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Spring distribution of shelled pteropods across the Mediterranean Sea

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Abstract

Shelled pteropods represent an excellent sentinel for indicating exposure to ocean acidification (OA). Here, for the first time, we characterise spring pteropod distribution throughout the Mediterranean Sea, a region that has been identified as a climate change hot-spot. The presence of a west-east natural biogeochemical gradient makes this region a natural laboratory to investigate how the variability in environmental parameters may affect pteropod distribution. Results show that pteropod abundance is significantly higher in the eastern Mediterranean Sea where there is a higher aragonite saturation state (Ωar), showing that distribution is positively correlated with Ωar. We also observed a resilience of pteropods to higher temperatures and low nutrient conditions, including phosphorous limitation. The higher abundance of pteropods in ultra-oligotrophic conditions (eastern Mediterranean Sea) suggests that this organism can play an important role as the prime calcifying zooplankton within specific oligotrophic regions.

1. Introduction

Thecosome pteropods are holoplanktic mollusks found in all major world oceans (Bednaršek et al., 2012). This organism plays an important role in the biogeochemical cycle (Manno et al., 2019) and in ocean food webs as bacterivores, (predominantly) herbivores, and as pray for higher trophic levels (Conley et al., 2018). Pteropods are very susceptible to changes in carbonate saturation state (Ω) due to their aragonite shell, which is a comparatively highly soluble form of calcium carbonate (Mucci et al., 1989), and they therefore represent an excellent sentinel for indicating the impacts of ocean acidification (OA) (Bednaršek et al., 2016; Manno et al., 2017).

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In the Mediterranean, pteropod species diversity, abundance and distribution are currently poorly documented. The studies that have incorporated information on pteropods in the Mediterranean Sea focus mostly on whole zooplankton communities, with data collected via different methods (i.e. net mesh sizes, collection depth) and in different regions (i.e. Ligurian, Tyrrhenian, Adriatic, Balearic, Ionian, Cretan and Levantine Seas) (Andersen, 2002; Andersen et al., 2004; Batistić et al., 2004; Fernández de Puelles et al., 2007; Mazzocchi et al., 1997). There are only two studies within the Mediterranean that focus solely on pteropod ecology (Howes et al., 2015; Manno et al., 2019) and both are limited to very restricted geographical regions. To our knowledge, there is no study on pteropod abundance and distribution across the Mediterranean Sea covering the whole basin and relatively large biogeochemical gradients. This is limiting our knowledge of this important calcifying zooplankton.

The Mediterranean Sea has been identified as a climate change hot-spot (Giorgi, 2006) that is particularly responsive and vulnerable to ecosystem changes (Lazzari et al., 2014). This region is undergoing rapid changes as a result of climatic and non-climatic forcing (Cramer et al., 2018) and is experiencing an increase in temperature that is exceeding global trends with a current (as of 2018) annual mean temperature of 1.4ºC above late-nineteenth-century level (Cramer et al., 2018). Sea temperatures are expected to rise by 1.5-2ºC by the end of this century, at a rate faster than the global average (Lazzari et al., 2014). Sea surface pH is predicted to decrease in line with the global average (approximately 0.3 to 0.4 units by 2100) (Flecha et al., 2015b; Geri et al., 2014; Kapsenberg et al., 2017) or even exceed the global average decrease (Hassoun et al., 2015). The impacts of climate change on marine systems will be diverse and complex, with predicted disruptions to population dynamics, geographical distributions and ecosystem functioning, as well as losses in biodiversity and species richness (Bulling et al., 2010; Harley et al., 2006; Lacoue-Labarthe et al., 2016). It is essential to improve our knowledge of key communities that are likely vulnerable to these changes in order to determine how organisms and communities will respond to ocean conditions under climate change.

The Mediterranean Sea has distinct biogeochemical regions that cross natural environmental gradients, with the shallow Strait of Sicily splitting the Mediterranean into east and west (Rohling et al., 2009). The eastern Mediterranean is characterised by higher temperatures and salinities than the western basin, which consists of Atlantic water entering from the Gibraltar

Strait that are modified moving eastward (Rohling et al., 2009). Surface-water circulation is mainly driven by thermohaline forcing as well as wind stress (Robinson and Golnaraghi, 1994). Using data collected from the MedSeA cruise (2013), the average Ωar (saturation state of aragonite) in the top 200m of the water column gradually increases from approximately 2.7 in the Atlantic to approximately 3.6 in the Eastern Mediterranean, meaning these waters are saturated with respect to aragonite. Phosphate and nitrate have higher concentrations in the west of the Mediterranean, with a sharp decrease moving to the east of Mediterranean, which is typified by phosphorus limitation and low concentrations of nitrate (oligotrophic system) (Krom et al., 1991). These stark changes in marine environmental parameters from west to east make the Mediterranean Sea a natural laboratory to investigate how the variability in environmental factor is affecting species distributions.

