Zooplankton abundance and community structure driven by tidal currents in a Mediterranean coastal lagoon (Boughrara, Tunisia, SW Mediterranean Sea)

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Abstract.

Lagoons and coastal marine zones are very productive and useful ecosystems, but they are threatened by the effects of global change and anthropogenic pressures. These effects have a negative impact on the zooplankton, weakening its function of phytoplankton consumer, leading to uncontrolled proliferation of microalgae in case of eutrophication. In this study we test the hypothesis that tidal exchanges with the sea can counteract these deleterious effect, by renewing the zooplankton community and by enhancing its top-down control of phytoplankton through selective retention of zooplankton grazers. Our study focused on the southern region of the Gulf of Gabes and the Boughrara lagoon which presents the highest tidal range in the Mediterranean. During two field campaigns (October 2016 and April 2017) we have analyzed zooplankton descriptive (taxonomic composition, abundance; biomass) and functional (ingestion rate, grazing pressure) variables and environmental variables during time series at a fixed station during ebb-flood sequences and at 8 stations along a sea-lagoon transect and during different tidal amplitude periods. Multivariate analyses of both environmental parameters and zooplankton taxa showed the existence of three distinct zones along the sea-lagoon transect, but also the influence of tidal circulation and water mixing on the renewal of the zooplankton community up to the innermost zones of the lagoon. Time series gave clear patterns for the input/output of marine/lagoon species and show a net import for different taxa and for the total zooplankton abundance and biomass (mean flood/ebb ratio = 2.2 for the total abundance and 2.4 for the biomass), leading to differential retention of zooplankton in the lagoon and to an

increase in the potential grazing pressure on phytoplankton (mean flood/ebb ratio = 2.8). We also estimated that the grazing pressure in the lagoon was twice higher during the periods of high tidal amplitudes (at or close to spring tide) compared to periods with low amplitude (neap tides), clearly showing that the retention of zooplankton significantly increases the grazing impact on phytoplankton. These results highlight the importance of the tidal forcing for maintaining the good status of the zooplankton structure and function in strongly anthropized coastal and lagoon ecosystems.

– Keywords: Metazooplankton, lagoon, abundance, biomass, diversity, grazing pressure physical forcing, tidal transport.

Highlights

Tidal circulation is a major forcing for coastal and lagoon ecosystems.

Tidal forcing maintains zooplankton diversity and community structure.

Tidal exchanges with the sea drive selective retention of zooplankton.

Zooplankton retention increases grazing impact on phytoplankton.

Tidal circulation may limit anthropization effects.

1.Introduction

Lagoons and coastal marine zones are both of great importance and high vulnerability at the same time. They are considered as hotspots for biodiversity and are among the most productive ecosystems in the world (Boudouresque, 2004; Basset *et al*., 2013). They play a key role in the biogeochemical cycles and have a major economic impact through the goods and services they provide (fishing, aquaculture, tourism, etc.). However, their biodiversity and their ecological functioning are threatened by the effects of global change and anthropogenic pressures causing degradation of the biotopes and the biocenosis (Kemp and Boynton 2012). For example, increased anthropogenic activities may accelerate the eutrophication process leading to dystrophic crises and/or irreversible deterioration (Bartoli *et al.*, 2001).

Due to their rapid response to fluctuating physical and chemical conditions, plankton communities are often used as bioindicators for ecological changes in these aquatic systems (Amengual-Morro *et al.*, 2012; Hemraj *et al.*, 2017). In particular, due to its key position in the food webs, zooplankton constitutes a sensitive tool for monitoring environmental changes (Etilé *et*

al., 2009; Hussain *et al.*, 2020). Zooplankton comprises larval stages of benthic and pelagic species of high ecological and commercial interest and is particularly abundant in coastal and lagoon systems. As the main consumer of phytoplankton, it constitutes a key factor for controlling proliferation of microalgae and deleterious effects of eutrophication (Rissik *et al.*, 2009). To better analyze the structure and functioning of these ecosystems, to predict, to anticipate and to manage any ecological issues, it is therefore essential to understand the combined effects of natural and anthropogenic forcing and drivers on zooplankton communities.

This was the main issue of the COZOMED-MERMEX project (2014-2018) that was designed to understand whether local physical forcing (including the tide and associated currents) can mitigate the impacts of human disturbance on the structure and functioning of planktonic coastal ecosystems. In particular, we have tested the hypothesis that tidal circulation helps to control the eutrophication through (i) the dilution of the nutritional inputs (bottom-up control) and (ii) retention/accumulation of zooplankton enhancing the grazing pressure on phytoplankton (top-down control). We hypothesize that in high tidal amplitude regions, responses of zooplankton to tidal effects should be considered as a major resilience factor of coastal and lagoon ecosystems against the negative effects of pollution and eutrophication together with the strictly physical effect of tides (dilution linked to increased water turnover rate; Chevalier *et al.*, 2017). According to this hypothesis, the areas under strong tidal influence would be less vulnerable to eutrophication than others.

Retention of zooplankton in such coastal zones is linked to their behavioral responses to tidal currents such as swimming against the flow, downward migration to the low current region and/or active substrate attachment (Alldredge and Hamner, 1980; Genin *et al.*, 2005; Leichter *et al.*, 2013). Tidal currents may also have a positive impact on the import-export dynamics of zooplankton and thus on the renewal of its communities and the maintaining of its biodiversity. The COZOMED-MERMEX project was focused on a Mediterranean coastal ecosystem (Boughrara lagoon – Gulf of Gabes, Tunisia) which has the highest tidal range in the Mediterranean Sea (maximum >2m). This emblematic ecosystem provides many eco-systemic services (around 65% of national fishing activities) despite very strong anthropogenic pressure (urban, industrial and agricultural), demonstrating a high resilience capacity (Bejaoui *et al.*, 2019). Thus we may wonder about the direct (eg. dilution) or indirect (zooplankton retention) roles of

the tidal hydrodynamics on the high resilience capacity of this ecosystem. Previously published results from the COZOMED-MERMEX project have shown the importance of the hydrodynamics in driving certain important ecological features of the Boughrara lagoon: heterogeneous water renewal between zones (Attoui *et al.*, 2020), control of the salinity level inside the lagoon compensating high evaporation (Ben Ismail *et al.*, 2017), accumulation of organic matter inside the lagoon (Ciglenečki *et al.*, 2020), control of toxic algal blooms through control of the distribution of dinoflagellate cysts (Abdelmouleh *et al.*, 2020).

Only few studies have been conducted on zooplankton patterns of distribution and community structure in this region. The first investigation on Boughrara and the southern Gulf of Gabes zooplankton was carried out by Daly Yahia and Romdhane (1994 and 1996) on the diversity and dynamics of the zooplankton community. Before the renovation of the historic Roman causeway, Daly Yahia and Daly Yahia-Kefi (2003) showed that the Boughrara lagoon displayed very high densities of phyto- and zooplankton linked to high water temperature and salinity (comparable to subtropical values) and high nutrient concentrations, particularly orthophosphates, characteristic of an eutrophic region. More recently, Drira *et al.* (2010) focused on the driving factors of the copepod community structure in the Gulf of Gabes showing the good adaptation of *Oithona nana* to high salinity and chlorophyll concentrations. However the effect of the tide on the zooplankton has never been investigated.

In this study, we focus on the spatial and time variability of zooplankton under contrasted tidal conditions. We aim to assess the impact of tidal currents on the distribution patterns and the retention of zooplankton to test the hypothesis that these processes may help in limiting the anthropization effects and the ecosystem resilience through maintaining the zooplankton biodiversity and favouring the control of phytoplankton proliferation.

2.Methods

2.1 Study site

The Gulf of Gabès is the marine region which has the highest tidal range in the Mediterranean Sea (maximum >2m) essentially due to the low slope of the continental shelf and the shallow depth, which maintains its horizontal dimensions close to the resonance condition (Bejaoui *et al.*, 2019). The tidal influence is particularly high in the south of the Gulf and in the Boughrara lagoon (Othmani *et al.*, 2017). The Gulf of Gabes is also highly productive and constitutes a paradox in the Eastern Mediterranean basin, which is known to be oligotrophic (Berman *et al.*, 1984; D'Ortenzio and d'Alcalà, 2009; Ben Brahim *et al.*, 2010; Krom *et al.*, 2010). Based on complementary biogeochemical and plankton criteria synthesized from recent regionalization analyses by Ayata *et al.* (2018), the Gulf of Gabès was recently identified as one of the eleven consensus ecoregions of the Mediterranean and classified as a shallow and phytoplankton bloom region. Linked to this planktonic richness, this area is an important nursery for several fish species (Koched *et al.*, 2015; Enajjar *et al.*, 2015) and contributes approximately 40% of the national fish production in Tunisia (DGPA, 2015). However, this singular and economically important region was recently identified as a 'hotspot' of anthropogenic pressures (Reygondeau *et al.*, 2017), strongly threatened by industrialization, particularly discharges from large-scale phosphate production plants, and overfishing, both potentially causing ecosystem disequilibrium and the decline of fish resources (Bejaoui *et al.*, 2019).

The Boughrara lagoon (33.35°N, 10.50°E) is a large (500 km^2) and shallow (average depth

about 5m) basin located in the southwest part of the Gulf of Gabes (Fig. 1). It receives freshwater inputs from small intermittent rivers (wadis) and communicates with the Gulf of Gabes through the Ajim-Jorf channel and with the open Eastern Mediterranean Sea through a 12 m pass under a Roman causeway linking Djerba Island to the continent. This pass was created in 2007 to promote water exchanges with the sea and water circulation in the lagoon and to make easier water oxygenation and greater mixing of the environment (Guetat et *al*., 2012). The tide is semi-diurnal with mean amplitude of 31 cm at neap tide and 73 cm at spring tide (Othmani *et al.*, 2017). Due to low freshwater inputs and high evaporation, the salinity of the lagoon is higher than in the surrounding sea, reaching values up to 43.6 in the central part of the lagoon and 50.9 at coastal stations, especially during the summer season (Daly Yahia *et al.*, 1994; Ben Aoun *et al.*, 2007).

2.2 S**ampling strategy**

Sampling was carried out during two campaigns within the frame of the COZOMED project: 4-13 October, 2016 (COZOMED 1); 11-14 April 2017 (COZOMED 2), both periods matching strong tidal conditions due to the proximity to equinox periods.

The tidal situation (water height) corresponding to the different samplings is shown in Fig. 2.

Sampling was performed in October 2016 and April 2017 at 8 stations: two stations in the marine coastal zone (st 1, 12m depth and st 2, 8m depth), one station in the Ajim-Jorf channel (st 3, 11m depth), one station in the lagoon close to the entrance of the channel (st4, 10m depth), three stations in the central part of the lagoon (st 5 and st 6, 14m depth, and st 7, 3 m depth) and one station in the eastern part of the lagoon close to the Roman causeway and the the pass communicating with the open Mediterranean sea (st 8, 2m depth). In October 2016, these stations were sampled three times to assess spatial variations in three contrasted tidal periods: (1) 4-5 October, with high tidal amplitude (mean = 0.58m) immediately following spring tide conditions (period called HA), (2) 8-9 October with low amplitude (0.22 m) during neap tide (LA) and (3) 11-12 October with medium amplitude (0.38 m) after neap tide (MA). Station 8 located in a very shallow area (as low as 1m depth in low water period) was sampled only once on October 5, but was abandoned afterwards due to navigation problems linked to the shallowness. In April 2017, stations 1 to 7 were sampled once (11-14 April) in spring tide conditions with high mean amplitude (0.67m).

In addition, three time-series were performed at station 4 for estimation of sea-lagoon exchanges over a tidal cycle and corresponding to different tidal sequences:

The first series (06 Oct 2016; HA) in post-spring tide period (mean amplitude = 0.49 m) started at the beginning of the ebb (10:00), slack water occurred at (15:00) and the two last sampling points were done in flood conditions.

The second series (10 Oct 2016; LA) done during neap tide (mean amplitude = 0.14m) started at the beginning of the flood (10:00), slack water occurred at (14:30) and the three last sampling points were done in ebb conditions.

The third series (12 Apr 2017; HA) performed in spring tide conditions (mean amplitude = 0.66 m) started at the beginning of the ebb (10:00), slack water occurred at (13:30) and the three last sampling points were done in flood conditions**.**

During each time-series, environmental parameters hourly sampling and zooplankton bi-hourly sampling were performed between 10:00 and 17:00. Note that we were not able to sample over a whole cycle (i.e., between two successive identical tidal situations), for safety reasons.

2.3 Physical and trophic variables

Sea level values were obtained from the hydrographic and oceanographic office of the French Navy (SHOM: Service Hydrographique et Oceanographique de la Marine; http://www.shom.fr/). As the available values from the SHOM concerned the Sfax coastal zone, we applied a 3-h time lag to estimate the values at Boughrara according to the numerical model developed by Othmani *et al*. (2017). Current velocity and direction were recorded at 10 minute intervals with a current-meter Argonaut D-1500 KHz (http://www.sontek.com/) moored on the bottom close to st 4 (see Fig 1) and deployed from October 6, 2016 for 47 days and from April 13 for 35 days (Attoui et al, 2020). Water origin and renewal time were estimated at each station from the hydrodynamic model described in Zayen *et al* (2020), using the procedures detailed in Chevalier et al. (2017).

Transparency was estimated with a Secchi disk. Salinity and temperature were recorded using a CTD probe (SBE 37 Sea-Bird Scientific) from surface to bottom. Water samples were collected at two depths (sub-surface and near bottom), using a 5 L Niskin bottle for measurements of suspended solids (SS), particulate organic matter (POM) and Chloropyll *a*. Chlorophyll *a*

was measured by optical density using a Jenway-7605 spectrophotometer. For SS and POM, water samples were filtered onto preweighed GF/F filters. After filtration, filters were dried at 60°C for 24 h and reweighed to determine SS. Afterwards, the filters were burnt at 550°C for 1.5 h and reweighed to estimate ash weight, POM and % of organic matter (%POM).

2.4 Zooplankton

The zooplankton was sampled with a WP2 200µm mesh net by vertical hauls from the bottom to the surface. The net was provided with a Hydrobios flowmeter to measure the length of the net trajectory and estimate the sample volume. In addition, samples were collected at two vertical levels (sub-surface and near bottom) with a 30 liter Schindler-Patalas plankton trap (Schindler, 1969) equipped with a 64 µm mesh filtering sock. The collected samples were immediately fixed with neutralized formaldehyde (4 % final concentration) in hermetically sealed PVC flasks. At the laboratory, before treatment, each sample was washed with 20µm filtered seawater, to eliminate the contained formaldehyde. For both counting and identifying zooplankton taxa, we used a Leica M 205C stereo microscope. For the WP2 samples, taxa were enumerated on sub-samples taken by wide bore piston pipettes, whereas for the trap samples, we counted the individuals on the whole sample. Zooplankton taxa were identified to species level when possible, according to Rose (1933), Tregouboff and Rose (1957), Boxshall and Halsey (2004) and Razouls *et al.* (2005-2020).

To estimate the body size of zooplankton organisms, selected samples of October 2016 (corresponding to Stations 1, 2, 4, 5, 6 and 7) were digitized with the ZooScan digital imaging system (Gorsky et al., 2010). When necessary, the sample was divided in 2 fractions (<1000 and>1000 mm) for better representation of rare large organisms in the scanned subsample. The resulting samples were poured onto the scanning cell and zooplankton organisms were manually separated with a wooden spike in order to avoid overlapping organisms. After scanning, each image was processed using ZooProcess, which is embedded in the ImageJ image analysis software (Gorsky et al., 2010). Finally, Plankton Identifier (http://www.obs-vlfr.fr/~gaspari/Plankton_Identifier/ index.php) was used for automatic classification of zooplankton into 7 categories: nauplii, copepod, other crustaceans, appendicularians, chaetognaths, other gelatinous organisms, meroplankton. The mean body area of zooplankton organisms category was then computed for each zooplankton category and for each station

2.5 Data analysis

2.5.1 Zooplankton abundance and diversity

Two datasets of zooplankton were considered:

- Subsurface and bottom zooplankton density (trap samples) to examine vertical distribution.
- Mean zooplankton density in the water column; we combined the datasets of the two sampling devices by selecting, for each taxon, the higher value between the trap (mean value of bottom and sub-surface) and the net sample.

