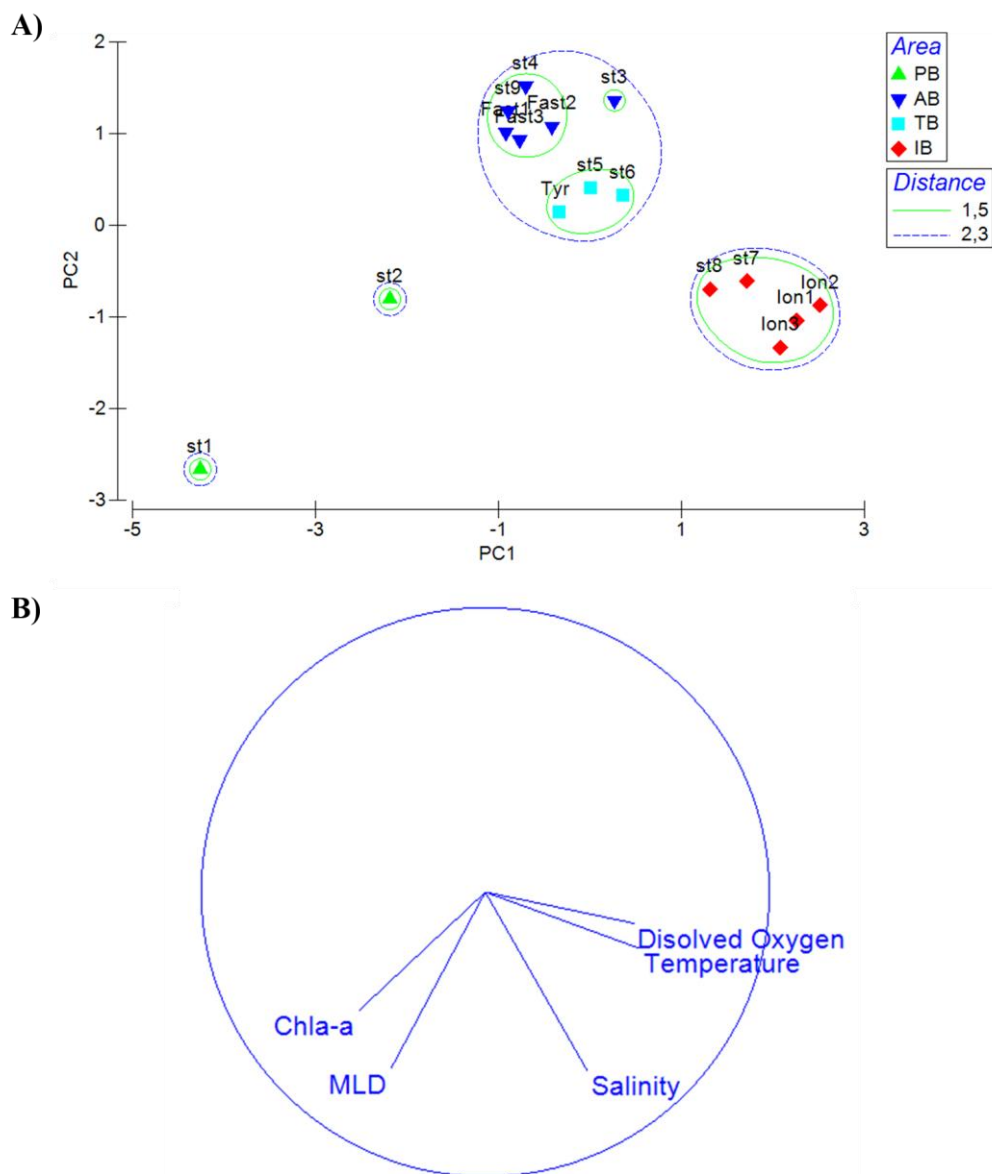
**Figure 3: Principal Component Analysis (PCA) ordination of five environmental indicators: Mixed/layer Depth (MLD), Integrated values of Chl-a concentration, mean values on the upper 0/300 m of temperature, salinity and dissolved oxygen. (A) Plots of the stations and (B) variables on the first factorial plan. AB: Algerian Basin, PB: Provencal Basin, TB: Tyrrhenian Basin, IB: Ionian Basin.**

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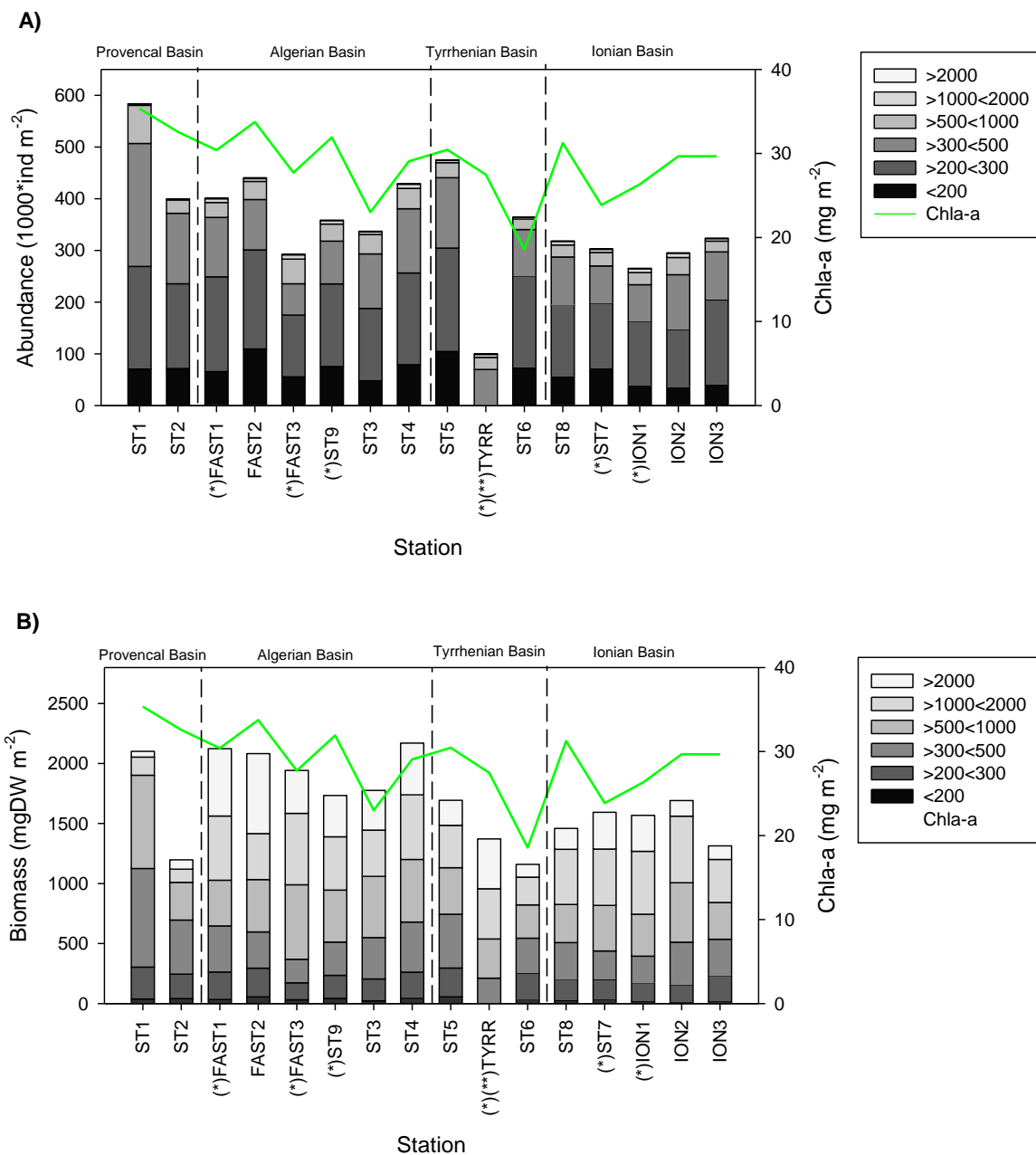