This study aims to investigate pteropod distribution across large spatial scales, such as the Mediterranean Sea, which has been identified as a gap within pteropod research, particularly in relation to understanding how these populations will respond to climate change (Bednaršek et al., 2016). In this region, the presence of a West-East natural environmental gradient enable us to investigate the interaction between pteropod distribution and environmental parameters during the spring season. We also present the relationship between pteropods and another major group of planktic marine calcifier, foraminifera (single-celled, calcareous zooplankton). Foraminifera were collected during the same research cruise campaign (Mallo et al., 2017) and are therefore directly comparable with this study on thecosome pteropods.

2. Materials and methods

Samples were collected from the Mediterranean Sea during the MedSeA (Mediterranean Sea Acidification in a Changing Climate) cruise from May 2nd to June 3rd, 2013 (Fig. 1) (Ziveri and Grelaud, 2015). The research cruise covered the majority of Mediterranean sub-basins, starting from the Atlantic Ocean crossing the western basin and moving through the Levantine Basin in the east, and then again starting from the north-eastern Ionian Sea, moving to the northern Algero–Provençal basin in the east (Fig. 1).

2.1 Hydrological and chemical collection analyses

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Temperature, salinity, oxygen and fluorescence were obtained from the correspondent conductivity-temperature-depth (CTD) stations using an ITS-90 and an oxygen sensor SBE 43 and considering the upper 200m towing depth. The overall accuracy for temperature is ± 0.001ºC and ± 0.0003 for salinity. To determine the seawater carbonate system, samples for total alkalinity (AT) and dissolved inorganic carbon (DIC) were collected from the top 200m of the water column (~5m, 10m, 20m, 40m, 50m and every 25m thereafter until 200m) (see Goyet et al. (2015). Methods for the analysis of water chemistry (total alkalinity and dissolved inorganic carbon) have been described in Gemayel et al. (2015; Hassoun et al., 2015). Ocean chemistry data were input into the program CO2sys to calculate pH, $p\mathrm{CO}_2$, aragonite saturation (Ωar) and $[\mathrm{CO}_3^{-2}]$ using the equilibrium constants of Mehrbach et al. (1973) refitted by Dickson and Millero (1987) . Photosynthetically active radiation (PAR) was measured at the beginning of each tow. Surface chlorophyll *a* concentration was obtained from MODIS Aqua L2 satellite data (NASA Goddard Space Flight Centre, 2013; Fig. 1). The nutrient concentrations (phosphate $[\mathrm{PO}_4]$ and nitrate $[\mathrm{NO}_3]$) were obtained using OGS (Italian National Institute of Oceanography and Experimental Geophysics) and analysed with a Bran+Luebbe3 AutoAnalyzer (see Grasshoff et al. 1999) and D'Amario et al. (2017) for a detailed methodology of the nutrient analysis).

2.2 Pteropod sample collection and analyses

Sampling for pteropods was conducted using BONGO nets (mesh size 150µm, 40cm diameter) from the surface to approximately 200m depth. A flow meter attached to the ring of the net was used to determine the volume filtered through the net. Please refer to Supplementary Table 1 for information pertaining to the date, time, location, environmental parameters and volume of water filtered in the plankton tow for each sampling station. From these tow samples, pteropod abundances were determined for each station. Samples were stored in 500ml polycarbonate bottles and kept at 4ºC in the dark. pH was measured in all the samples, at the beginning, during and the end of the storing period to ensure that the state of the pteropod shells were not affected by the preservation technique. Pteropod abundance was determined for each station and species were identified and counted using a Leica z16 APO binocular light microscope. Pteropod abundance within the water column was calculated as individuals per cubic meter (ind. m^{-3}). Pteropods were grouped into four target families: Heliconoididae, Limacinidae, Cavoliniidae and Cresedai; and further into seven target species: *Heliconoides inflata*, *Limacina trochiformis*, *Limacina bulimoides*, *Cavolina inflexa*, *Creseis acicula*,

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Creseis concia and *Styliola subula.* The online plankton portal (www.planktonportal.org) was used to aid in the identification of pteropods to species level.

2.3 Statistical methods

All environmental parameters used in the analyses were averaged from 5-200m depth. Using the environmental parameters (temperature, salinity, oxygen, fluorescence, NO_3, PO_4, pH, pCO_2, CO_3^{-2} and Ωar) a principle component analysis was conducted (PCA, varimax rotation). After an initial analysis, PAR was removed as it did not significantly contribute to the variation of environmental parameters. Based on the PCA results, a Kruskal-Wallis Test was used to determine any significant differences in total and individual species abundance between western stations (1-7a and 19-22) and eastern stations (9-'16-18'). A parsimonious canonical correspondence analysis (CCA) was used to determine the significant environmental parameters affecting pteropod species composition. Using Factor 1 and Factor 2 values from the PCA and the environmental parameters for each station, alpha values were obtained to conduct a binary logistic regression model (BLRM) which predicts the odds of having a low-density station (classified as stations with >1 ind. m^{-3} pteropod). Stations were binned according to the total density (13 high density stations, 7 low density stations) and were modelled against Factor 1 and 2, as well as each environmental variable. Pearson's correlation coefficients were calculated to determine if there were any significant relationships between the environmental parameters and total and individual species abundance. The CCA was analysed using R version 3.6.0 and all other statistical analyses were performed using IBM SPSS v23.