In the three time-series at st 4, for better comparison between the three periods, zooplankton abundance was standardized for each period (x/x_{max})

The species richness S is represented by the total or average number of counted species per unit of area. The taxonomic diversity was estimated using the Shannon-Wiener Index (H') and Pielou Equitability Index (J ') (Harris *et al.*, 2000). The Pielou Equitability index allows measurement of the distribution of the individuals in each species, independently of the species richness. Its value varies from 0 (dominance of one species) to 1 (equal distribution of the individuals of the species). These indexes were calculated for water column values only, using Primer 6 (Plymouth Routines in Multivariate Ecological Research) Software. To better understand the changes in the community structure, the Rank Frequency Diagrams (RFD) were constructed by plotting the logarithms of the ranks of all species on the x-axis (in decreasing order of frequency) against their logarithmic frequency value on the y-axis (Pinca & Dallot, 1997). The Importance Value Index (IVI) for the different taxa was determined by summing the values of relative frequency, relative abundance and relative dominance (Curtis, 1959).

2.5.2 Zooplankton biomass and zooplankton grazing pressure

The mean body weight of each zooplankton category analyzed with the Zooscan (expressed as µg C ind^{-1}) was calculated using the area – carbon body weight relationships from Lehette and Hernandez-Leon (2009). These estimates (based on the analysis of selected samples of October 2016) were averaged per zone (Sea, Transition and Lagoon) and applied to the whole data set. The zooplankton biomass (mg C m^{-3}) was thus computed by summing the products of the mean individual body weight of each zooplankton category by its density in the water column (ind m^{-3}).

To estimate the grazing pressure of zooplankton on phytoplankton, we computed the carbon demand of zooplankton (ZCD) based on estimates of its biomass and ration:

ZCD (mgC m^{-3} d^{-1}) = Ration x Bzoo

where Bzoo is the biomass of zooplankton in mgC m^{-3}, and Ration is the amount of food consumed per unit of biomass, calculated as:

Ration (d^{-1}) = (gz + r) / A

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

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

as a function of sea water temperature (T, °C), food availability (Ca, mgC m-3, estimated from Chl-a), and weight of individuals (w, mgC).

Following Nival et al. (1975) and Alcaraz et al. (2007), we considered constant values of A (0.7 d^{-1}) and r (0.16 d^{-1}) respectively.

We compared ZCD to the phytoplankton stock, converted to carbon assuming a classical C:Chl-a ratio of 50:1, to estimate the potential clearance of phytoplankton by zooplankton.

2.5.3 Statistical and multivariate analyses

Sampling point-matrix were created for environmental data (tidal amplitude TA, Secchi depth, SD, temperature T, salinity S, NOx, PO4, Chl (*a*), suspended solids SS and % particulate organic matter %POM) and zooplankton taxa abundance (the 85 taxa reported in Table S1). In each matrix, the columns correspond to the environmental or zooplankton data and the lines to the sampling points. Zooplankton and environmental data were transformed (lnx+1) before analyses, in order to tend towards normal distribution.

Analysis of variance (ANOVA) was performed to compare mean values of zooplankton and environmental variables between depths, zones and periods. Prior analyses, log transformed data were tested for homogeneity; no case of non-homogeneity was detected.

The spatial and temporal variability of selected environmental variables, the most representative to define zooplankton habitats (temperature, salinity, suspended solids and % of POM), was investigated using principal component analysis (PCA). The spatial and temporal variability of the zooplankton community was measured using Nonmetric Multi-Dimensional Scaling

(NMDS) on taxon abundances, based on ordination of similarity matrices using the Bray-Curtis Dissimilarity (Harris *et al.*, 2000). A SIMPER (percentage of similarity) analysis was performed to identify the species contributing most to similarity and dissimilarity between stations for the station groups identified by NMDS. Permutational multivariate analysis of variance (PERMANOVA) was used to compare the station groups defined by the PCA and the NMDS, and test the hypothesis of no differences in community structure among these groups. The analyses were performed using Primer 7 (Plymouth Routines In Multivariate Ecological Research) Software.

According to the interpretation we made on the NMDS on zooplankton, we used the scores of the sampling points on the factorial axes as a proxy to define the "lagoon" or the "marine" character of the zooplankton communities. Then we searched for relationships between these proxies and the water origin (estimated from the hydrodynamic model using the procedures detailed in Chevalier et al., 2017).

3. Results

Environmental and trophic variables

For the October 2016 campaign, the PCA on environmental variables explained 34% and 33% of the total variance on the first two components, respectively (Fig.3). The plots of the sampling points on the first axis opposed the coastal marine stations (st 1 and 2) to all other stations characterized by higher salinity, lower SS and higher POM for the three considered tidal periods (HA from 4 to 6 October, LA from 8 to 10 October and MA from 11 to 13 October) (Fig 3A). The second axis tends to oppose the typical lagoon stations (st 5, 6 and 7) to the transitional water stations (st3 and 4 close to Ajim-Jorf channel) characterized by lower temperature and lower SS. This pattern on the second axis is followed during the three transects except for st 7 during the MA period, due to a decrease in temperature in this period.

For the April 2017 campaign, the PCA explained 67% and 28% of the total variance on the first two components, respectively. The plot of the sampling points (only one transect in HA period), as for October 2016, shows an opposition between marine and lagoon stations (Fig. 3B).

For both periods, the PERMANOVA shows significant differences between the three zones (lagoon, transition area and sea): pseudo F=6.3 and p=0.001 for October and pseudo F=6.9 and

p=0.02 for April. However, in both periods, pairwise tests show that the differences between the sea and the transition zone or between the sea and the lagoon are more pronounced than the differences between the transition zone and the lagoon, $p<0.01$ and $p<0.05$ respectively.

The mean value of the environmental parameters for each zone and each parameter are shown in Table 1. Temperature and salinity were significantly higher in October than in April (ANOVA, $p<0.001$), and in both periods the highest mean values were always found in the lagoon and the lowest in the sea. There was a clear horizontal salinity gradient with salinity increasing from sea (st 1-2) to lagoon (st 5, 6 and 7) with values from 40 to 46 in October and from 38.5 to 42.5 in April. In addition, in both periods, the water was slightly stratified in lagoon and sea zones with a significant difference between bottom and surface salinity (ANOVA, $p<0.01$), but the stratification disappeared in the transition zone. Transparency was higher in October than in April in the lagoon and the transition zone, and the difference was particularly high in the transition zone where the highest values were recorded for both seasons (ANOVA, $p<0.01$).

Suspended solid and Chlorophyll *a* showed no clear spatial pattern, with no significant difference between zones or between bathymetric levels (ANOVA, $p>0.1$), but were significantly higher in October than in April. Conversely, the percentage of POM was 1.2 to 1.7 times lower in October than in April in all zones.

Zooplankton abundance

The comparison of surface and bottom zooplankton density values obtained in the samples collected with the plankton trap shows that in October 2016 there was a clear vertical gradient of total zooplankton abundance (expressed as the bottom/surface ratio), with higher abundance near the bottom compared to the surface in the coastal marine stations throughout the survey, and in the transition area during HA period (Fig. 4A). Total zooplankton abundance as well as abundance of the most important taxa (*Oithona nana* and gastropod larvae) were on average higher in bottom samples than in surface samples when considering the stations as a whole (ANOVA, $p<0.001$). However, when considering each zone separately, the bottom – surface difference was significant only in the coastal marine zone (two-way ANOVAs for bottom-surface and station effects within each zone, $p<0.05$). Besides, the relative abundance of the main zooplankton groups (calanoids, cyclopoids and harpacticoids copepods, gelatinous organisms, other holoplankton and meroplankton) displayed no significant variation between surface and

bottom samples either globally or when considering each zone separately. In April 2016, the bottom - surface ratio varied between 0.5 and 4 according to stations (Fig. 4B), but neither depth nor zone effects were significant for zooplankton abundance or for the percentage abundance of main zooplankton groups (ANOVA, $p>0.1$).

Mean integrated water column values of total zooplankton abundance varied between 3600 and 50000 ind/m^3 in October 2016, with high variation according to stations and tidal periods (Fig. 4C). If we except a very low value recorded at station 8, close to the pass under the Roman causeway, sampled only once on October 5th, overall the zooplankton abundance tended to increase from marine stations (st 1 and 2) to lagoon stations (station 5, 6 and 7) in HA and MA periods, whereas no clear spatial pattern was detected during the LA period. The two-way ANOVA (zone and tidal period effects, Table 3) showed that the total zooplankton abundance as well as the abundance of the two most important taxa (*Oithona nana* and gastropod larvae) were significantly more abundant in the lagoon than in the coastal zone. The percentage of gelatinous organisms significantly increased in the lagoon compared to the sea, mainly due to appendicularians (*Oikopleura dioica*), whereas the percentage of copepods decreased. Among copepods, the relative abundance of the main groups also changed spatially with decreased importance of Calanoida versus Cyclopoida and Hapacticoida in the lagoon compared to the sea. No significant difference in total abundance or in abundance of the main taxa was observed between tidal periods except for *Oithona nana* which was significantly more abundant during LA than during MA and HA in the marine and transition zones and conversely in the lagoon.

In April 2017, mean integrated water column zooplankton abundance varied between 1400 and 11000 ind/m^3 with highest values found in the innermost lagoon stations st 6 and st7 (Fig 4 D), but no significant difference in total abundance or in abundance of the main taxa was observed between zones except for the percentage of non-copepod and non-gelatinous taxa that was significantly higher in the lagoon than in the coastal area (Table 2).

Overall, the zooplankton abundance was significantly lower in April 2017 than in October 2016 both when considering the three zones separately and for the whole data set (ANOVA, $p<0.01$)

Zooplankton community

We identified 116 taxa including 64 copepods, 13 non-copepod holoplanktonic crustaceans, 14 gelatinous organisms and 25 meroplanktonic larvae (table S1 in annex). Copepods were always dominant (62% - 92% of total abundance) but, in both periods, their percentage decreased from marine to lagoon stations except at station 8 sampled only during HA period in October 2016. Meroplankton, strongly represented by gastropod and bivalve larvae, was the second more important group (4% - 34%) and its relative abundance increased from marine to lagoon zone. Gelatinous zooplankton, mainly including appendicularians and chaetognaths, represented < 0.1%-13% abundance. Their relative abundance increased from sea to lagoon during October 2016, mainly due to appendicularians (*Oikopleura dioica*), but displayed an inverse pattern during April 2016.

Among copepods, *Oithona nana*, *Acartia latisetosa, Euterpina acutifrons and Paracalanus parvus* were overall the most important species in the 3 zones (sea, lagoon and transition) and in the two periods with IVI ranging between 80 and 130, however *A. latisetosa* was more prominent in April compared to October (Table S1, Fig. 5). Several other copepod species were recorded only in April (eg *Acartia clausi* and *Tortanus* sp.), whereas other species were recorded only in October (eg. *Oithona helgolandica, Lubbockia* sp., *Microsetella* sp. and *Pontella mediterranea*). Most copepod species were recorded in the three zones but several species were absent from the lagoon (*Ctenocalanus* sp., *Pontella mediterranea, Farranula sp., Metridia* sp., *Heterorhabdus* sp.) whereas some others were never recorded in the coastal marine zone (*Platycopia pygmea, Oithona simplex, Microsetella* sp.).

Among non-copepod taxa, meroplanktonic larvae (namely gastropods, bivalves, polychaetes and cirripedes) as well as the appendicularian *Oikopleura dioica* were the most strongly represented, with IVI ranging from 60 to 160. Cladocerans, mostly represented by *Podon* and *Evadne* genera, were more represented in the lagoon (IVI between 60 and 120) than in the coastal zone (IVI between 0 and 67).

The species richness (S) varied between 20 and 51 with the minimum value found at station 8. It was significantly higher in October 2016 than in April 2017 (ANOVA, $p<0.001$). In October 2016, S increased from the sea to lagoon, but displayed the reverse pattern during April 2017. However, species richness and diversity indexes (J' and H') showed no significant difference

either between zones in both periods or between tidal periods. H' was significantly higher in October than in April, whereas J' showed no significant difference between the two periods.
The Rank Frequency Diagrams (RFD) had similar convex shapes in both periods and zones except for station 8 in October (Fig. 6). In October, the RFD diagrams were very similar in the 3 considered zones, but station 8 was atypical compared to the other zones, with clear drops after the 1st and the 3rd ranks showing low diversity and evenness compared to the other zones. In April, the RFD of sea and lagoon zones were very similar up to rank 20 but they differed afterwards with spectacular decrease in frequency for the lagoon zone. We can note that in both periods, the RFD observed in the transition zone differed from those of the marine and lagoon zone with slight a drop-off from the 4th (October) or the 6th (April) rank.
In October 2016, *Oithona nana* was the rank1 species in the three considered zones but differences were observed from rank2, with *Phaenna spinifera* in the sea zone, *Oikopleura dioica* in the lagoon and Gastropod larvae in the transition zone (Table 4). Station 8 was dominated by *Acartia latisetosa* and harpacticoid copepods. In April 2017 the community was dominated by *Oithona nana* in the marine zone and by gastropod larvae in the transition zone and the lagoon. The NDMS on the relative abundance of the zooplankton taxa clearly discriminated between the two periods sampled (October 2016 and April 2017) as well as between the three identified zones (Fig 7A). In addition, station 8 was clearly distinguished from all other stations. In both periods, the PERMANOVA shows significant differences between the three zones (lagoon, transition area and sea) but with a better discrimination in October (pseudo $F=5.7$ and $p=0.001$) than in April ($F=2.7$ and $p=0.017$). In both periods, pairwise tests show that the differences between the sea and the transition zone or between the sea and the lagoon are more pronounced than the differences between the transition zone and the lagoon $p<0.01$ and $p<0.05$ respectively.

In October 2016, to better assess the influence of tidal periods on the lagoon zooplankton community, we performed a NDMS analysis on the relative abundance of zooplankton taxa for the lagoon zone stations (St 5, 6 and 7) during the three tidal periods (Fig. 6B). The plot of the sampling points shows a clear separation between the low tidal amplitude period (LA) and periods with higher amplitude (MA and HA). In the latter case, the lagoon stations tend to be

grouped and correlated with the most abundant species (*Oithona nana*), whereas during the LA period, the sampling points are more scattered.

Zooplankton biomass and zooplankton grazing impact on phytoplankton

The total zooplankton biomass followed the same spatial and temporal patterns as the zooplankton abundance. The mean biomass values ranged from 5.8 to 36.7 mg C m-3 with highest values recorded in the lagoon and the transitional zones and the lowest in the coastal marine zone and much higher values in October 2016 than in April 2017 (Table 5). The mean ratio between phyto- and zooplankton biomasses ranges between 8 and 27%. The mean daily grazing pressure represented 4.3 to 15.3 % of the phytoplankton stock, with higher values in October 2016 than in April 2017.

The comparison between tidal periods in October 2016 shows that zooplankton biomass and the zooplankton grazing pressure (ZCD) in the lagoon was on average twice higher during the periods of tidal amplitudes (MA and HA) compared to period with low amplitude (LA), whereas no clear variation was observed between tidal periods in the coastal sea and transitional zones.

Tidal variability at the fixed station

The total zooplankton abundance increased overall during the ebb period and reached the maximum at low water and until mid-flood, when current velocity was at a maximum and oriented inwards into the lagoon, and tended to decrease afterwards during the end of the flood (Fig. 8A). The percentage of zooplankton present at the surface was highly variable but tended to decrease during the ebb, reaching minimum values from beginning to mid-flood (Fig 8B).