Figure 4: Values of zooplankton abundance (A) and biomass (B) cumulated by ESD size classes along different stations of the PEACETIME cruise. Integrated Chl-a concentrations (green line). (*)Stations sampled during the night.(**) At station TYR, only 705 **the abundance and biomass values above 500 μm obtained with the 200 μm mesh size net are presented.**
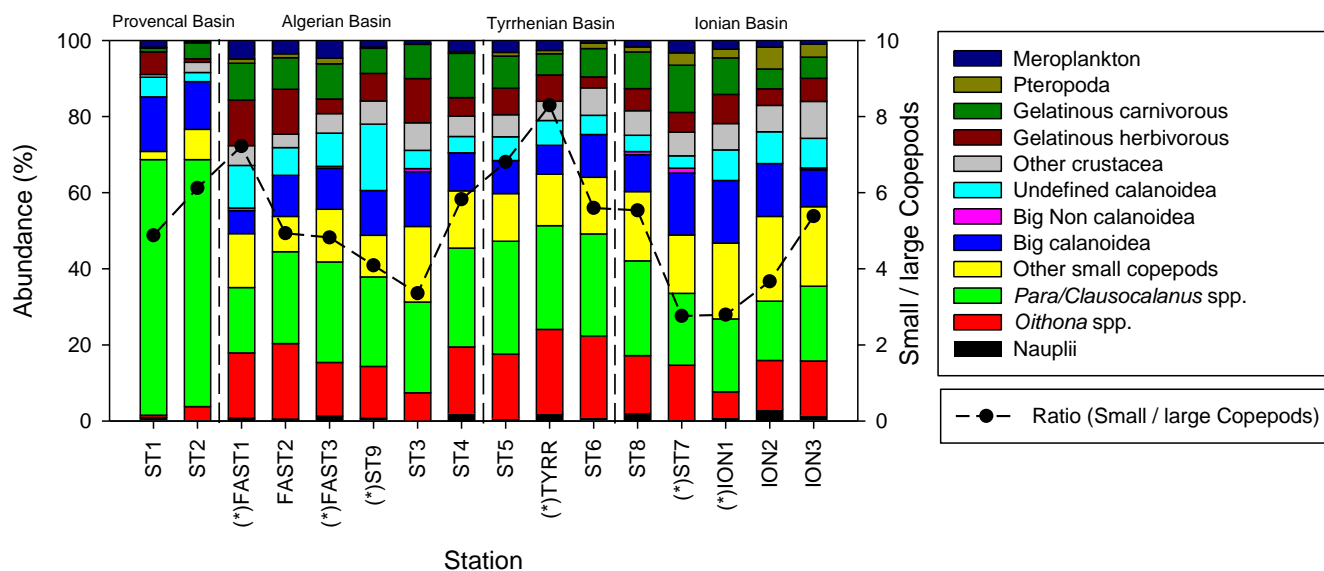