3. Results

The mean absolute abundance of pteropods collected in the Mediterranean Basin was 1.27 ± 1.62(SD) ind. m^{-3} (STable 2). The highest abundance was recorded in the Otranto Straight toward the southern end of the Adriatic Sea with 5.21 ind. per m^{-3} (STable 2, Fig. 2). There were no pteropods sampled in the Northern Alguero-Balear region (station 20), and the lowest mean standing stock was recorded at the Catalan-Balearic Station, off the coast of Spain (STable 2, Fig. 2). The eastern Mediterranean Sea had higher overall pteropod abundances with an average abundance of 2.13 ind. m^{-3}, which was approximately 5x greater than the average

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pteropod abundance in the western basin (0.42 ind. m^{-3}), where the lowest abundances were recorded.

A total of five different pteropod families and 11 species were identified. Limacinidae was the most abundant family (77.7%), which dominate the eastern part of the Mediterranean basin, followed by Creseidae (15.4%) and Cavolinidae (6.8%). *Heliconoides inflata* was the most abundant species in the Mediterranean (29.4%) and recorded at all stations, followed by *L. bulimoides* (23.8%) and *L. trochiformis* (23.2%). The three species in Limacinidae followed a similar distribution pattern with high abundances in the Ionian Sea and the Antikythera Strait and lower abundances to the south of the Balearic Sea. *Cavolina inflexa* (6.8%), *C. acicula* (7.7%) and *Creseis conica* (6.8%) all presented the highest abundance in the Eastern Ionian Sea while *S. subula* (0.68%) abundance was at a maximum in the east of Levantine basin (STable 2). Specimens within the target families that were unidentifiable to species level made up 1.4% of the total abundance.

3.1 Relationship with environmental parameters

The Kruskal-Wallis Test confirmed significantly greater total pteropod abundance and abundance of *H. inflata, L. trochiformis, L. bulimoides* and *C. inflexa* in eastern stations (STable 3). The results of the Pearson's Correlation show that total pteropod abundance over the whole Mediterranean Sea was positively correlated with Ωar, O_2, pH, salinity and temperature and negatively correlated with NO_4, PO_3 and pCO_2 (STable 3).

The PCA performed on the environmental parameters reveals separation between stations in the east and the west of the Mediterranean Basin (Fig. 3). The western basin is characterised by greater nutrient content, lower temperatures and salinities (Fig. 3). The eastern basin is characterised by ultra-oligotrophic conditions as well as higher temperatures, salinities and aragonite saturation (STable 1). Factor 1 and 2 together explain approximately 77.55% of the variation in the environmental parameters. Factor 1 explains approximately 58.08% of variation in environmental parameters. This factor exhibited positive loadings for temperature and O_2 (and to a lesser extent Ωar and salinity) and a negative loading for the nutrients PO_4 and NO_3 (and to a lesser extent fluorescence). Factor 2 explains approximately 19.47% of variation in environmental parameters. This factor is characterised by positive loadings for pH, salinity and Ωar, and a negative loading for pCO_2. Factor 2 is interpreted as the carbonate system in the Mediterranean Sea, with a higher pH and Ωar in the east compared to the west. Abundance scores for total pteropod and individual species counts were overlaid onto the PCA plot (Fig. 3 and SFig. 1). Stations in the eastern Mediterranean generally have a greater total abundance of pteropods and are more positively associated with Factor 1 and 2; namely, greater temperatures, salinities, pH levels, Ωar and O_2 (Fig. 3). In general, the western stations have a lower total abundance and are more positively associated with $p\mathrm{CO}_2$, nutrients and greater nutrient availability.

The parsimonious CCA reveals that temperature, pH, Ωar and salinity affect pteropod community composition in the Mediterranean and that species group by family, with species belonging to Limacinidae showing a positive relationship with pH, Ωar and salinity, and *H. inflata* showing a strong positive correlation with temperature (Fig. 3). Species in Creseidae also group together yet do not correlate positively with temperature, pH, Ωar and salinity (Fig. 3), reflecting the lower proportion of total abundance for this family in the east of the Mediterranean. *Cavolina inflexa* does not group with the other families, and the results do not indicate a positive correlation with any environmental factor.