The comparison of the mean values between ebb and flood periods (Fig 9, Table 5) allows assessment of the net tidal exchange of particulate matter and zooplankton between the sea and the lagoon. There was no significant difference between ebb and flood for Chl *a*, SS and P concentrations (Table 5). In each of the three time-series, the water column integrated total zooplankton abundance and biomass were significantly higher during the flood than during the ebb (Fig. 9). Significant differences between ebb and flood were also found for the water column abundances of copepods (either as total or by larval phases or families), and of the most important copepod species *O. nana* and *E. acutifrons,* with flood/ebb ratio ranging from 2 to 6 (Table 5). The same patterns were noted for the same zooplankton taxa and additionally for

total meroplankton and *O. dioica* in bottom strata, but no significant ebb-flood differences were detected in surface water, except for *E. acutifrons* during the first time-series (October 2016). The water column zooplankton abundance was on average 2.2 higher during the flood than during the ebb, and this increase was even more important for the zooplankton biomass (x 2.4) and for the zooplankton grazing pressure on phytoplankton (x 2.8).

The NMDS performed on the relative abundance of the zooplankton taxa during the two time-series of October 2016 shows a clear separation between HA and LA periods and between ebb and flood within each period (Fig.10). The first axis clearly shows an opposition between lagoon influence (on the right), through correlation with meroplankton larvae (gastropods, bivalves, polychaetes, fishes, etc) and copepods such as *O. nana* and *E. acutifrons,* and marine influence (on the left), characterized by more typical marine taxa such as Chaetognaths, *Lucifer* sp., and copepods such as *Metridia* sp. LA period was characterized by higher lagoon influence and MA by higher marine influence. Each tidal cycle starts with a relatively marine zooplankton assemblage at high water which then evolves towards a more lagoon assemblage during ebb with a return towards the marine assemblage at the end of the next flood. It can be noted that the return to the marine assemblage is slower than the passage to the lagoon assemblage, particularly during the LA period. Besides, as previously noted spatially in the NMDS for the lagoon stations (see Fig 9), a higher variability was observed in LA conditions compared to HA conditions.

4. Discussion

Main characteristics of the Boughrara lagoon zooplankton: *do they reflect a disequilibrium?*

As in many other Mediterranean coastal or lagoon ecosystems (see Table 7), the zooplankton of the Boughrara lagoon is characterized by a community strongly dominated by copepods (62% - 92% of total abundance), but also with high relative abundance of meroplanktonic larvae

(4% - 34%; mostly gastropod larvae). Several differences were observed between the two studied periods, with lower abundance and diversity in April 2017 than in October 2016, perhaps reflecting a post spring-bloom situation in April with quick development of some suspension-feeders (namely, gastropod larvae, and small copepods, see Table 4). This is in agreement with the seasonal variability described by Daly Yahia and Ben Romdhane (1994) for the Boughrara lagoon both in terms of zooplankton abundance and community structure, and similar to the seasonal pattern observed in another Tunisian lagoon: Ghar el Melh (Ziadi *et al.*, 2015).

As in most examples given in Table 7, *Oithona nana*, *Acartia latisetosa*, *Euterpina acutifrons* and *Paracalanus parvus* were overall the most dominant copepod species in the study area in both periods. The high frequency of *O. nana* in the Boughrara lagoon and in its riverine coastal area, both highly anthropized, is not surprising, since this species was already reported at very high and unusual abundance in highly polluted urban bays such as the bay of Toulon in the NW Mediterranean (Richard and Jamet, 2001) or in the bay of Tunis (Daly Yahia *et al.*, 2004). Moreover, the Oithonidae seems to be a family having high affinity for anthropized marine systems, and as such were shown to be a potentially good indicator of anthropization (Serranito *et al.*, 2016) having high dominance in lagoon ecosystems (Williams and Muxagata, 2006). In their pioneering study carried out in 1992-93, Daly Yahia and Ben Romdhane (1994) reported zooplankton abundance in the Boughrara lagoon 2-4 times higher than that recorded in our study in the same seasonal periods, but more than two decades earlier. Furthermore, *Centropages kroyeri,* which represented 6-10% of the Boughrara copepod abundance in 1992-93, was almost totally absent in our 2016-2017 samples and was replaced by *C. ponticus* (2-13% copepod abundance in the lagoon), recognized as a dominant copepod species throughout the Tunisian lagoons (Neffati *et al.*, 2013). Perhaps this decrease in zooplankton abundance and the replacement of *C. kroyeri* by *C. ponticus*, more adapted to eutrophic conditions, constitute the signs of disturbance of the lagoon plankton ecosystem, in relation to increased anthropization over the last decades, mostly due to chemical pollution which has led to the degradation of the water quality and the erosion of benthic communities (Ben Aoun *et al.*, 2007). Despite these signs of disturbance, the zooplankton community in our study was characterized by a high diversity and evenness and rank frequency diagrams having a convex shape reflecting a relatively mature and equilibrated zooplankton community (*sensu* Frontier 1976) in the three investigated zones, with the exception of station 8 in October 2016, more characteristic of a young zooplankton community at the beginning of an ecological succession. Conversely other coastal

Mediterranean ecosystems, strongly anthropized but not under tidal influence, display very low zooplankton diversity, e.g. the small bay of Toulon, where the community is strongly dominated by only one species, *Oithona nana* reprensenting 60-90% of the zooplankton abundance) (Jamet and Corbel, 1996).

Another important characteristic of the zooplankton of the Boughrara lagoon is its high abundance, much higher than in the open Mediterranean sea (up to 50000 ind/m^3, in our study vs <10000 ind/m^3 in most open Mediterranean regions (Siokou Frangou *et al*., 2010). In comparison with other lagoons, the zooplankton abundance in the Boughrara lagoon is slightly higher than in the northern Tunisian coastal lagoons, such as Bizerte lagoon (Gueroun *et al.*, 2020) and Tunis lagoon (Annebi Trabelsi *et al.*, 2005), but lower than in the shallow Ghar El Melh lagoon (Ziadi *et al.*, 2015), and within the same range of values as those reported for north-western Mediterranean lagoons such as Thau and Bages-Sigean (Marques *et.al.*, 2015), whereas much higher values are recorded either in highly anthropized sites such as Berre lagoon (Delpy *et al.*, 2012) or in lagoons under low Human pressure (protected areas) such as Sacco del Canarin, (Po Delta, Italy) (Ferrari *et al.*, 1985) and Bardawil (Egypt) (Mageed, 2006). It is interesting to note that the zooplankton abundance and species composition (notably dominance of *O. nana*) in Boughrara are very similar to those recorded in another highly anthropized and meso-tidal Mediterranean lagoon, Venice lagoon (Italy) (Riccardi, 2010).

With regard to the Gulf of Gabès, the zooplankton abundance recorded in the southern coastal zone is within the range of that recorded by Drira *et al.* (2017) in the northern coastal zone close to Sfax and by Drira *et al.*, (2010) in the neritic area (<50m depth), Daly Yahia *et al.* (2004) found similar zooplankton abundance values in the Bay of Tunis. However, much lower values were recorded in the oceanic areas (>50m depth) of the gulfs of Gabès (Drira *et al.*, 2010) and Tunis (Ben Lamine *et al.*, 2015).

In summary, despite several signs of disturbance lightened (? alleviated) by the taxonomic composition and presumably linked to the anthropization, the zooplankton community of the Boughrara lagoon is still characterized by high abundance and high diversity reflecting a rather good health status. The rather high biomass ratio between zooplankton and phytoplankton (7-28%, comparable to values reported for coastal marine zones 12-23%, Gasol *et al*., 1997), as well as the high zooplankton grazing rate (representing 4.3 to 15.3 % of the phytoplankton stock per day comparable to the values recorded in the open Mediterranean Sea: 9.5 to 19.3% d^{-1}; Feliu *et al*., 2020), are also good signs reflecting an efficient transfer between the first levels of the pelagic food chain. In comparison, other highly anthropized lagoon ecosytems present abnormally low zoplankton/phytoplankton biomass ratio (e.g. 2% in the Ebrié lagoon, Ivory Coast, Pagano and Saint-Jean, 1994; 1% in Sontecomapan, VeraCruz, Mexico, Benitez-Diaz Miron *et al*., 2019) or very low zooplankton grazing impact (e.g. <1.7% d^{-1} in the Berre Lagoon, NW Mediterranean Sea, Gaudy, 1989), leading to phytoplankton accumulation and episodic dystrophic crisis. Finally, the increasing zooplankton abundance in the Boughrara lagoon compared to the coastal marine area and to the open Mediterranean Sea (see above) suggests zooplankton retention in relation with the morphology (low slope), advection process and the tidal influence, as discussed below.

Tidal influence on community structure and retention of zooplankton: do these processes help maintain zooplankton biodiversity and control phytoplankton?

Our study highlights very clear spatial gradients of environmental and trophic variables between the coastal zone of the Gulf of Gabès and the Boughrara lagoon, but do these changing conditions explain the spatial variability of the zooplankton community and the increasing gradient of zooplankton abundance between the sea and the lagoon? As discussed below, our results suggest rather an important contribution of tidal Lagrangian transport and mixing of organisms from different zones in structuring the zooplankton communities and driving the spatial gradient of zooplankton abundance through selective retention of organisms in the lagoon.

The impact of tidal circulation on the exchanges of zooplankton between the sea and the lagoon was clearly shown in the 3 time-series observations performed at station 4 in the transition zone. At this station, the zooplankton community has a relatively marine character at high water which then evolves towards a more lagoon character during the ebb, with a return towards marine character at the end of the next flood (see Fig. 10). In addition, the return to the marine

character is slower than the passage to the lagoon character, suggesting a dynamic lag between the input and the output of zooplankton from the sea to the lagoon, as observed in hysteresis situations. This pattern is observed in LA and HA periods, but LA, compared to HA, is characterized by having a more lagoon character over the whole tidal cycle, a higher variability in community structure between ebb and flood, and longer time lag from lagoon to marine character (see Fig. 10). This pattern and its variation between LA and HA periods can be explained by the relative contribution of marine and lagoon water in the transition area simulated by the hydrodynamic model (Fig 11A). HA conditions are characterized by an important marine water contribution (Concentration Ratio ≥ 60%) compared to lagoon water (15-35%) (Fig.11A). In LA conditions, the mixing of water is more intensive with a contribution of lagoon water (55-70%) that is higher than the contribution of marine water (30-50%). This may explain the higher variability of the zooplankton community over a tidal cycle during LA than during HA in the transition zone. Furthermore, in each situation, the lagoon character of the community (as defined by the scores of the first axis of the NMDS analysis of Fig 10A) increases when the relative contribution of the lagoon water increases in relation with the tidal cycle (Fig 11B). The lag time for the return to a marine community can be explained by the higher distance of st 4 from the marine coastal zone (st 2) than from the typical lagoon zone (st 5). Thus, the time-variability of the zooplankton community in the transition zone results from mixing of zooplankton taxa differentially transported from the coastal marine area of the Gulf of Gabes and from the innermost part of the lagoon. Tidal exchanges with the open Mediterranean Sea through the Roman causeway in the north-eastern part of the lagoon were not directly investigated, but the very different community recorded at Station 8 compared to the other lagoon stations (see Figs 6 and 7), also suggests intense tidal exchanges and mixing between coastal marine and lagoon zooplankton. Estimates of the water origin and renewal time from the hydrodynamic model confirm the high contribution of the external Mediterranean water (>50%) and the intense water renewal (<10 days; Atoui *et al*., 2020) in this zone of the lagoon. This can thus be considered as a transition zone between the sea and the lagoon, similarly to the north-western zone close to Ajim-Jorf channel (St 3 and St4).

Spatial gradients of zooplankton community structure were clearly demonstrated in both periods (Fig 7A). These gradients appear to be strongly driven by tidal advection transport, as suggested by the positive relationships between the lagoon character of the community at the different lagoon stations and the relative contribution of the lagoon water at these stations (Fig 11 C). In the lagoon, spatial gradients of the zooplankton community were clearly higher in LA conditions compared to MA and HA conditions when the strong tidal circulation probably generates mixing and homogenization of the zooplankton communities (see Fig. 7B). This suggests that during high tidal amplitude periods, the communities are spatially homogenized even in the innermost part of the lagoon (st 6 and 7), whereas low amplitude periods favour spatial gradients of zooplankton communities. High tidal amplitudes also favour gradients of abundance (see Fig 4C) linked to a retention phenomenon (see below), but with mixing and homogenization of the community composition linked to higher tidal exchanges with the sea. Conversely, low tidal amplitude would attenuate the gradient of abundance (through lower retention), but would favour a spatial gradient of community composition.

The higher zooplankton abundance recorded in the Boughrara lagoon compared to the adjacent coastal zone in the Gulf of Gabès seems to result from a retention phenomenon associated with tidal currents, as shown by the net import balance of zooplankton especially for the most important copepod species *O. nana* and *E. acutifrons*, during the tidal cycle (see Fig. 9 and Table 5). Rawlinson et al (2005) also advanced a net tidal transport to explain the higher abundance of mesozoplankton species (including *Oithona helgolandica*) in a semi-enclosed Irish ecosystem compared to the adjacent Atlantic Ocean. Similarly to our observations in the transition area (st 4), Krumme and Liang (2004) observed higher zooplankton abundance during the ebb with highest values occurring at low water in a Brazilian macro-tidal cul-de-sac channel, suggesting zooplankton retention. However, the higher proportion of meroplankton in the Boughrara lagoon compared to the coastal zone could also indicate that higher zooplankton abundance in the lagoon may arise from local production of meroplanktonic larvae by benthic adults in the lagoon, as mentioned by Archambaud *et al.*, (1988) among different hypotheses to explain increased abundance of organisms inside and outside embayments. Nevertheless, rather high mean flood/ebb ratio for meroplankton abundance (l.4 for the water column and 2.3 for bottom water with significant ebb – flood difference) argue more in favor of meroplankton retention in the lagoon rather than local production of adults. Although we have no current data on benthic communities in the study area, we know that the coastal zone of the Gulf of Gabes

close to Boughrara hosts a macroinvertebrate benthic community very similar to the one in the lagoon (Khedhri *et al.,* 2016). Moreover, the strong variability of the flood/ebb ratio between the different taxa suggests a selective retention of zooplankton in the lagoon, with copepod and particularly harpacticoids (mostly *Euterpina acutifrons*) and to a lesser extent the cyclopoid *Oithona nana* being the most retained taxa. Such selective retention could be partly explained by a behavioral tendency of some species to congregate in the depths during ebb tide, as observed for *Acartia* in Newport Bay, California, by Trinast (1975). Among Oithonidae, *Oithona davisae* was shown to have the ability of selective retention and an extremely high adaptive plasticity in Black Sea environment (Svetlichny *et al.,* 2016) and *O. plumifera* increased abundance in shallow nearshore waters off the south coast of South Africa could also be explained by physical aggregation (Porri *et al.,* 2007).

In our study, significant ebb-flood differences were observed for bottom strata but not in surface waters, also suggesting aggregation of zooplankton at depth during ebb tide, limiting their export from the lagoon. Very similar results were recorded in another mesotidal Mediterranean lagoon (Sacca del Canarin, Adriatic Sea) by Ferrari *et al.* (1985) who observed particularly high abundance of *Acartia clausi*, *Paracalanus parvus*, *Oithona nana* and *Euterpina acutifrons* at flood tide compared to ebb tides, as well as daily positive input-output balance for calanoids, cyclopids and harpacticoids over a 24-h cycle. In contrast, Brugnano *et al*. (2010) in a non-tidal lentic ecosystem of the southern Adriatic region (lagoon Lesina) observed an increasing abundance trend from the lagoon towards the sea, highlighting the relative confinement of this lagoon. Besides, this lagoon, similarly to other non-tidal lentic Mediterranean lagoons (e.g. Lakes Ganzirri and Faro, Zagami and Guglielmo, 1995), is characterized by rather low (<10000 ind/m^3) zooplankton abundances in contrast to other Mediterranean lagoons such as Boughrara, characterized by intense hydrodynamics and water exchanges with the sea.