Figure 5: spatial variation of taxonomic groups (stock bars) and small (length< 1 mm)/large (length> 1 mm) copepod ratio (dashed line). (*)Stations sampled during the night.

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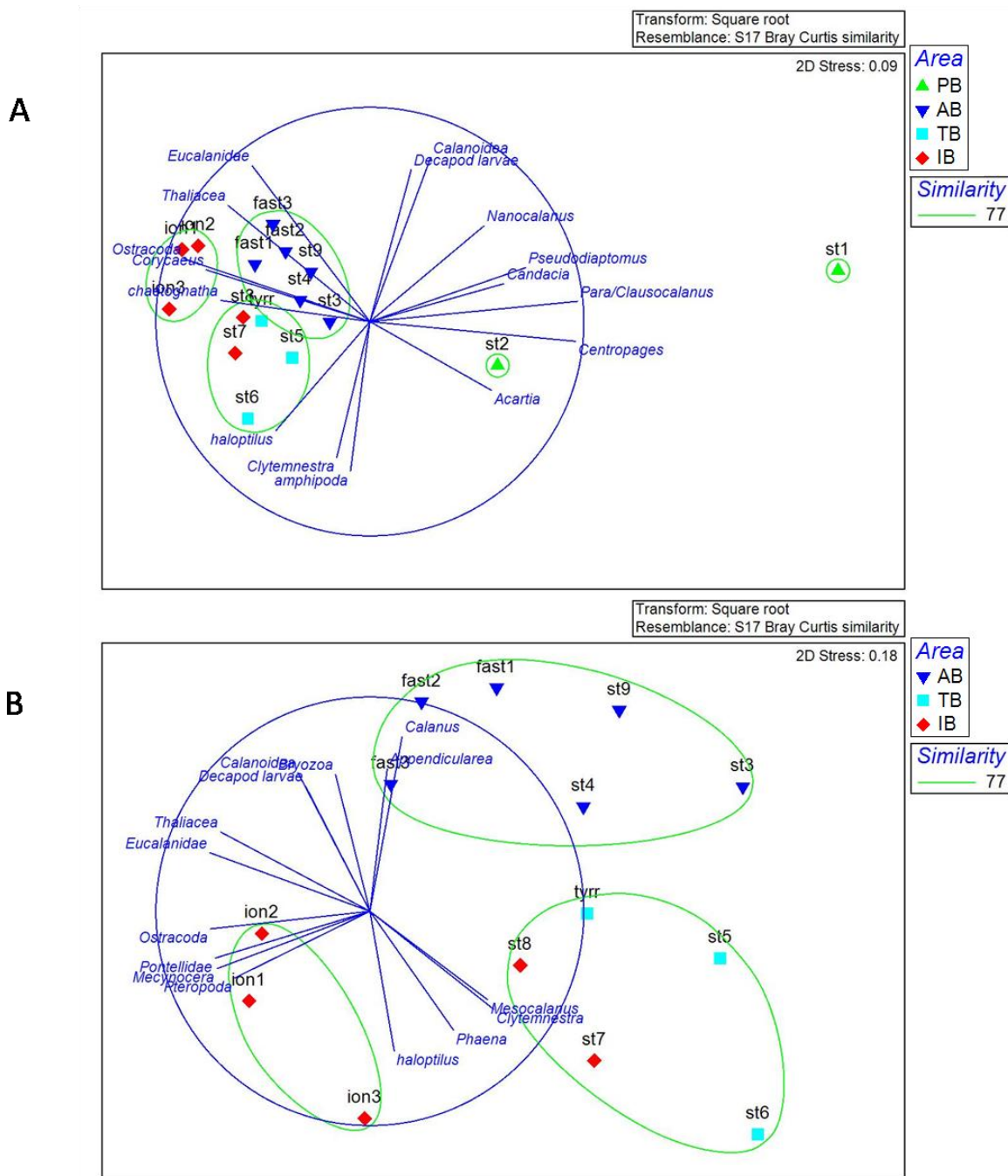
Figure 6: NMDS analysis of the zooplankton taxa for the whole stations (A) and with exclusion of st 1 and st2 (B): plot of the stations and the taxa correlated at >0.65 with the axes. Colour of the stations represents