The BLRM predicts (90% CI) that an increase in temperature and, to a much greater extent Ωar, will increase the odds of having a station with a total abundance >1 ind. m^{-3}. Increasing nitrate will reduce the odds of having a station with a total abundance >1 ind./m^{-3} (STable 3). These results are likely influenced by the higher abundance of family Limacinidae in the east of the Mediterranean Sea. The BLRM correlates well with the CCA results in that pteropod community composition is driven by a similar suite of environmental factors, namely Ωar, pH, salinity, and to a lesser extent, temperature.

4. Discussion

This study shows that springtime shelled pteropod distribution in the Mediterranean Sea is positively correlated with Ωar saturation across the whole basin. We also found that the variability in Ωar influences community composition and that changes to the level of Ωar is likely to cause changes to pteropod populations. These results are driven by the positive relationship of Ωar with the most abundant family Limacinidae (76.4% of total abundance) and suggest that overall, pteropod distribution is strongly dependent on Ωar distribution.

The energetic costs associated with calcification indicate that calcifying organisms will spend more energy on building their shells under low Ωar conditions (Waldbusser et al., 2015). A recent study found that under reduced Ωar (control - 2.8; reduced - 2.1 Ωar), calcification in *H. inflatus* decreased and metabolic rate increased (Moya et al., 2016), revealing that even in oversaturated conditions, variability in Ωar can generate stress. Small variations in over saturated aragonite conditions may incur an energetic cost (however small), which can result in variations in pteropod geographical distribution. Species distribution often reflects environments containing their optimal parameters in order to optimise energy expenditure (Parsons, 1990) and our results show that pteropods have a preference for areas with higher Ωar in which they will likely devote less energy to building their shell and be under less metabolic stress. A study in the Mediterranean at CO_2 vents in the Gulf of Naples investigated pteropod calcification and abundance along an Ωar gradient (1.9-2.7) (Manno et al., 2019). Similar to our study, there was a positive correlation of *Creseis conica* abundance with Ωar in oversaturated conditions. The focus of this paper however, was to a very small geographic region in the Tyrrhenian Sea and involved a non-static system (CO_2 vent), whereas in the present study, we utilised stronger gradients of multiple environmental parameters over a large geographic scale. The findings in our study indicate that springtime pteropod distribution in the Mediterranean is strongly dependent on Ωar distribution.

The Ωar in this study ranged from 2.68 in the west of the Mediterranean to 3.61 in the east (Fig. 4A). It is difficult to determine seasonal or inter-annual variability for Ωar within the Mediterranean, as studies on carbonate chemistry are either at a single time point over latitudinal gradients (Álvarez et al., 2014; Millero et al., 1979; Schneider et al., 2007) or a mid to long-term data series at a single coastal location (Ingrosso et al., 2016; Kapsenberg et al., 2017). In the case of the long-term data series by Ingrosso et al. (Ingrosso et al., 2016) in the Gulf of Trieste in the north Adriatic Sea and Kapsenberg et al. (Kapsenberg et al., 2017) in the Ligurian Sea, samples for Ωar analysis were collected from shallow coastal locations (~15m and ~75m respectively) and as such are not reflective of the open sea environments where sampling in our study was undertaken. Seasonal variation of Ωar in open ocean waters such as the North Atlantic (upper 50m and 100m depths; Ωar 0.4-0.6) (Kim et al., 2015) is likely more reflective of the seasonal fluctuations experienced in deeper Mediterranean waters, and as such, the seasonal variability in Ωar that pteropods are experiencing is not in the range of the geographical variability within the Mediterranean Sea (up 200m). As Ωar is the biggest driver of pteropod distribution, we suggest that the general population trend in this study will be

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maintained throughout the year, as the eastern Mediterranean will be consistently higher in Ωar and therefore more energetically favourable than the west in terms of calcification.

We found that to a lesser extent, temperature and NO_3 are also drivers of spring pteropod distribution within the Mediterranean sea, with increases in temperature and decreases in NO_3 predicted by the BLRM to slightly increase the odds of higher pteropod abundance. In the Mediterranean, sea surface temperatures vary by about 10°C over the year, with the north-western Mediterranean have a winter average around 10°C and a summer average of 21°C, while the south-eastern Mediterranean winter average is around 15°C and the summer around 26°C (Rohling et al., 2009) with a consistent west to east gradient (Fig. 4C). Most of the recorded temperatures in this study will be experienced at some point over the course of the year for all pteropod populations, except for the eastern Mediterranean during summer, which is warmer than the west year-round (Rohling et al., 2009). In light of the ongoing warming of the Mediterranean Sea, further studies should address the potential implication connected to the observed positive relationship between pteropod abundance and temperature.