In this study we observed net import balances of total zooplankton abundance (mean flood/ebb ratio = 2.2) and biomass (mean flood/ebb ratio = 2.4) during the semi-diurnal tidal cycles leading to an increase of the potential grazing pressure on phytoplankton (mean flood/ebb ratio = 2.8). We also estimated that the grazing pressure in the lagoon was twice higher during the periods of high tidal amplitudes (MA and HA) compared to period with low amplitude (LA),

clearly showing that the retention of zooplankton significantly increases the top-down control of phytoplankton thus help controlling the proliferation of phytoplankton.

In summary the high tidal exchanges (particularly during spring tide periods) favour mixing and homogenization of the community as well as retention and accumulation of zooplankton in the Boughrara lagoon. These processes help maintain the zooplankton biodiversity even in the innermost part of the lagoon. They also lead to an increase in the zooplankton abundance and biomass and its grazing impact on phytoplankton.

Conclusion

The comparison of our results with previous historical studies highlights several changes in the zooplankton community composition, probably due to the degradation of environmental and trophic conditions linked to increasing anthropisation. However, several results in our study (high diversity, high abundance and biomass, equilibrated biomass ratio between phyto-and zooplankton, high potential grazing impact) reveal a rather good current health status of the planktonic ecosystem in agreement with our hypothesis of a buffer effect of the tidal flow likely to limit the effects of this anthropization, Our study clearly shows the effect of the tidal forcing (i) on the time variability and on the spatial gradients of community structure and abundance between the marine coastal zone and the innermost part of the lagoon, and on (ii) maintaining high abundance, biomass and grazing pressure in the lagoon. These results suggest the importance of the tidal forcing for maintaining the zooplankton diversity and biomass at a good level in a strongly anthropized ecosystem, thus fulfilling (quantitatively and qualitatively) the stock of zooplankton prey available for the upper trophic levels (zooplanktophagous organisms, e.g. small pelagic fishes) and ensuring a good top-down control of phytoplankton. The top-down control on phytoplankton may be also partly exerted by the micro-zooplankton as shown by Sakka Hlaili *et al.*, (2006) for the Bizerte lagoon where a large ciliate community was shown to prey upon upon large diatom cells. Since there is also an important ciliate community in the Boughrara-Gabès system (Rekik *et al.*, 2020), further studies may necessarily extend the investigations to the whole of the zooplankton (including proto- and metazooplankton) in order to better understand how tidal forces can minimize the devastating impact of eutrophication and contamination.

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Legends of figures

Fig. 1. Map of the study zone showing the location of the different sampling stations. AJC= Ajim Jorf Channel; RC=Roman causeway.

Fig. 2. Tidal situation during the different samplings: position of the sampling points in relation with water height in October 2016 (A) and April 2017 (B). HA, LA and MA (with associated horizontal lines) position the periods of high, low and medium tidal amplitude, respectively.

Fig 3. PCA analysis of the mean values of the main environmental variables (salinity, temperature, SS, POM) for the radial stations in October 2016 (A) and April 2017 (B). HA= high amplitude, LA=low amplitude and MA=medium amplitude. Trans = Transition zone, Lag= Lagoon zone).

Fig.4. Bottom/surface ratio of total zooplankton abundance along coastal marine – lagoon water transects in three tidal periods (HA= high amplitude, LA=low amplitude and MA=medium amplitude) in October 2016 (A) and under high amplitude conditions in April 2017 (B) and total integrated water column zooplankton abundance in the same situations (C and D respectively).

Fig. 5. Importance Value Index (IVI) for the copepod taxa in the three zones in October 2016 and April 2017.

Fig 6. Mean Rank Frequency Diagrams (RFDs) of zooplankton taxa for the two campaigns October 2016 (A) and April 2017 (B) and for the three zones (plus St 8 in October).

Fig 7. Non-Metric Multidimensional Scaling (NMDS) of the relative abundance of the zooplankton taxa (square root transformed). Ordination of the sampling points and the zooplankton taxa having correlation >0.7 for (A) the two campaigns and (B) for the lagoon stations in October in the three tidal periods. The sampling points of October are symbolized as follows: the station number is followed by -LA, -MA or –HA indicating the tidal period.

Fig 8. Time series of zooplankton abundance standardized for each series (x/xmax) (A) and of % abundance of zooplankton sampled at the surface (surface x 100 / bottom + surface) (B) during ebb/flood at station 4 during the three distinct studied periods. The dashed and continuous black lines correspond to the mean standardized values (between the periods) of water height and current velocity, respectively. For better comparison between the three periods, the results are presented on

a common x time scale by positioning the sampling points at the elapse time between the sampling time and the preceding high water.

Fig 9. Comparison of the mean values of total zooplankton abundance (top) and of percentage abundance of the zooplankton groups (bottom) between ebb and flood periods during the three time-series at Station 4.

Fig 10. Non-Metric Multidimensional Scaling (NMDS) of the abundance of the zooplankton taxa (square root transformed) during the two time-series performed at station 4 in October 6 (HA) and 10 (LA) in 2016. Ordination of the sampling points (A), and the zooplankton taxa having correlation >0.7(B). HW+ number means the elapse time between the sampling time and the preceding high water (e.g. HW+5 means 5 hours after the preceding high water).

Fig 11. Time variation of the relative contribution of lagoon and marine water (derived from the hydrodynamic model; see Methods) at station 4 in October (A), and relationships between the percentage of water of lagoon origin and the 'lagoon character' of the zooplankton during the two time-series at St 4 in October (B) and for the whole set of stations sampled during the two periods (C). The lagoon character of the zooplankton corresponds to the scores of the sampling points of the first axis of the NMDS of Fig 10A for the time-series, and to the scores of the stations on the second axis of the NMDS of Fig 7A for the spatial variations.

Legends of Tables

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Table 4. Zooplankton taxa having the first 10 ranks in the RFD diagrams shown in Fig.6.

Table 5. Mean and standard deviation (SD) values for integrated water column values of phyto- and zooplankton biomasses and for zooplankton grazing pressure in the 3 different zones and the tidal periods. MA+HA are considered together for comparison with LA.

Table 6. Mean ratio between flood and ebb periods for chlorophyll and particulate matter and for the abundances of total zooplankton and of zooplankton groups or taxa calculated for the integrated water column (Col.) and for the surface (Surf.) and bottom (Bot.) strata and for the biomass and grazing pressure of total zooplankton; T-tests between ebb and flood tide means reveal significantly different means with $p<0.05$ (*). Ratio corresponding to significant ebb-flood differences are in red characters.

Table 7. Comparison of total zooplankton abundance in different lagoon and coastal ecosystems of the Mediterranean Sea.

Table S1. Importance value indexes (IVI) for the taxa inventoried during the two COZOMED campaigns in October 2016 and April 2017 in the three zones and at station 8.

Figures

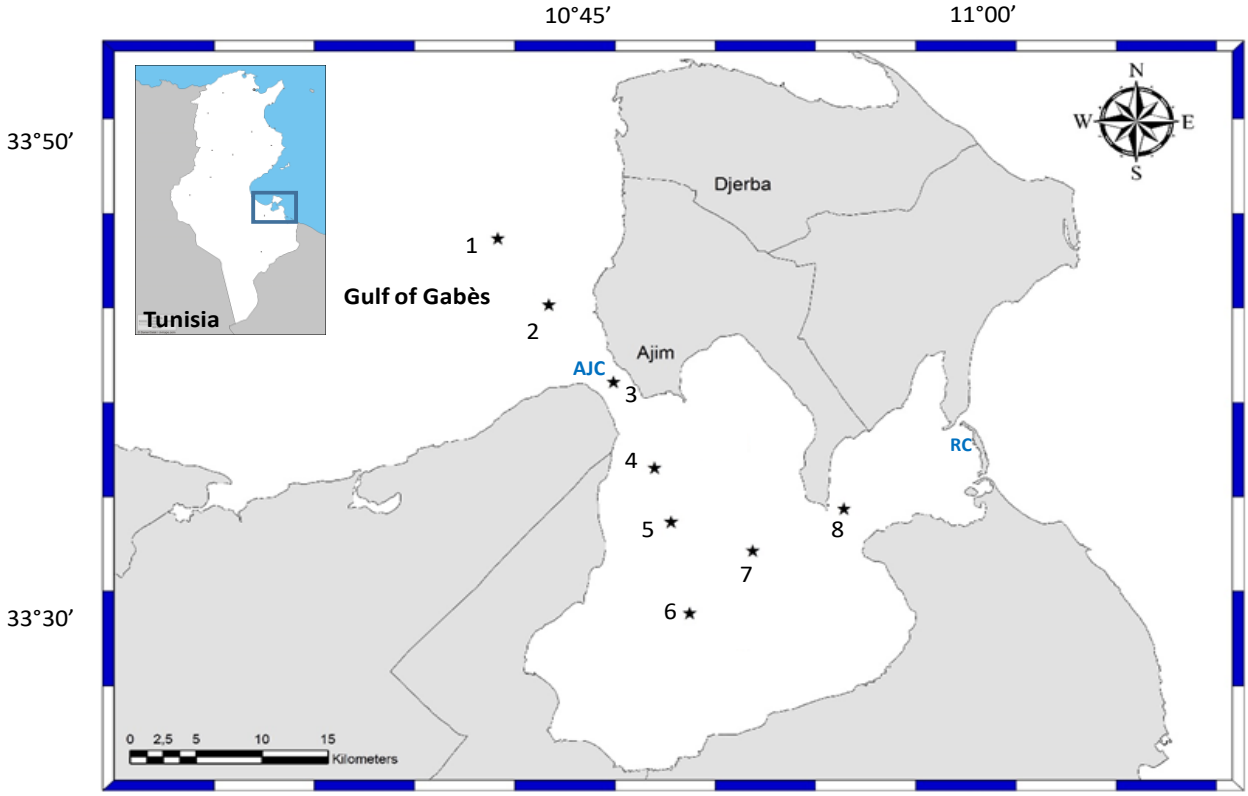


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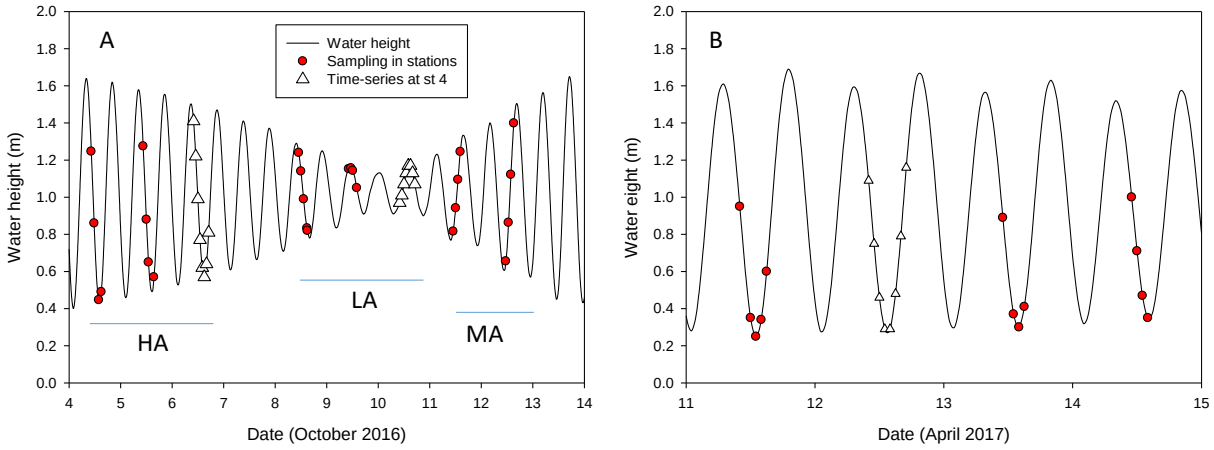


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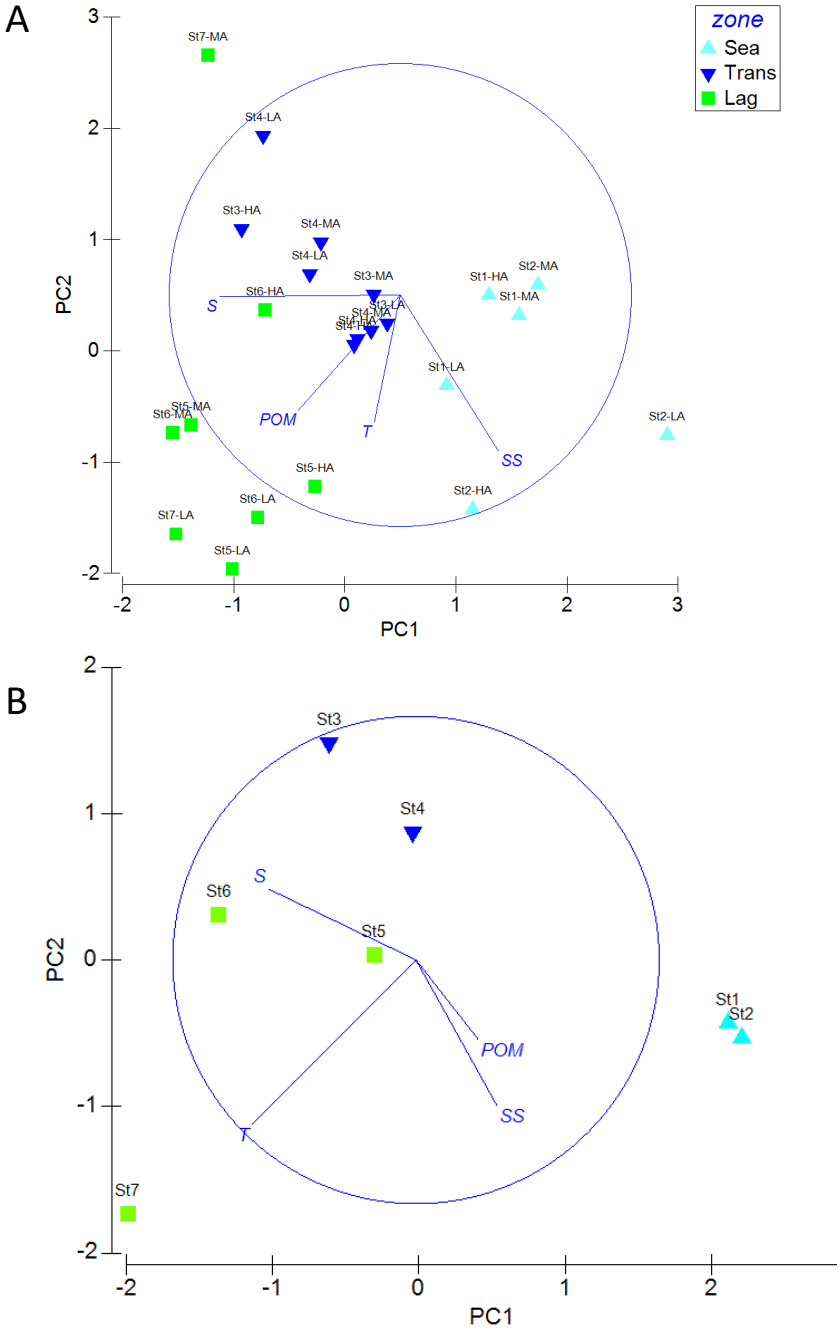