the eco-regions identified by the PCA on the environmental analysis (see Fig. 2). This analysis was performed on the zooplankton collected with the data from N$_{200}$. PB: Provencal Basin, AB= Algerian Basin, TB =Tyrrhenian Basin, IB = Ionian Basin.

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$$y = -0.603x + 1.031$$
$$r^2 = 0.864$$
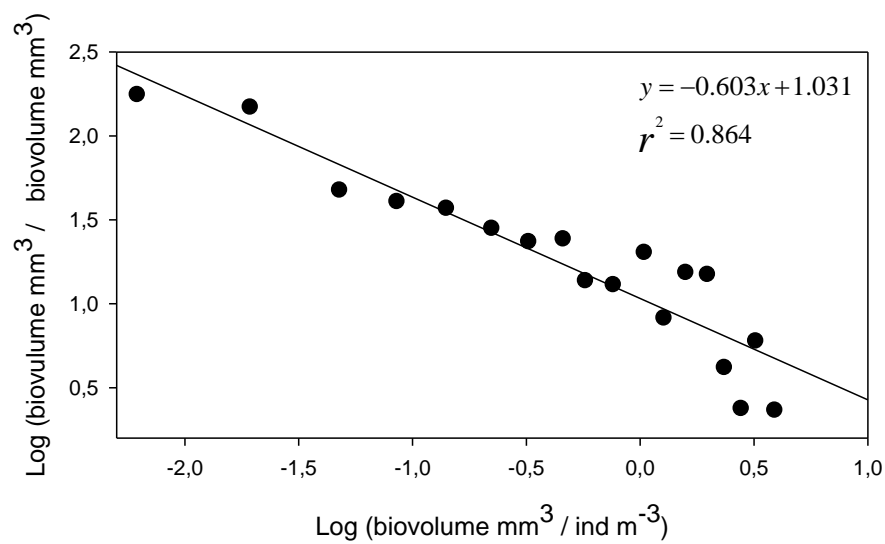
Figure 7: Example of a Normalized biomass size spectrum (NBSS) and slope of STION1.