For NO_3, there is a well-known east-west gradient of oligotrophy in the Mediterranean (Fig. 4B) that does not have much annual variability(Pasqueron de Fommervault et al., 2015). In our study, pteropod abundance was ~5x greater in the ultra-oligotrophic eastern Mediterranean. The negative correlation of pteropod abundance with favourable nutrient conditions (in particular nitrate) is unexpected, as pteropod global distribution has been previously correlated with high productivity and nutrient content (Bednaršek et al., 2012; Burridge et al., 2017). A study of pteropod distribution along a longitudinal gradient in the Atlantic Ocean (Burridge et al., 2017) found that areas with the highest biomass corresponded to areas with the highest concentrations of chlorophyll *a* (Huot et al., 2007). However, because in Burridge's study chlorophyll *a* was correlated with temperature, it is unclear which of the two variables was the main driver of pteropod distribution. As only two environmental parameters were investigated, Burridge's study is limited in its' ability to determine how other biologically relevant parameters for pteropods affect their distribution, such as Ωar. In the Atlantic Ocean over a range spanning more than the 45ºN to 45ºS in Burridge's study, the upper 200m is supersaturated with respect to aragonite (Jiang et al., 2015) and there is little variability in Ωar (Takahashi et al., 2014). If Ωar is a primary driver of pteropod distribution, as indicated by this study, when waters are supersaturated and there is little variability in Ωar, other factors such as temperature or nutrients may be secondary driving forces affecting pteropod abundance, as seen in Burridge's study. As we found that Ωar is the main driver of pteropod distribution in the Mediterranean, it is likely that the negative correlation with NO_3 is not directly causing a negative effect on pteropod abundance and distribution. Pteropod abundances are higher in the oligotrophic and highly aragonite-saturated eastern basin, resulting in a negative correlation with NO_3.

We are aware that this study is only a snapshot in time, which limits our ability to predict the distribution of pteropods within the Mediterranean over large temporal scales. However, this study represents the first description of pteropod distribution along the whole Mediterranean basin and their relation with relevant environmental parameters. On the basis of the observed correlation between pteropods and the natural geographical variability of Ωar, we suggest that future research should focus on long-term, Mediterranean-wide monitoring to detect potential changes of pteropod populations.

4.1 Pteropod and foraminifera interaction

Planktic foraminiferal abundance and distribution presented in Mallo et al. (2017) were compared to the pteropod data from this study. The tow samples from Mallo et al. (2017) were collected during the same cruise and within the same nets as the pteropods of the present study, allowing a direct comparison of the two groups of key planktic calcifiers.

Spring pteropod and foraminiferal abundances present an opposite pattern distribution between the west and east of the Mediterranean (Fig. 5). A clear difference in the composition of pteropod and foraminiferal communities is evident in the CCA (Fig. 4), showing foraminiferal communities are positively related to fluorescence and NO_3, and pteropod communities positively related to temperature, pH, salinity, O_2 and Ωar. Pteropod abundance is distinctly greater in the eastern ($\bar{x}$=2.13 ind. m^{-3}) Mediterranean than in the west ($\bar{x}$=0.47 ind. m^{-3}), while foraminifera populations are characterised by higher abundances in the west ($\bar{x}$=1.87 ind. 10 m^{-3}) than in the east ($\bar{x}$=0.96 ind. 10 m^{-3}) (Fig. 5). There was a significant correlation in abundance between western Mediterranean stations (r=.757*), but not the eastern stations. Although total abundance is distinctly greater for pteropod populations across the entire Mediterranean, abundance for both organisms follows a similar pattern in the western stations (Fig. 5).

Experimental evidence indicates that planktic foraminifera are vulnerable to OA conditions under which they experience reduced calcification and an increased metabolic rate (Davis et al., 2017; Lombard et al., 2010; Manno et al., 2012). Foraminiferal distribution and abundance appear to be driven more by nutrient levels than carbonate saturation levels, as suggested in Mallo et al. (2017). The skeleton of foraminifera is made of calcite, a less soluble form of calcium carbonate than aragonite (Mucci et al., 1989; Subhas et al., 2018). Both pteropods and foraminifera are sensitive to OA due to their carbonate skeletons, however it is likely that foraminifera are less sensitive to carbonate variability due to the lower solubility of their calcite skeleton compared with aragonite. Foraminifera have been shown to be nutrient limited (Gregg and Casey, 2007; Schiebel et al., 2004), and Mallo et al. (2017) suggested that the lower foraminiferal abundance in the eastern Mediterranean (ultra-oligotrophic sector) results from reduced reproduction due to limiting food resources.