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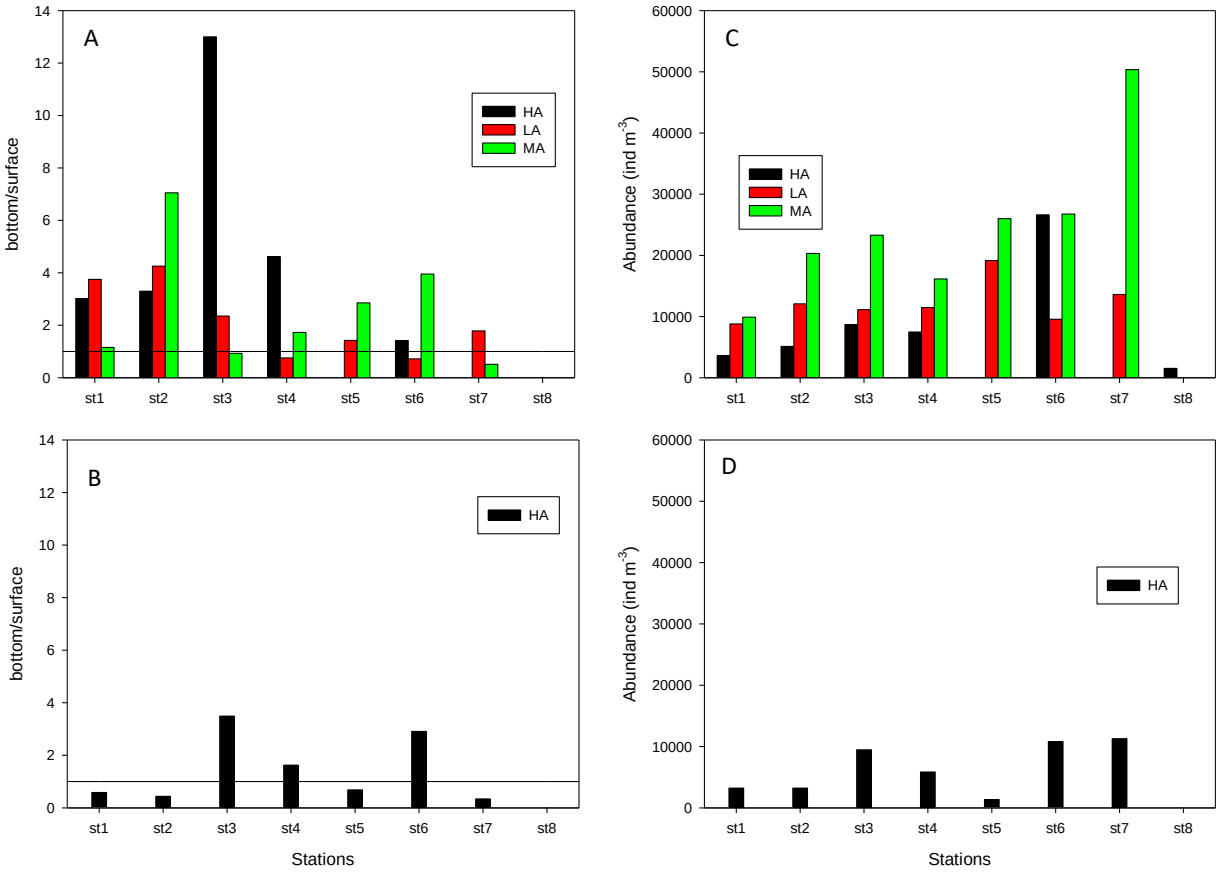


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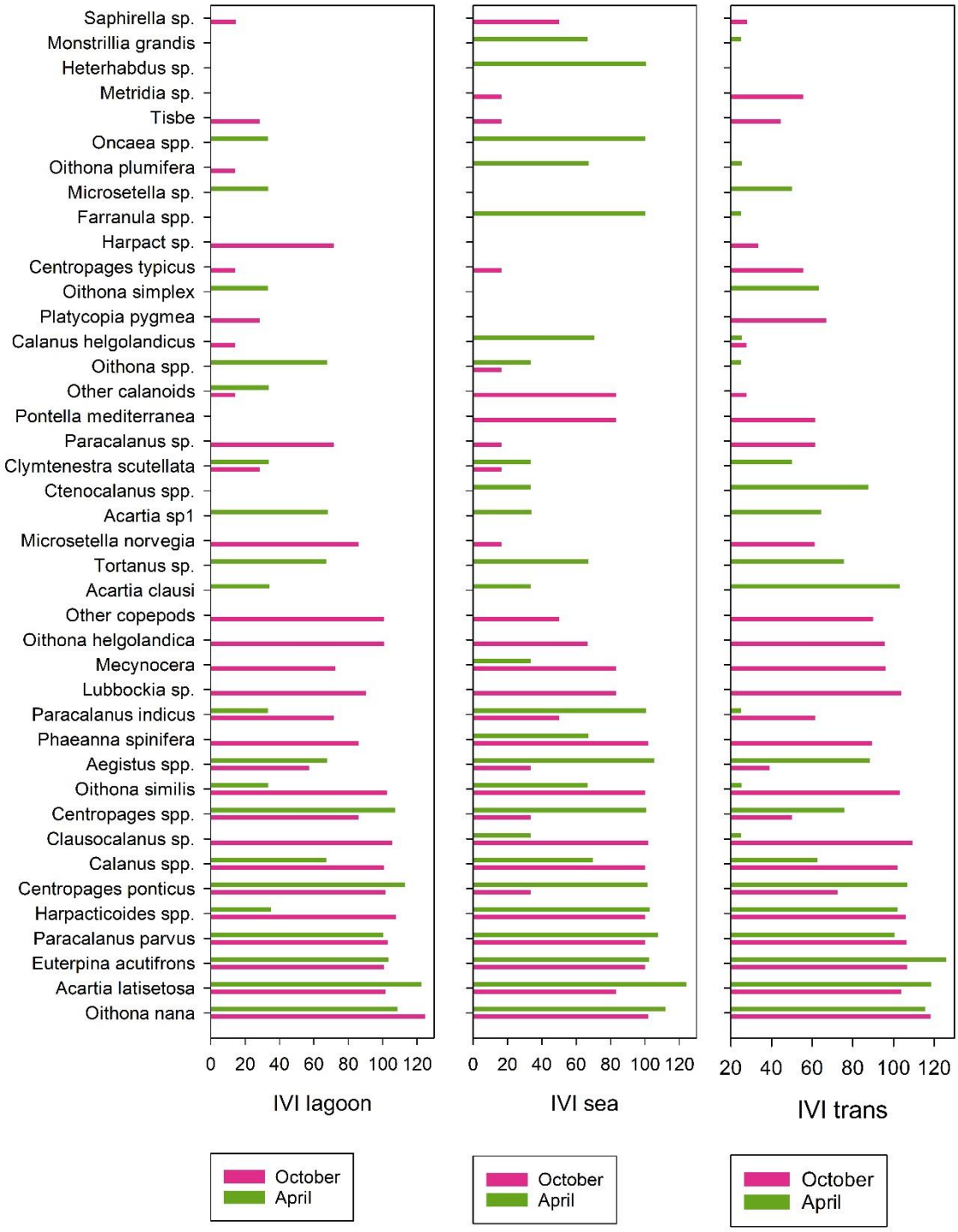


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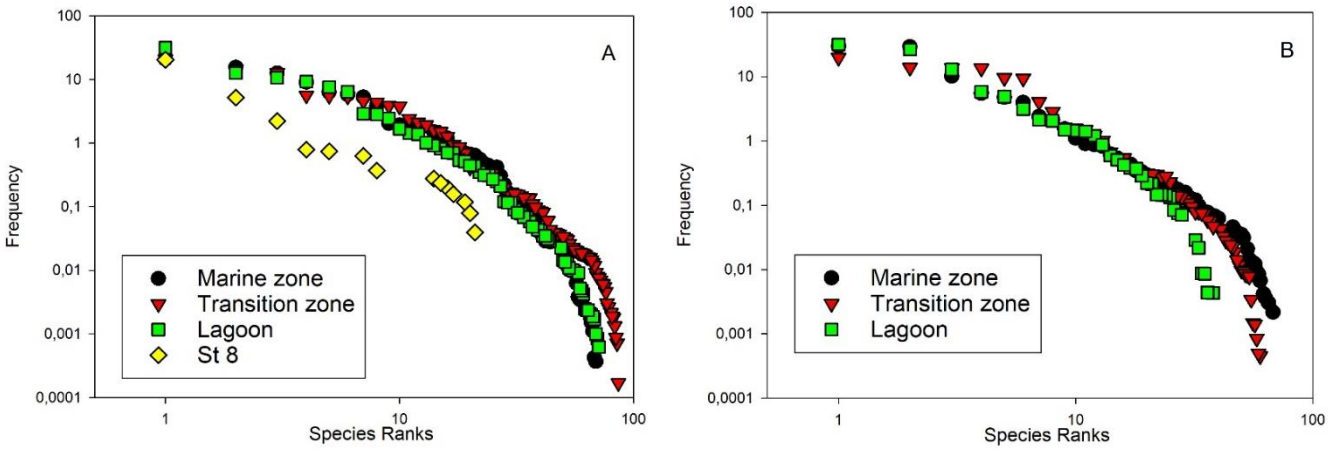


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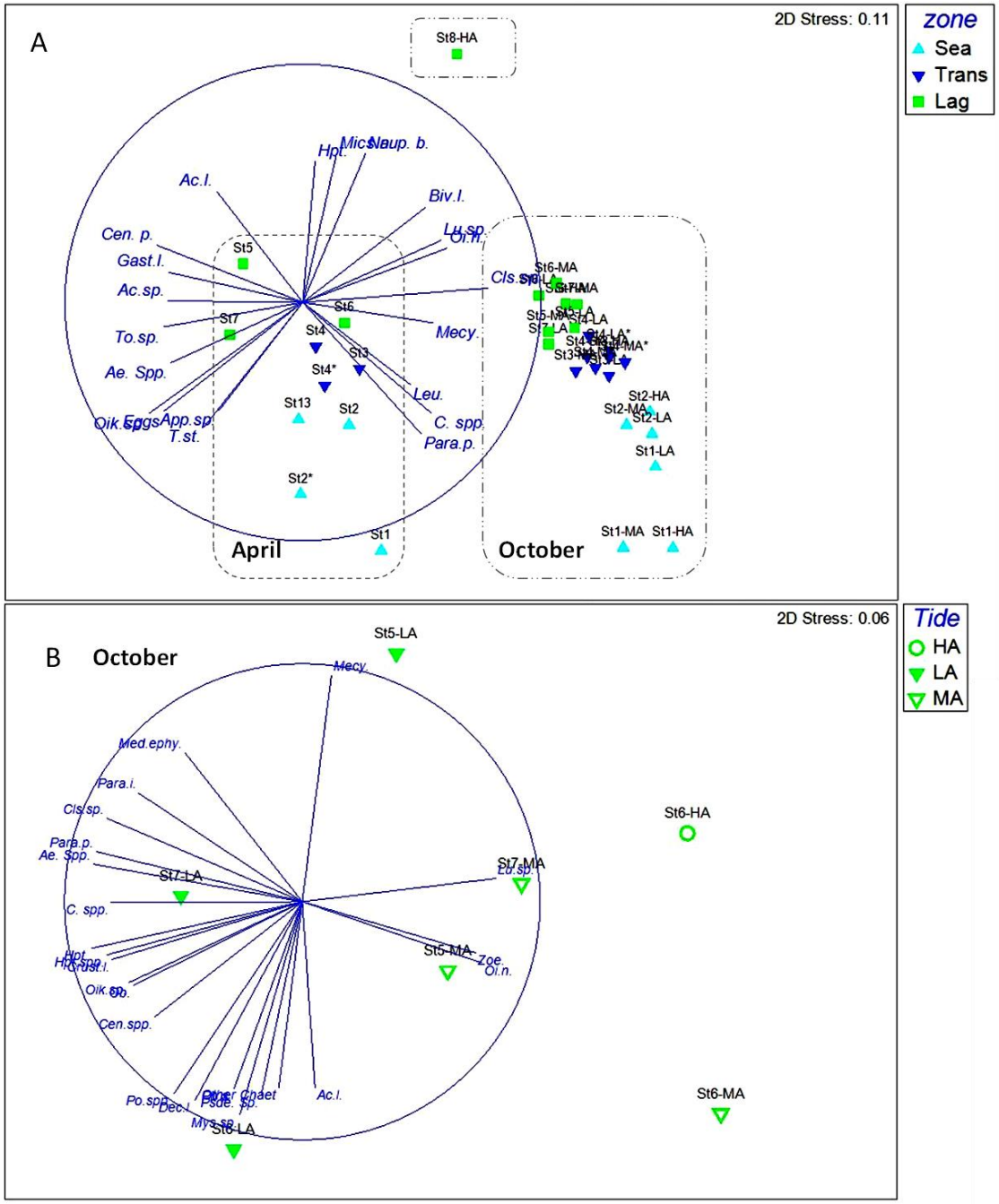


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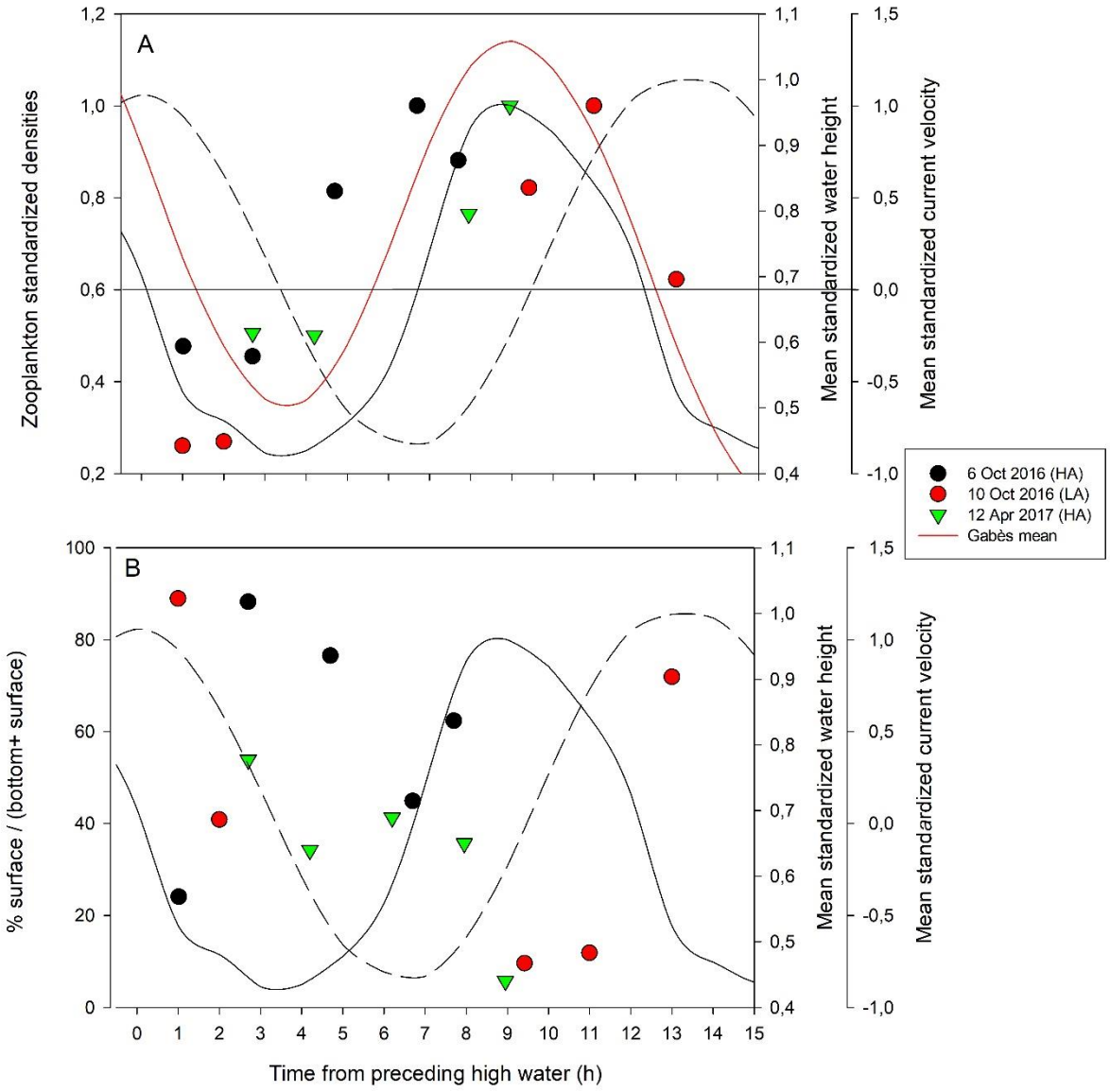