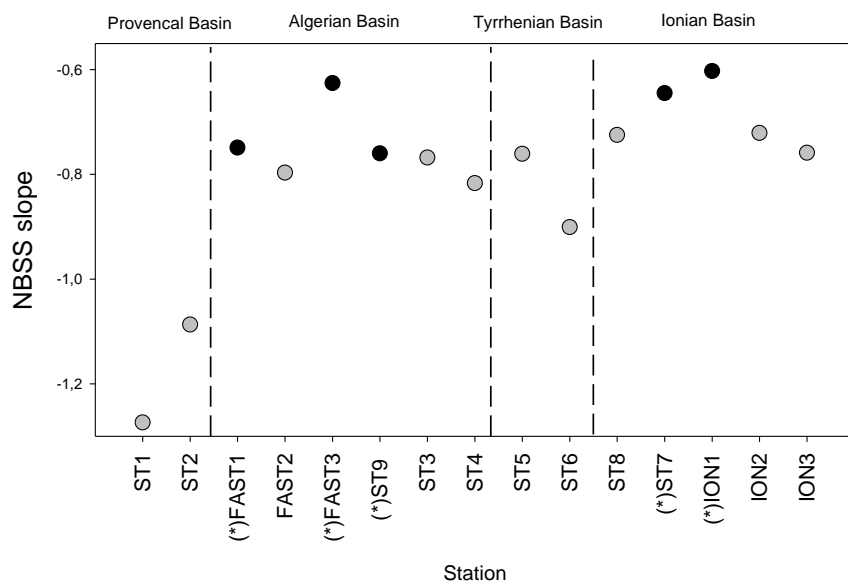
Figure 8: NBSS slope for all stations during PEACETIME survey.
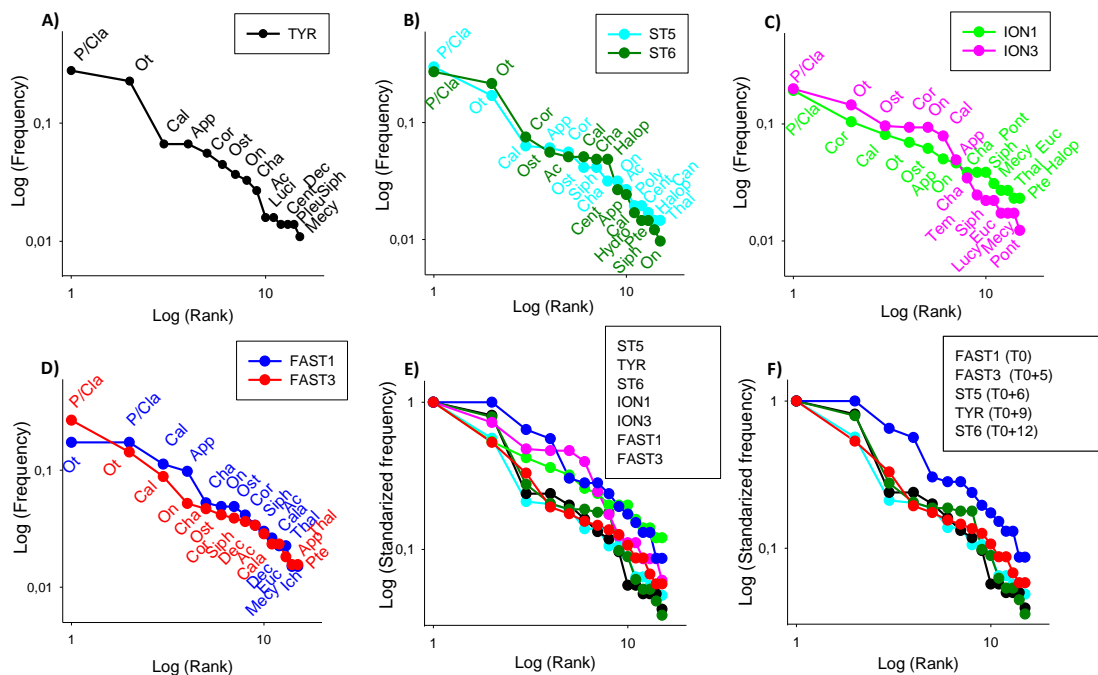
Figure 9: Rank frequency diagram on long station TYR (A), ST5 and 6 (B)ION (C) FAST (D) and Log standardized frequency for all stations (E) and station influenced by dust deposition (F). Ac: *Acartia* spp.; Cal: Calanoid copepods; Cala: *Calanus* spp.; Cent: *Centropages* spp.; Cor: *Corycaeus* spp.; 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.