Conversely, nutrients and food availability do not appear to be a limiting factor for pteropods and their abundance is ~5x higher in the oligotrophic sector of the Mediterranean than the west. The majority of pteropods belong to the Thecosome order and have a unique feeding method involving the production of a large mucous web that is suspended in the water column, which passively entraps organic particles and motile organisms, enabling them to filter water at high rates (Conley et al., 2018). To ingest the material collected by the mucous webs, they draw the webs into their mouth via ciliary action, a feeding method that may allow them to overcome low food condition due to their ability to capture and filter through relatively large amounts of organic matter (Hamner et al., 1975). In contrast to foraminifera, pteropods are also able to actively swim (Hamner et al., 1975; Lalli and Gilmer, 1989) and potentially search for more favourable food conditions. Further, the survival of pteropod *H. helicina* (Limacinadae family) does not appear to be affected when expose to prolonged starvation (7 days) (Busch et al., 2014). We suggest that, in the western Mediterranean, pteropods are more able to adapt to low food availability than foraminifera which may be due to a combination of both their feeding method and their ability to withstand starvation.

Thus the difference in the pattern of distribution between foraminifera and pteropods in the eastern Mediterranean may be due to the unfavourable oligotrophic conditions for foraminifera and that pteropods are more dependent upon higher Ωar than nutrient levels. In the west, with relatively higher concentrations of nutrients, Ωar is lower, accounting for the reduced abundance pteropods, with foraminiferal and pteropod abundance following the same pattern, as a secondary factor of importance for pteropods, namely nutrients, affects their distribution here. On the other hand, in the eastern oligotrophic conditions, pteropod abundance is distinctly greater than foraminifera, as it is more strongly driven by the higher Ωar saturation, and foraminiferal and pteropod abundance no longer follow the same pattern, as the region is very nutrient poor, negatively affecting foraminiferal abundance.

There have been only a handful of studies that investigate the relationship between pteropod and foraminiferal communities. A multi-decadal study of calcareous holo-zooplankton at two sites off the coast of Southern California and Central California (1951-2008) showed no relationship between foraminifera or pteropod abundances (Ohman et al., 2009), unlike our study. In the Gulf Stream, Sargasso Sea and the Gulf of Mexico, pteropod and foraminifera densities followed a similar pattern, with density decreasing closer to oligotrophic conditions (Casey et al., 1979). In Schiebel et al. (2001), foraminifera and pteropod production in the North Atlantic was positively correlated with chlorophyll-*a*. The correlation of abundance for pteropods and foraminifera with nutrients in Casey et al. (1979) and Schiebel et al. (2001) are similar to the findings for the west of the Mediterranean in our study. These studies did not incorporate the carbonate system and our study is the first to utilise a complete spectrum of environmental parameters to investigate the relationship between pteropods and foraminifera.

5. Conclusions

The relationship of shelled Mediterranean pteropods to the natural variability in Ωar adds to the growing body of support for using pteropods as a bioindicator of changes in ocean carbonate chemistry (Bednaršek et al., 2019; Manno et al., 2017). Overall, we suggest that the higher abundance of pteropods in the eastern than the western Mediterranean sea is a combination of higher Ωar that is energetically favourable for calcification and their unique method of feeding and/or ability to withstand starvation, allowing them to fill the ecological role in the east of the Mediterranean as the prime calcifying zooplankton. With the increase in OA, the positive correlation between Ωar and pteropod distribution stresses the need for regular, long-term monitoring of pteropod populations throughout the entire Mediterranean Sea. This study provides new insight into the ecology of shelled pteropods and foraminifera and highlights that, in specific oligotrophic regions, ecological competition could also play an important role in regulating the pelagic calcifier zooplankton communities.

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Figure Legends

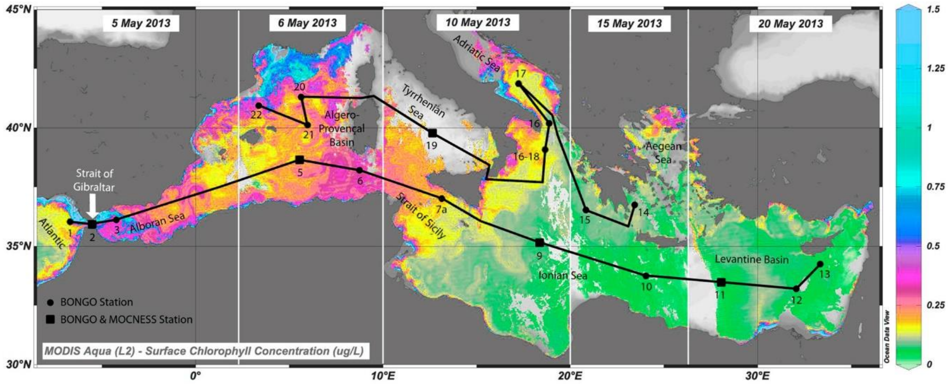

Figure 1. The sampled stations with BONGO nets are indicated by dots. The numbers in the picture represent the station codes: First leg: 1 to 13, second leg: 14 to 22. The colour scale represents the values of surface chlorophyll concentration (in µg/l), retrieved from *MODIS Aqua (L2)*, from the closest day to the start of the first transect. Figure made using Ocean Data View. Also in Mallo et al. (2017).