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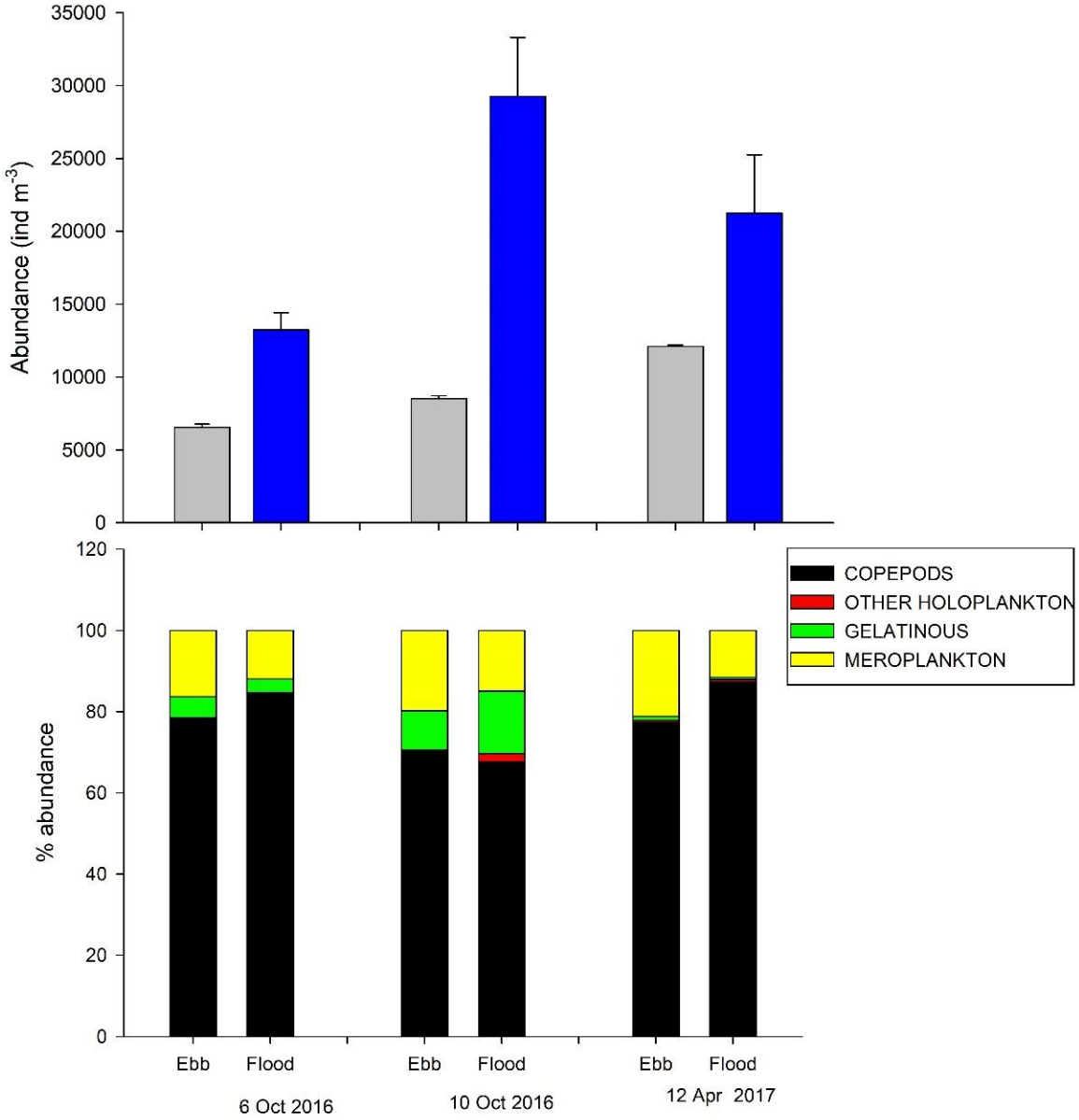


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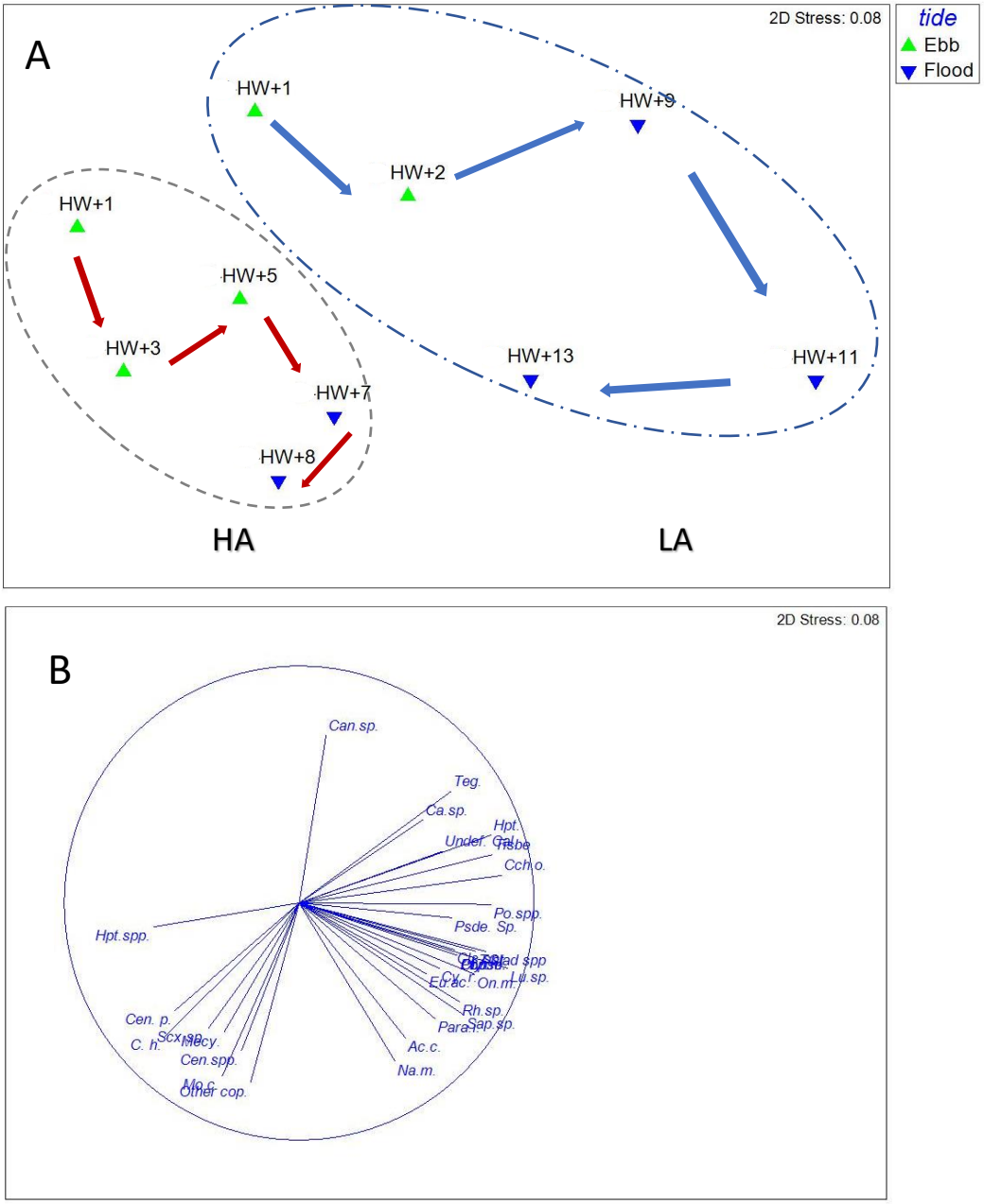


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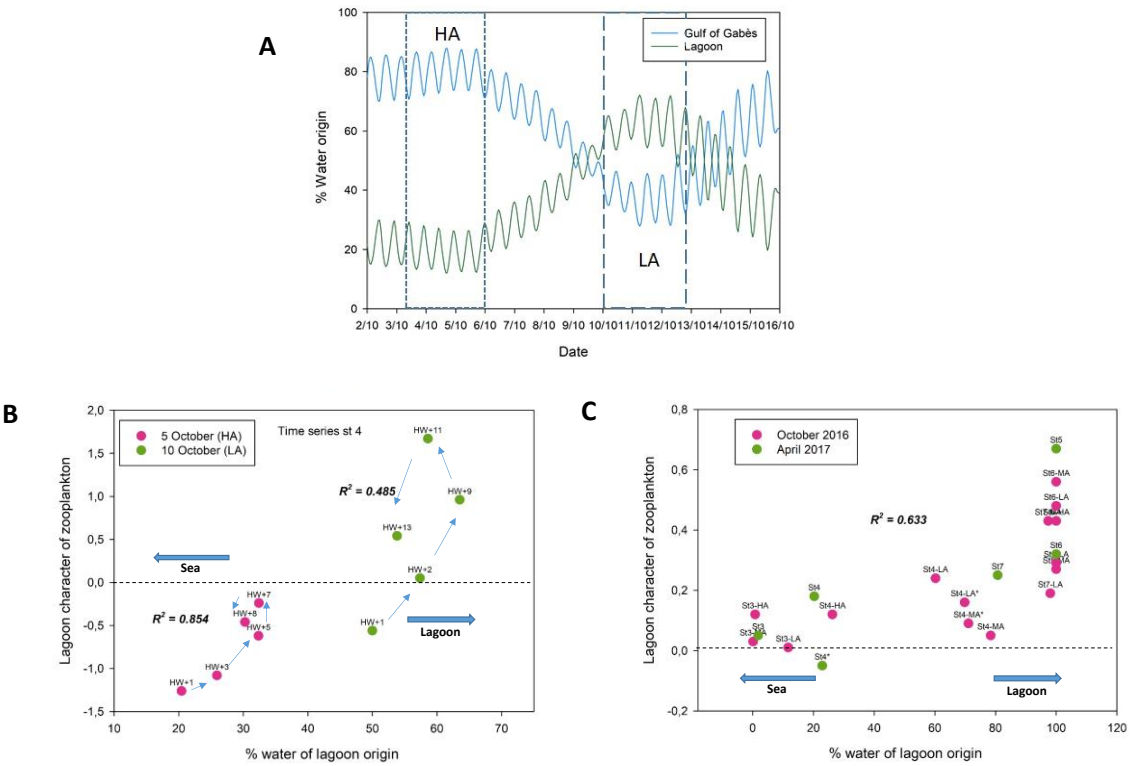


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Tables

Table 1. Mean values (± SD) of environmental variables in the different zones predefined by the PCA analysis.

	October 2016									April 2017								
	Sea			Trans.			Lagoon			St8	Sea			Trans.			Lagoon		
Salinity	40.33	±	0.33	43.97	±	0.67	**45.48**	±	**0.38**	nd	38.52	±	0.17	42.49	±	0.01	**42.58**	±	**0.15**
Temperature (°C)	26.66	±	0.14	26.73	±	0.11	**26.91**	±	**0.22**	nd	17.65	±	0.26	18.06	±	0.28	**19.46**	±	**1.24**
Transparency (m)	3.90	±	0.89	**7.24**	±	**0.14**	4.80	±	1.39	3.00	3.65	±	0.89	**4.63**	±	**0.18**	4.30	±	1.72
Suspended Solids (µg/L)	24.62	±	2.32	21.39	±	0.69	23.64	±	1.89	**28.20**	11.17	±	3.31	11.16	±	3.26	**12.57**	±	**2.24**
Organic Matter (%)	24.54	±	4.03	**28.81**	±	**1.46**	28.49	±	2.64	15.60	**41.84**	±	**7.66**	36.88	±	0.60	33.31	±	3.34
Total Chl (µg/L)	2.98	±	0.40	2.40	±	1.43	**5.64**	±	**3.09**	3.19	0.78	±	0.27	0.97	±		**1.50**	±	**1.35**

Table 2. Mean and standard deviation (SD) values for zooplankton variables in the trap samples collected in subsurface (Surf.) and near bottom (Bot.) for the three zones and the two periods (October and April) and two-way ANOVAs (p values) for the differences between zones and depth; none of the interaction between these effects was significant. Degree of freedom (df) of error were 37 and 12 for October and April, respectively. Significant values of p are in red characters.

		OCTOBER 2016								APRIL 2017							
		Mean values						ANOVA (p values)		Mean values						ANOVA (p values)	
		Sea		trans.		lagoon		zone	depth	Sea		trans.		lagoon		zone	depth
		n=6		n=8		n=7		df=2	df=1	n=6		n=3		n=3		df=2	df=1
		Surf.	Bot.	Surf.	Bot.	Surf.	Bot.			Surf.	Bot.	Surf.	Bot.	Surf.	Bot.		
Abundances (ind/m³)																	
Zooplankton	**mean**	**4389**	**15294**	**9867**	**15967**	**20986**	**27210**	***0.008***	***0.033***	**3722**	**1922**	**4189**	**8300**	**7433**	**7144**	*0.277*	*0.770*
	sd	*2626*	*11023*	*7015*	*5885*	*20200*	*12082*			*880*	*1435*	*1859*	*4100*	*7706*	*7394*		
O. nana	**mean**	**411**	**2106**	**1408**	**2738**	**2205**	**3043**	***0.023***	***0.008***	**244**	**122**	**456**	**956**	**400**	**511**	*0.177*	*0.459*
	sd	*421*	*2119*	*1145*	*1408*	*1649*	*1897*			*192*	*84*	*171*	*738*	*371*	*685*		
L gastero	**mean**	**89**	**211**	**779**	**896**	**1238**	**1943**	***0.003***	***0.023***	***489***	***178***	**478**	**1900**	**2156**	**2022**	*0.246*	*0.693*
	sd	*72*	*117*	*986*	*833*	*1628*	*1432*			*704*	*126*	*184*	*1467*	*2911*	*2528*		
% total abundance																	
Copepods	**mean**	**76.6**	**89.5**	**77.4**	**82.2**	**72.6**	**69.0**	***0.013***	*0.217*	**79.0**	**76.1**	**77.0**	**67.7**	**73.5**	**71.2**	*0.730*	*0.443*
	sd	*20.2*	*4.3*	*9.8*	*5.2*	*7.3*	*8.1*			17.7	17.7	*8.1*	*5.5*	*15.0*	*8.2*		
Gelatinous	**mean**	**0.8**	**0.7**	**2.8**	**3.4**	**8.1**	**11.6**	***0.000***	*0.090*	***2.1***	***3.0***	**1.6**	**4.6**	**2.0**	**0.1**	*0.437*	*0.602*
	sd	*0.6*	*1.2*	*1.6*	*2.0*	*4.1*	*3.6*			*1.8*	*5.2*	*1.4*	*3.4*	*1.5*	*0.1*		
Other	**mean**	**0.7**	**0.1**	**1.0**	**0.1**	**0.9**	**1.2**	*0.728*	*0.419*	**0.0**	**0.3**	**0.2**	**0.0**	**0.1**	**2.3**	*0.126*	*0.104*
	sd	*0.7*	*0.2*	*2.9*	*0.2*	*0.9*	*1.7*			*0.0*	*0.6*	*0.3*	*0.0*	*0.1*	*2.3*		
Meroplank.	**mean**	**21.9**	**9.7**	**18.7**	**14.3**	**18.5**	**18.3**	*0.585*	*0.109*	***18.9***	***20.6***	**21.3**	**27.7**	**24.4**	**26.4**	*0.774*	*0.636*
	sd	*20.0*	*3.5*	*9.1*	*3.9*	*9.8*	*6.4*			*19.3*	*20.1*	*9.6*	*7.1*	*16.1*	*10.2*		
% copepod abundance																	
Calanoida	**mean**	**72.0**	**58.8**	**33.4**	**33.8**	**26.1**	**28.0**	***0.000***	*0.368*	**43.1**	**42.0**	**26.4**	**26.4**	**63.1**	**49.8**	*0.083*	*0.637*
	sd	*17.6*	*15.0*	*6.2*	*10.4*	*13.2*	*10.3*			*23.6*	*12.4*	*6.5*	*9.8*	*34.2*	*25.0*		
Cyclopoida	**mean**	**15.8**	**27.3**	**37.1**	**41.8**	**49.7**	**46.7**	***0.000***	*0.247*	***38.8***	***37.6***	**40.8**	**41.8**	**26.5**	**31.4**	*0.376*	*0.830*
	sd	*11.3*	*13.3*	*8.2*	*14.1*	*18.6*	*12.5*			*16.7*	15.2	*3.2*	*7.8*	*25.6*	*12.9*		
Harpacticoida	**mean**	**10.4**	**13.3**	**27.8**	**22.5**	**22.6**	**24.1**	***0.000***	*0.709*	**18.1**	**20.4**	**32.8**	**31.8**	**10.4**	**18.4**	*0.052*	*0.583*
	sd	*8.5*	*4.8*	*5.6*	*6.5*	*12.8*	*4.7*			*7.1*	*12.2*	*9.6*	*12.6*	*9.1*	*16.6*		
Other copepods	**mean**	**1.7**	**0.6**	**1.6**	**2.0**	**1.6**	**1.2**	*0.648*	*0.677*	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.38**	*0.397*	*0.337*
	sd	*2.5*	*1.4*	*2.7*	*1.5*	*2.2*	*1.2*			*0.00*	*0.00*	*0.00*	*0.00*	*0.00*	*0.66*		