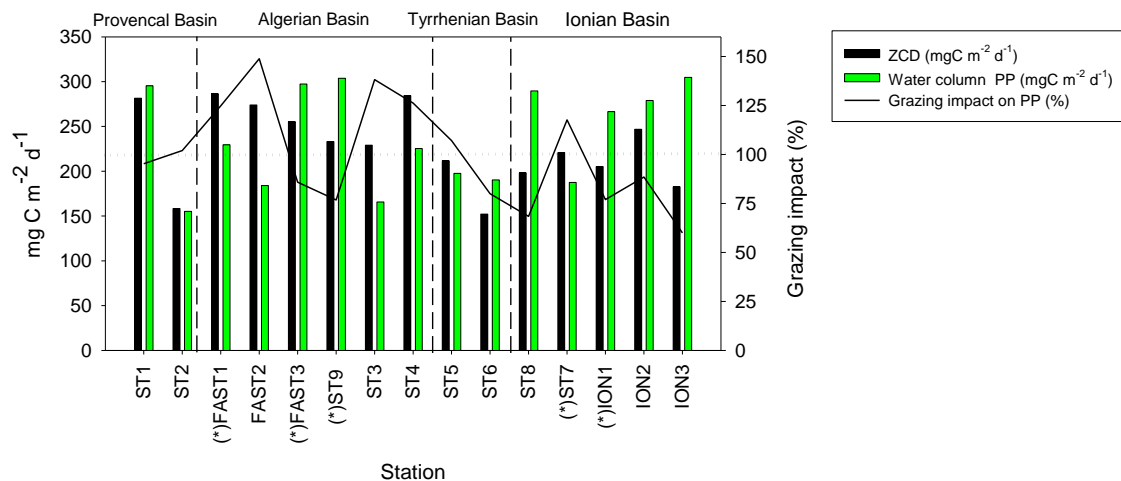
735 **Figure 10. Changes in Zooplankton carbon demand (black bars), primary production (green bars) and daily grazing impact from zooplankton to primary production (straight line). (*)Stations sampled during the night.**

Table 1. Sampled stations during the PEACETIME survey: geographical information, date and time of zooplanktonnet 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	04/06/2017	22:15
FAST2	AB	37°56,81	2°54,99	06/06/2017	9:50
FAST3	AB	37°56,81	2°54,99	08/06/2017	23:45

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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				Tyrrhenian Basin				Ionian Basin			
	st1	st2	fast1	fast2	fast3	st9	st3	st4	st5	st6	st8	st7	ion1	ion2	ion3
Grazing impact															
Phytoplankton stock (mg C m^{-2})	1749	1632	1554	1691	1412	1805	1161	1458	1526	933	1582	1212	1376	1587	1587
Primary Production (mgC m^{-2}d^{-1})	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 (mg C m^{-2} d^{-1})	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
NH4 zooplankton contribution															
Excretion (mg N-NH4 m^{-2} d^{-1})	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
Phytoplankton needs (mgN m^{-2} d^{-1})	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
PO4 zooplankton contribution															
Excretion (mg P-PO4 m^{-2} d^{-1})	2,3	1,3	2,0	1,9	1,8	1,7	1,8	2,1	1,6	1,3	1,6	1,6	1,5	2,0	1,5
Phytoplankton needs (mg P m^{-2}d^{-1})	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

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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		Gaudy et al. (2003)
NWMS - Gulf of Lions shelf	Jan 1999	80-200	0-200	4.73 ± 2.53		Gaudy et al. (2003)
NWMS - Provencal sea	Mar 1969	200	0-200	0.4 - 53		Nival et al. (1975)
NWMS - Provencal sea	Apr 1969	200	0-200	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
Tyrrhenian Sea	Autumn 1986	200	0-50	3.6 - 32		Fonda Umani and de Olazábal (1988)
Coastal Tyrrhenian sea	1984-2006	200	0-50		1708	Mazzocchi et al. (2011)
Tyrrhenian sea	Sep/Oct 1963	60-300	0-700	0.15-0.3		Cited in Champalbert, (1996)
Tyrrhenian sea	Jun/Jul 2008	200	0-200	3.2	1250	Nowaczyk et al. 2011
Tyrrhenian sea	Jun 1968	Not specify	0-200	5.8**		Cited in Kovalev et al. (2003)
Tyrrhenian sea	May/Jun 2017	100-200	0-300	4.8 ± 1.1	1398 ± 108	This study
Ionian sea	Apr/May 1999	200	0-100	6.0 ± 0.8 (eastern)		Mazzochi et al. (2003)
Ionian sea	Apr/May 1999	200	0-100	8.2 to 13.4 (western)		Mazzochi et al. (2003)
Ionian sea	Spring 1992	200	0-300		219	Mazzochi et al. (2003)
Ionian sea	Spring 1999	200	0-300		193	Mazzochi 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
Ionian sea	May/Jun 2017	100-200	0-300	5.1 ± 0.5	1003± 76	This study