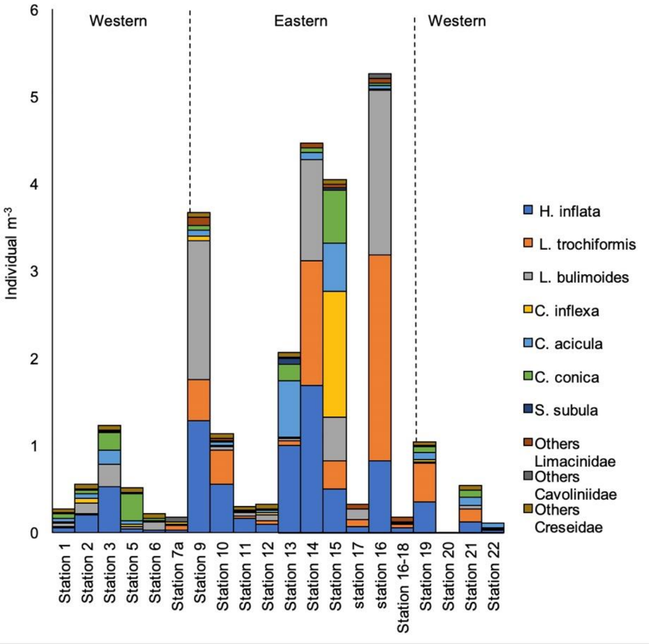

Figure 2. Absolute abundance of planktic pteropods from stations 1-22 on the MedSeA cruise. The category of 'Others' for each family includes specimens that were not a target species in this study or that were unidentifiable to the species level.

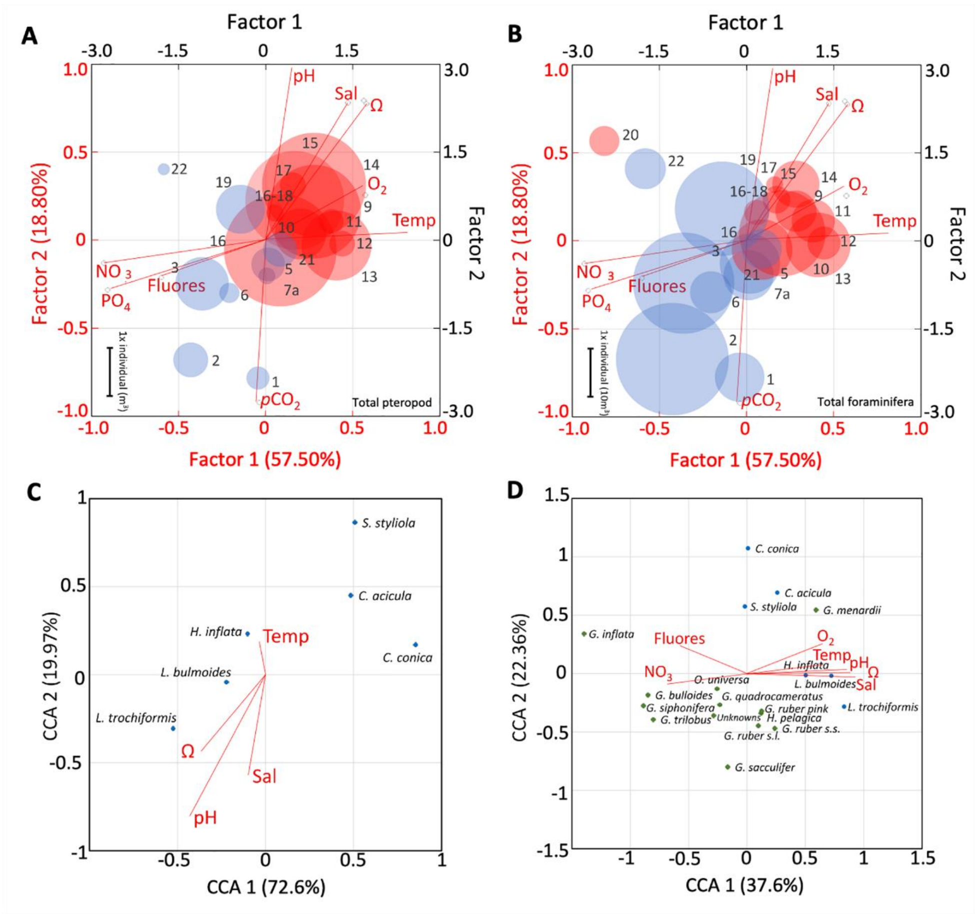

Figure 3. PCA graphs of environmental factors overlaid with absolute abundance values on station scores of **A** pteropods at all stations (ind. per m^{-3}) and **B** foraminifera at all stations (ind. per 10m^{-3}). The red axes are associated with PCA coordinates and the black axes are associated with the station coordinates. CCA graphs indicating **C** pteropod community composition and **D** pteropod (blue dots) and foraminifera (green dots) community composition. Family Cavoliniidae (*Cavolinia inflexa*) is not indicated on the graph as they were not related to any environmental factor or species groupings. Coordinates for *C. inflexa* in **C** (1.55, 0.59) and **D** (0.63, 2.33).