Table 3. Mean and standard deviation (SD) values for integrated water column zooplankton variables in the 3 different zones and for st 8, and one way (April) or two-way (October) ANOVAs (p values) to test the differences between the 3 zones and the 3 tidal periods (LA, HA and MA in October only). Significant values of p are in red characters.

		OCTOBER 2016						APRIL 2017			
		mean values				ANOVA (p values)		mean values			ANOVA (p values)
		Sea	trans.	lagoon	St. 8	*zone*	*Tide*	Sea	trans.	lagoon	*zone*
		n=6	*n=8*	*n=7*	*n=1*	*df=2*	*df=1*	*n=3*	*n=3*	*n=3*	*df=2*
Abundances (ind/m³)											
Zooplankton	**mean**	9974	12143	24581	1537	0.010	0.055	3223	7055	7823	0.319
	sd	2425	1983	5002				1110	1502	3231	
O. nana	**mean**	1258	2000	2624	17	0.063	0.034	183	706	456	0.245
	sd	449	373	537				109	223	245	
L gastero	**mean**	150	646	1590	17	0.004	0.193	333	1189	2090	0.259
	sd	31.3	257.1	391.0				397	468	1041	
% total abundance											
Copepods	**mean**	85.2	81.8	69.8	91.1	0.001	0.204	80.7	74.3	73.1	0.612
	sd	3.0	1.6	2.4				9.8	0.8	7.8	
Gelatinous	**mean**	0.8	3.1	9.6	1.2	0.000	0.970	3.2	3.6	1.0	0.268
	sd	0.4	0.6	0.7				1.7	1.5	0.5	
Other	**mean**	0.6	0.7	1.2	0.3	0.542	0.929	0.2	0.2	1.1	0.013
	sd	0.3	0.3	0.4				0.3	0.2	0.1	
Meroplank.	**mean**	13.4	14.4	19.5	7.3	0.083	0.131	15.9	21.9	24.8	0.613
	sd	2.8	1.4	2.3				11.1	2.1	8.3	
% copepod abundance											
Calanoida	**mean**	61	34	28	86	0.004	0.658	65.9	43.5	64.3	0.295
	sd	6	2	4				15.2	8.1	13.0	
Cyclopoida	**mean**	25	41	47	1	0.016	0.191	23.7	30.6	22.4	0.580
	sd	5	3	5				9.6	3.4	7.4	
Harpacticoida	**mean**	13	24	23	13	0.0412	0.3845	10.3	25.9	13.1	0.125
	sd	2	2	3				5.9	5.3	5.4	
Other copepods	**mean**	1	1	1	0	0.991	0.495	0.1	0.0	0.2	0.541
	sd	1	0	0				0.1	0.0	0.2	
Specific Richness (S)	**mean**	37.2	39.5	43.0	21.0	0.642	0.111	36.0	32.3	25.0	0.284
	sd	4.4	5.3	5.5				5.3	11.0	5.6	
Equitability (J')	**mean**	0.71	0.73	0.68	0.42	0.058	0.224	0.70	0.69	0.61	0.457
	sd	0.07	0.02	0.05				0.10	0.07	0.09	
Shannon-Wiener (H')	**mean**	3.70	3.85	3.69	1.85	0.078	0.156	3.59	3.39	2.84	0.112
	sd	0.43	0.09	0.24				0.34	0.22	0.50	

Table 4. Zooplankton taxa having the first 10 ranks in the RFD diagrams shown in Fig.6.

	Rank	Sea	Transition	Lagoon	Station 8
October 2016	1	*Oithona nana*	*Oithona nana*	*Oithona nana*	*Acartia latisetosa*
	2	*Phaeanna spinifera*	Gastropods Larvae	*Oikeuplora dioica*	*Harpacticoides spp.*
	3	*Paracalanus parvus*	*Clausocalanus sp.*	Bivalve Larvae	*Phaeanna spinifera*
	4	*Calanus spp.*	*Euterpina acutifrons*	Gastropods Larvae	Bivalve Larvae
	5	*Clausocalanus sp.*	Larve bivalve sp1	*Clausocalanus sp.*	*Nauplii balanus*
	6	*Euterpina acutifrons*	*Oikeuplora dioica*	*Lubbockia sp.*	*Oithona nana*
	7	Mecynocera	*Paracalanus parvus*	*Harpacticoides spp.*	*Euterpina acutifrons*
	8	Decapods larvae	*Harpacticoides spp.*	Nauplii chthamalus	*Microsetella norvegia*
	9	Annelid polychet larvae	*Oithona similis*	*Paracalanus parvus*	*Oikeuplora dioica*
	10	Bivalve Larvae	*Lubbockia sp.*	*Oithona similis*	Nauplii chthamalus
	Rank	**Sea**	**Transition**	**Lagoon**	
April 2017	1	*Oithona nana*	Gastropods Larvae	Gastropods Larvae	
	2	*Oikeuplora dioica*	*Euterpina acutifrons*	*Oithona nana*	
	3	Gastropods Larvae	*Acartia latisetosa*	*Centropages ponticus*	
	4	*Euterpina acutifrons*	*Oithona nana*	*Acartia latisetosa*	
	5	*Acartia latisetosa*	*Centropages ponticus*	*Euterpina acutifrons*	
	6	*Paracalanus parvus*	*Oikeuplora dioica*	Annelid polychet larvae	
	7	*Lubbokia acuelata*	*Harpacticoides spp.*	*Harpacticoides spp.*	
	8	*Aegistus spp.*	Annelid polychet larvae	*Centropages spp.*	
	9	*Harpacticoides spp.*	*Acartia sp1*	*Acartia sp1.*	
	10	*Calanus helgolandicus*	*Acartia clausi*	*Podon spp.*	

Table 5. Mean and standard deviation (SD) values for integrated water column values of phyo- and zooplankton biomasses and for zooplankton grazing pressure in the 3 different zones and the tidal periods. MA+HA are considered together for comparison with LA.

		OCTOBER 2016						**APRIL2017**		
		Sea		transition		lagoon		Sea	trans	lagoon
		LA	HA+MA	LA	HA+MA	LA	HA+MA	HA	HA	HA
Biomasses (mgC m-3)										
Phytoplankton	mean	169.7	138.5	128.6	137.2	219.8	196.0	51.4	48.6	74.8
	sd	*4.9*	*15.0*	*54.3*	*72.0*	*68.8*	*64.0*	*25.0*	*25.0*	*67.6*
Zooplankton	mean	19.3	18.6	20.1	24.6	16.6	36.7	5.8	13.2	8.3
	sd	*3.2*	*13.0*	*6.6*	*13.8*	*2.3*	*11.5*	2.6	3.2	3.4
		0.11	*0.13*	*0.16*	*0.18*	*0.08*	*0.19*	*0.11*	*0.27*	*0.11*
% zooplankton biomass										
Copepod	mean	85.5	81.2	68.8	65.7	62.9	64.2	69.0	59.5	63.8
	sd	*8.1*	*31.3*	*10.1*	*16.7*	*14.3*	*9.8*	*6.7*	*10.9*	*0.0*
Gelatinous	mean	1.3	1.8	4.8	7.0	14.1	14.3	7.3	4.6	0.8
	sd	*0.5*	*0.7*	*1.7*	*2.1*	*3.2*	*2.9*	*0.2*	*0.1*	*0.7*
Other	mean	1.1	1.1	0.9	7.2	8.5	4.7	0.7	1.6	6.7
	sd	*0.4*	*0.9*	*0.8*	*7.3*	*5.8*	*2.7*	*0.9*	*1.9*	*4.6*
meroplankton	mean	12.1	15.9	25.5	20.2	14.5	16.8	23.0	34.3	28.6
	sd	*1.0*	*8.2*	*14.0*	*13.4*	*3.9*	*7.5*	*22.6*	*34.9*	*84.5*
Zooplankton grazing pressure										
ZCD (mg m^{-3} d^{-1})	mean	13.7	13.0	14.2	17.1	12.2	26.1	2.2	5.1	3.7
	sd	*2.3*	*9.0*	*5.0*	*9.6*	*1.6*	*7.0*	1.0	1.2	1.5
%phyto d^{-1}	mean	8.1	9.4	11.3	14.6	6.1	15.3	4.3	10.6	5.0
	sd	*1.6*	*6.8*	*0.9*	*8.3*	*2.3*	*9.4*	4.0	5.0	2.3

Table 6. Mean ratio between flood and ebb periods for chlorophyll and particulate matter and for the abundances of total zooplankton and of zooplankton groups or taxa calculated for the integrated water column (Col.) and for the surface (Surf.) and bottom (Bot.) strata and for the biomass and grazing pressure of total zooplankton; T-tests between ebb and flood tide means reveal significantly different means with $p<0.05$ (*). Ratio corresponding to significant ebb-flood differences are in red characters.

	WHOLE DATA			OCTOBER 6, 2016			OCTOBER 10, 2016			APRIL 13, 2016		
	Col.	**Bot.**	**Surf.**	**Col.**	**Bot.**	**Surf.**	**Col.**	**Bot.**	**Surf.**	**Col.**	**Bot.**	**Surf.**
Chlorophyll	1.56	nd	nd	1.07	nd	0.72	1.72	nd	1.56	0.67	nd	nd
SS	0.82	0.75	0.88	0.78	0.82	0.75	0.93	0.86	1.01	0.72	0.59	0.88
POM	0.86	0.72	1.02	0.78	0.56	1.02	1.00	0.92	1.08	0.80	0.67	0.96
Abundance (ind m^{-3})												
Total Zooplankton	**2.22** *	**3.21** *	1.07	**2.02** *	2.04	2.05	**3.44** *	**8.59** *	0.58	**1.75** *	**2.80** *	0.83
Copepods	**2.37** *	**3.37** *	1.26	**2.18** *	2.09	2.46	**3.30** *	**9.54** *	0.60	**1.98** *	**3.03** *	0.99
Gelatinous	1.66	**2.40** *	0.62	1.32	2.00	0.96	**5.56** *	**10.45** *	0.60	0.99	1.33	0.40
Other holoplankton	2.33	2.93	1.52	1.78	abs	0.50	19.96	35.50	0.00	1.91	0.50	10.00
Meroplankton	1.40	**2.26** *	0.65	1.47	1.64	1.01	2.59	4.87	0.48	0.96	1.78	0.46
Copepod nauplii	**1.99** *	**2.66** *	0.87	1.91	2.40	1.63	**5.04** *	**19.30** *	0.61	1.17	**1.49** *	0.65
Copepodites	**1.91** *	2.34	1.08	**1.69** *	1.53	1.83	**3.42** *	**11.71** *	0.54	1.33	1.52	0.86
Calanoids	**2.17** *	**3.59** *	1.57	2.41	**2.88** *	2.91	1.98	**3.47** *	1.08	2.18	6.95	1.62
Cyclopids	**1.93** *	**2.88** *	0.97	**3.71** *	3.46	4.03	1.43	3.65	0.13	1.64	2.04	0.86
Harpacticoids	**2.80** *	**3.12** *	1.80	1.73	1.06	3.92	4.64	14.82	0.50	**4.22** *	**7.23** *	1.32
Other copepods	1.28	3.22	0.38	2.01	1.50	4.00	1.12	9.00	0.00	0.97	abs	0.00
Acartia latisetosa	1.94	3.70	2.34	1.28	2.10	1.29	6.75	8.75	6.08	2.63	30.56	3.50
Paracalanus parvus	1.20	1.95	0.66	2.40	1.92	3.05	1.46	**3.82** *	0.46	0.34	1.00	0.00
Oithona nana	**2.14** *	**3.12** *	0.99	**4.28** *	3.82	4.86	1.76	**4.58** *	0.10	1.65	2.00	0.88
Euterpina acutifrons	**4.54** *	**4.12** *	2.87	**3.21** *	2.09	**6.71** *	16.67	26.71	2.60	**4.55** *	**6.91** *	1.55
Oikeuplora dioica	1.56	**2.02** *	0.70	1.26	1.85	0.96	**5.60** *	**10.29** *	0.61	1.00	1.17	0.67
Cirriped larvae	1.32	2.36	0.59	6.35	2.50	abs	1.63	1.29	0.00	0.29	abs	0.14
Bivalve larvae	1.01	1.14	0.57	0.94	0.27	1.25	2.05	3.39	0.35	0.50	0.67	0.40
Gastropod larvae	1.16	2.31	0.50	0.73	1.47	0.51	5.56	21.64	0.78	0.97	1.70	0.41
Polychaete larvae	**2.45** *	2.33	1.35	6.00	1.00	abs	**4.25** *	**13.00** *	1.33	1.36	2.09	0.21
Zoopl. biomass (mg C m^{-3})	**2.41** *	nd	nd	**2.00** *	nd	nd	**3.49** *	nd	nd	**1.82** *	nd	nd
Zooplankton grazing pressure :												
ZCD mg C m^{-3} d^{-1})	**2.76** *	nd	nd	**2.10** *	nd	nd	**4.10** *	nd	nd	**2.06** *	nd	nd
% phytoplankton stock d^{-1}	**2.49** *	nd	nd	**2.11** *	nd	nd	**2.37** *	nd	nd	**3.09** *	nd	nd

Table 7. Comparison of total zooplankton abundance in different lagoon and coastal ecosystems of the Mediterranean Sea.