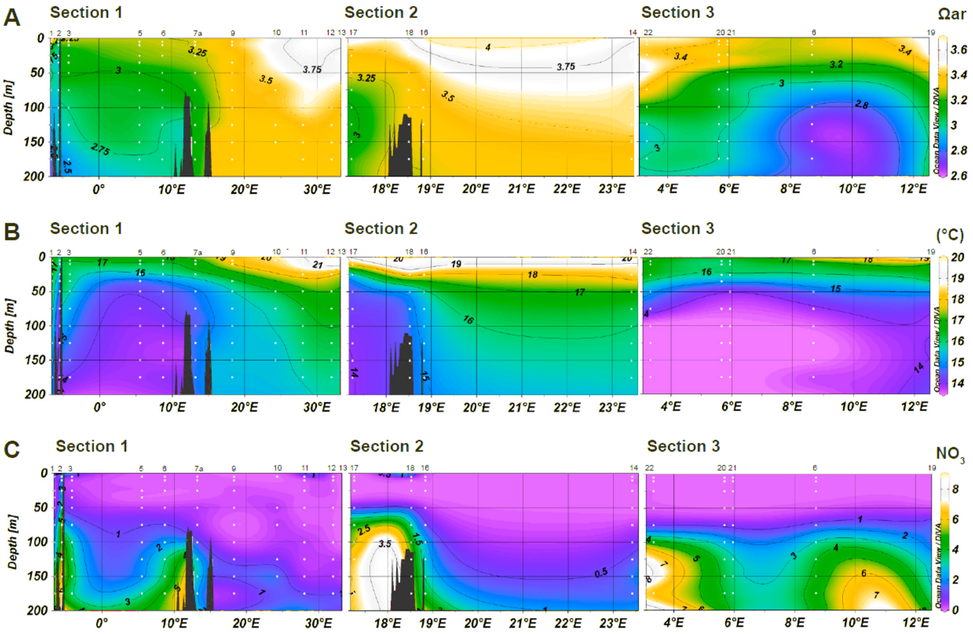

Figure 4. Depth profiles from 0-200 m depth highlighting the gradients of **A** Aragonite saturation (Ωar) **B** Nitrate (NO_3) and **C** Temperature (C^o) from the west to the east of the Mediterranean Basin (Section 1), within the Adriatic Sea (Section 2) and in the North-Eastern Mediterranean (Section 3) for factors affecting abundance and the community composition of pteropods. Figures made using Ocean Data View.

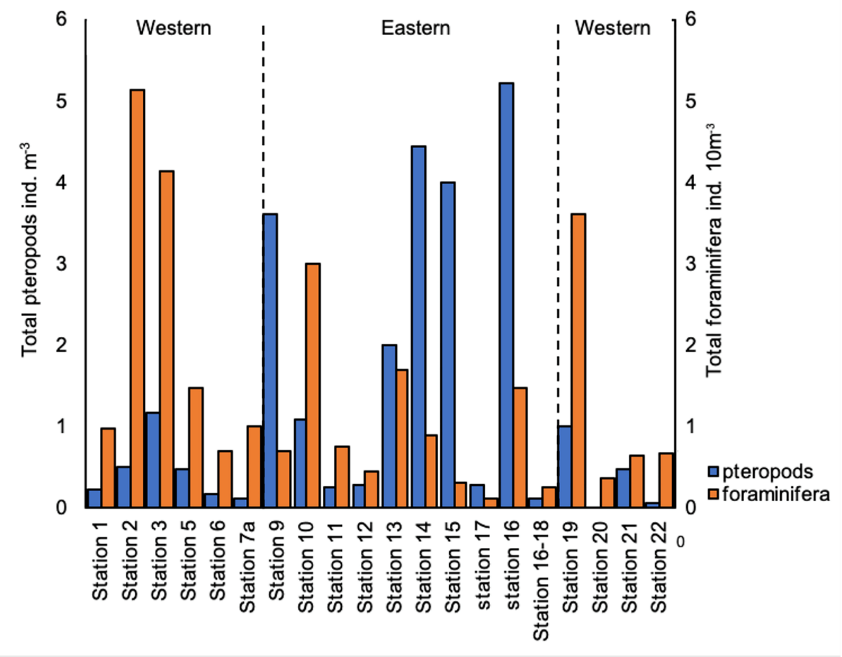

Figure 5. A comparison of absolute total abundance for pteropods and foraminifera at each station. Note that the scale of foraminifera abundance is distinctly lower than pteropod abundance (ind. 10 m^{-3} and ind. m^{-3} respectively), however this graph serves to illustrate similarities and differences in patterns of abundance.