Site	Sampling period	Net mesh size	Depth	Salinity	Abundance (ind m-3)		Dominant taxa	Reference
					mean	range		
Bizerte lagoon, Tunisia	Nov 2012 - Augt 2014	200µm	7-8 m	34-38	2978	(400 - 11000)	Calanoid copepods	Gueroun et al.,2020
Tunis lagoon, Tunisia	March2001 - Sept 2002	70 µm	1,5 m	35-44	9300	(200-76000)	Oithona nana, Acartia clausi, Euterpina acutifrons, Centropages kroyeri, Stephos marsalensis, Oithona helgolandica, Acartia discaudata,	Annabi Trabelsi et al., 2005
Tunis Bay, Tunisia	Dec 1993 - Nov 1995	55µm-300µm	3-30m	37-38	3962	(2500-20000)	O. nana, O. helgolandica, A. clausi, Euterpina acutifrons, Centropages kroyeri	Daly Yahia et al., 2004 (from their Fig. 5)
Gulf of Tunis, Tunisia	Dec 2007- Apr 2008	220µm	10-100m		870	(350-2600)	Paracalanus parvus, Clausocalanus lividus, Centropages kroyeri and Acartia clausi	BenLamine et al.,2015 (from their Table 1a)
Ghar El Meh lagoon, Tunisia	Feb 2011 - Jan 2012	100 µm	1-2 m	27-51		(95000-390000)	O. nana, A. clausi, P. parvus, bivalve larvae, gastropod larvae, polychaet larvae	Ziadi et al., 2015
	oct-17	**60µm-200µm**	**8-10m**	**45-46**	**24600**	**(9600-50000)**	**Oithona nana, Acartia latisetosa, Euterpina acutifrons, Paracalanus parvus , gasteropod, bivalve, polychaete larvae**	**this study**
Boughrara lagoon, Tunisia	**Apr 2017**	**60µm-200µm**	**8-10m**	**42-43**	**7800**	**(1400-11300)**		
	Summer 1992	55µm	14m	40-51	44845		O. nana, Paracalanus parvus, Euterpina acutifrons,Centropages kroyeri, A. clausi, A. latisetosa, Clytemnestra rostrata,	Daly Yahia and BenRomdhane, 1994
	Automn 1992	55µm	14m		46552			
	Winter 1992-1993	55µm	14m		27224			
	Spring 1994	55µm	14m		28089			
Gulf of Gabés coastal (South), Tunisia	**October2017**	**60µm-200µm**	**8-12m**	**40-41**	**9974**	**(3600-20300)**	**Oithona nana, Acartia latisetosa, Euterpina acutifrons, Paracalanus parvus , gasteropod, bivalve, polychaete larvae**	**this study**
	April2017	**60µm-200µm**	**8-12m**	**38-41**	**3223**	**(2100-5600)**		
Gulf of Gabés coastal (North), Tunisia	March 2013	100µm	0.5-4m	37-40	10250	(1400-48000)	Oithona nana , Paracalanus parvus , Tisbe battagliai, Euterpina acutifrons, Oithona plumifera, Calanus helgolandicus Acartia latisetosa	Drira et al., 2017
Gulf of Gabès open sea, Tunisia	July 2005	100µm	<50m	37-38	7410	(1460-43000)	Acartia clausi, Oithona nana, Temora longicornis, Oithona helgolandica, Paracartia grani	Drira et al., 2010
			>50m	37-38	1372	(200-5500)		
Bardawil lagoon, Egypt	October 2002	20 µm	0.5-2m	40-63	122000	(66000-216000)	O. nana, Lucicutia flavicornis, Centropages calaninus, Clausocalanus furcatus, molluscs larvae	Mageed, 2006
Thau Lagoon, South France	March 1982-March 1983	150µm	1-11m	35-40		(11 - 20000)	Acartia clausi, A. discaudata, A. bifilosa, A. latisetosa, Oithona nana, Oithona helgolandica, Euterpina acutifrons, Paracalanus parvus, Centropages kroyeri	Lam Hoai, 1985
	2010-2011	80µm	4.8m	35-40		(99 -55826)		Marques et al., 2015
Berre Lagoon, France	2008-2010	80µm-700µm	1-9m	nov-36	42000	(8000-280000)	Acartia clausi, A. tonsa, Oithona nana, Centropages typicus, Paracalanus parvus, cirriped larvae	Delpy et al., 2012
Sacca Del Canarin, Po Delta, Italy	Aug 1981	90µm	1m	15-35	92000		Acartia clausi, Paracalanus parvus , Oithona nana, Euterpina acutifrons	Ferrari et al., 1985
Venice Lagoon (central part), Italy	1995	80µm	0.8-1.5m	5-37	18302,5	(2800-38000)	Oithona nana, Oncaea waldemari, Bivalvia larvae, Acartia tonsa, Euterpina acutifrons, Paracalanus parvus	Riccardi, 2010

Supplementary material

Table S1. Importance value indexes (IVI) for the taxa inventoried during the two COZOMED campaigns in October 2016 and April 2017 in the three zones and at st 8.

		October 2016					April 2017			
	Abrev.	Sea	Trans.	Lag.	Station8	Total	Sea	Trans.	Lag.	Total
Number of taxa		**66**	**81**	**67**	**21**	**93**	**53**	**57**	**39**	**68**
COPEPODA CALANOIDA										
Acartia clausi	**A. clausi**						33.4	103.2	34.0	73.4
Acartia latisetosa	**A. latis.**	83.3	103.8	101.5	272.3	104.8	124.2	118.8	122.4	115.4
Acartia sp.	**A. sp1.**						34.1	64.4	68.2	58.7
Aegistus spp.	**Ae. Spp.**	33.3	38.9	57.2	101.0	43.8	105.4	88.3	67.5	87.5
Other calanoids	**Oth. Cal.**	83.3	27.8	14.3		34.4		12.5	33.5	14.3
Calanopia minor	**Cp. minor**		5.6			3.1				
Calanopia sp.	**Cp. sp1**							12.5		7.2
Calanus helgolandicus	**Cal. Helgo.**		27.8	14.3		18.8	70.6	25.4		29.7
Calanus spp.	**Cal. Spp.**	100.0	101.9	100.8	100.6	103.0	69.8	62.6	67.3	65.2
Canuella sp.	**Canuella. sp.**		5.6			3.1				
Centropages ponticus	**Cen. Pont.**	33.3	72.6	101.5		69.3	101.6	106.7	112.9	107.0
Centropages spp.	**Cen. Spp.**	33.3	50.2	85.9		53.3	100.8	75.9	107.4	88.0
Centropages typicus	**Cen. typicus**	16.7	55.7	14.3		37.6				
Clausocalanus sp.	**Claus. sp.**	102.1	109.4	105.5		120.5	33.4	25.1		21.5
Ctenocalanus spp.	**Cten. spp.**						33.4	87.6		57.2
Heterhabdus sp.	**Heter. sp.**						100.8	12.5		28.7
Mecynocera	**Mecyno.**	83.3	96.0	72.3		86.2	33.4			7.1
Metridia Maetidea sp2.	**Metridia**	16.7	55.6			34.4				
Nannocalanus minor	**N. minor**	16.7				3.1				
Paracalanus indicus	**P. indicus**	50.0	61.5	71.6		59.7	100.5	25.0	33.3	43.0
Paracalanus parvus	**P. parvus**	100.0	106.6	102.8		103.1	107.5	100.7	100.2	102.0
Paracalanus sp.	**P. sp.**	16.7	61.4	71.5		53.3				
Phaenna sp.	**Phae. sp.**	16.7				3.1				
Phaeanna spinifera	**Phae. Spini.**	102.1	89.3	85.9	102.8	99.8	67.2	12.5		21.5
Platycopia pygmea	**P. pygmea.**		66.9	28.6		43.9				
Pontella mediterranea	**Pont. Med**	83.3	61.5			50.4				
Pseudodiaptomus sp.	**Pseudo. sp.**						33.4			7.1
Rhincalanus sp.	**Rhin. sp.**						33.4			7.2
Scolecitrix sp.	**Scolx. sp.**						100.5			21.5
Temora stylifera	**T. stylifera**						100.4			21.5
Tortanus sp.	**Tor. Sp.**						67.2	75.7	67.4	72.1
COPEPODA CYCLOPIDA										
Farranula spp.	**F. spp.**						100.3	25.0		35.8
Lubbokia acuelata	**L. acuelata**	16.7				3.1				
Oithona helgolandica	**O. helgo**	66.7	95.7	100.9		88.5				
Oithona nana	**O. nana**	102.1	118.4	124.5	101.3	167.4	111.8	115.5	108.5	112.7
Oithona plumifera	**O. plumif**		5.6	14.3		6.3	67.3	25.3		28.9
Oithona similis	**O. similis**	100.0	103.1	102.5		99.4	66.7	25.2	33.4	35.9
Oithona simplex	**O. simplex**							63.4	33.3	43.4
Oithona spp.	**O. spp.**	16.7	16.7			12.5	33.4	25.2	67.5	36.0
Oncaea borealis	**Onc. borealis**		5.6			3.1				
Oncaea mediterranea	**Onc. Med**		33.4	14.3		21.9				
Oncaea minuta	**Onc. minuta**	16.7				3.1				
Oncaea spp.	**Onc. spp.**		11.1			6.3	100.2		33.4	28.6
Sapphirina sp.	**Sap. sp**		11.2			6.3				
Saphirella sp.	**Sapl. sp.**	50.0	28.0	14.4		28.4				
COPEPODA HARPACTICOIDA										
Clymtenestra scutellata	**Clyt. Scut**	16.7		28.6	100.1	12.5	33.4	50.0	33.5	42.9
Clytemnestra sp.	**Clyt. Sp.**							25.1		14.4
Euterpina acutifrons	**E. acuti**	100.0	106.7	100.9	101.3	105.1	102.6	126.1	103.3	114.6
Euterpina sp.	**E. sp.**	16.7	11.1			9.4	33.4			7.1
Harpact sp.	**H.sp.**		33.4	71.5	100.7	37.5				
Harpacticoides spp.	**H. spp.**	100.0	106.2	107.5	107.9	111.6	102.7	102.0	35.1	87.8
Lubbockia sp.	**L. sp**	83.3	103.9	90.2		94.2				
Macrosetella spp.	**M. spp**	16.7	33.5	28.7		28.2				
Metis ignea	**M. ignea**		33.4	14.3		21.9				
Microsetella norvegia	**M. norvegia**	16.7	61.3	85.9	101.3	59.6				
Microsetella rosea	**M. rosea**		5.6			3.1				
Microsetella sp.	**M. sp.**							50.0	33.4	35.8
Tegastidae	**T. Tegastidae**		11.1			6.3				
Tisbe	**T. Tisbe**	16.7	44.7	28.6		34.5				
OTHER COPEPODA										
Cymbasoma rigidum(Monstril	**Cym. rigid.**		11.1			6.3				
Monstrilla clavata	**M. clavata**		16.7	28.6		15.6				
Monstrillia grandis	**M. grandis**						66.7	25.0		28.6
Caligidae	**C. Caligidae**							12.5	33.4	14.3
Other	**Other**	50.0	90.0	100.5		82.1				

Table S1. (follow)

		October 2016					April 2017			
	Abrev.	Sea	Trans.	Lag.	Station8	Total	Sea	Trans.	Lag.	Total
CRUSTACEAN										
Amphipode spp.	**A. spp.**		66.7	14.3		40.6	33.4	50.0	66.8	50.1
Cladocera sp.	**Clad. sp.**	66.7	27.8	14.3		31.3				
Evadne sp.	**E. sp.**		16.7	86.0	100.3	31.3				
Pseudoevadne tergestina	**P. tergestina**	66.7	55.6	86.2		62.7	0.0	12.5	0.0	7.2
Podon spp.	**P. spp.**	16.7	27.8	71.6		34.4	33.4	75.3	101.7	72.0
Conchoecia obstustata	**Con. obstustata**		55.9	100.9		53.5				
Cypridina globosa	**Cyp. globosa**		5.6			3.1				
Cypridina mediterranea	**Cyp. mediterranea**		5.6			3.1				
Cytheridea sp.	**Cyt. sp.**		11.4			6.4				
Ostracode spp.	**O. spp.**	33.3	44.5	42.9	100.1	43.8	33.6	87.8	66.7	71.6
Crustacean spp.	**C. spp.**		5.6			3.1				
Mysidacea	**M.**	83.3	44.7	71.5		56.4		25.1		14.3
GELATINOUS										
Appendicular	**App.**	16.7	11.1	14.3		12.5	34.2	12.6		14.5
Oikeuplora dioica	**Oik. dioica**	83.3	108.7	121.5	101.3	121.1	103.7	102.6	101.5	102.6
Oikopleura spp.	**Oik. Spp.**			85.7		18.8	101.2	87.9	66.9	86.3
Chaetognathes spp.	**Chae. spp.**	33.3	27.8	57.2		34.4				
Sagitta lyra gazellae	**S. gazellae**	16.7		71.6		18.8				
Sagitta setosa	**S. setosa**	100.0	66.9	72.0		72.1	67.3	100.1	33.3	78.8
Sagitta sp.	**S. sp.**	33.3	44.5	28.6		37.5				
Anthomedusa	**A. spp.**						33.4			7.1
Jellyfish medusa	**E. méduse**		66.8	57.2	100.1	53.2				
Clytia roliformis	**Abrev.**			14.3		3.1				
Leptomedusa spp.	**L. spp.**	16.7	5.6			6.3		12.5		7.2
Obelia sp.	**O. sp.**	16.7	22.2	71.5		31.3	100.5	12.5		28.7
Muggia kochi	**M. kochi**						66.8			14.3
Siphonophore spp.	**S. spp.**						67.0			14.4
MEROPLANKTON										
Ascidea larvea	**Asc. L.**		61.4	85.8	100.1	56.4		37.6	33.3	28.6
Balanus Nauplii	**Balanus**	66.7	95.8	101.6	102.2	91.9	33.4	75.5	67.2	64.7
Chthamalus Nauplii	**Chthamalus**	100.0	103.9	102.5	101.3	102.9		62.9	67.5	50.4
Bivalva larvae	**Biv. L.**	100.0	106.7	112.4	102.6	107.1	66.8	88.1	100.4	86.2
Crustacean larvea	**Crust. L.**	100.0	89.0	86.4	100.8	90.9		37.5		21.4
Lucifer	**Leu.**	100.0	44.5	14.3		47.2	33.4			7.1
Decapods larvae	**decap. L.**	100.0	44.6	71.5		60.2		12.5		7.2
zoe crab larvea	**Crab L.**	100.0	72.7	57.2		72.3	100.6	75.1	66.8	78.8
blue crab zoe larvea	**Blue crab L.**						66.8	62.5	33.4	57.2
Palaemon elegans Larvea	**P. elegans**	83.3	61.1	57.2		62.5				
Sicyonia carinata protozoe	**Sic. Prot.**	83.3	16.7			25.0				
Crustacean zoe	**Z. crus.**	50.0				9.4				
Nauplii sp.	**N. sp.**	33.3		14.3		9.4				
Gastropod larvae	**Gastero. L.**	100.1	108.7	112.7	101.3	114.1	141.7	119.0	157.9	125.2
Spider	**Spider**		16.7	28.6		15.6				
Actinotroc Larvae	***Actino. L.***							12.6	33.4	14.4
Argule	***Arg.***							25.0		14.3
ND larvae	***Larve ND***	33.3	61.4	85.8	100.4	62.7	33.4	37.5	33.3	35.7
Echinoderm larvae	***Echino. L.***	16.7				3.1				
Mollusc larvea	***Mollusc L.***	16.7	5.6			6.3				
Fish larvae	***F.L.***	16.7	33.4	42.9		31.3	33.4	87.5		57.2
Fish eggs	***F. eg.***	83.3	22.3	72.0		44.0	67.2	62.7	67.2	64.6
Diverse eggs	***Div. eg***	100.0	95.0	101.3		94.8	109.8	92.3	103.1	98.4
Polychet annelids larvae	***Polych. L.***	100.0	83.9	102.1		88.7	102.8	102.6	103.6	102.9
Polychet annelids eggs	***Polych. Eg.***	33.3				6.4				