



# Shelled pteropod abundance and distribution across the Mediterranean Sea during spring

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## ABSTRACT

Thecosome pteropods are a dominant group of calcifying pelagic molluscs and an important component of the food web. In this study, we characterise spring pteropod distribution throughout the Mediterranean Sea, an understudied region for this common group of marine calcifying organisms. This semi-enclosed sea is rapidly changing under climatic and anthropogenic forcings. The presence of surface water biogeochemical gradients from the Atlantic Ocean/Gibraltar Strait to the Eastern Mediterranean Sea allowed us to investigate pteropod distribution and their ecological preferences. In the ultra-oligotrophic Eastern Mediterranean Sea, we found the mean upper 200 m pteropod standing stock of 2.13 ind. m<sup>-3</sup> was approximately 5x greater than the Western basin (mean 0.42 ind. m<sup>-3</sup>). Where standing stocks were high, pteropods appeared largely in the same family grouping belonging to Limacinidae. Temperature, O<sub>2</sub> concentration, salinity, and aragonite saturation ( $\Omega_{ar}$ ) explain 96 % of the observed variations in the community structure at the time of sampling, suggesting that pteropods might show a preference for environmental conditions with a lower energetic physiological demand. We also document that pteropods and planktonic foraminifera have an opposite geographical distribution in the Mediterranean Sea. Our findings indicate that in specific pelagic ultra-oligotrophic conditions, such as the Eastern Mediterranean Sea, different feeding strategies could play an important role in regulating calcifying zooplankton distribution.

## 1. Introduction

The Mediterranean region is undergoing rapid changes as a result of climatic and non-climatic forcings (Cramer et al., 2018; MedECC, 2020) and is experiencing warming at a rate that exceeds global trends, with atmospheric temperatures rising as much as 20 % faster than the global average (Lazzari et al., 2013; Lionello and Scarascia, 2018). Sea surface pH is projected to decrease in line with the global average (approximately 0.3 to 0.4 units by 2100) (Flecha et al., 2015; Geri et al., 2014; Kapsenberg et al., 2017), or to exceed the global rate of decline (Hassoun et al., 2022; Gemayel et al., 2015). Within this scenario, it is essential to improve our knowledge of how Mediterranean marine ecosystems might respond to ocean conditions under climate change and ocean acidification.

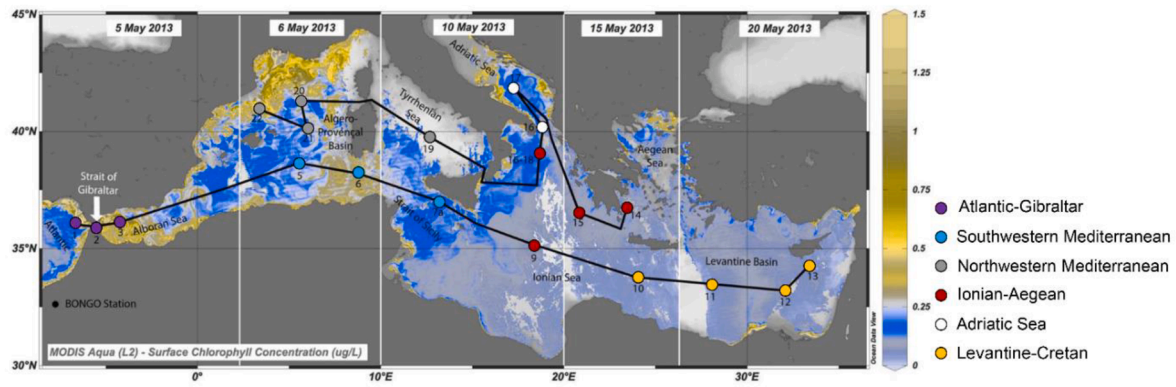
Ocean acidification is a direct consequence of the surface ocean uptake of carbon dioxide from the atmosphere, resulting in a reduction of seawater pH, carbonate ion concentrations, and carbonate saturation

state (Caldeira and Wickett, 2003; Gattuso et al., 2015). Calcifying zooplankton, such as pteropods and foraminifera, are sensitive to changes in seawater carbonate chemistry as they biomineralise their CaCO<sub>3</sub> exoskeleton (Bednaršek et al., 2019, 2016; Davis et al., 2017; Kuroyanagi et al., 2021). Pteropods in particular are known for their sensitivity to ocean acidification (e.g. Bednaršek et al., 2019; Bednaršek et al., 2016; Comeau et al., 2012a; Lischka et al., 2011; Maas et al., 2017; Manno et al., 2012), mainly due to their aragonite shell, which is a more soluble form of calcium carbonate compared to other mineral forms such as calcite (Mucci et al., 1989). As there are notorious difficulties associated with maintaining pteropods in captivity through a full life cycle (Howes et al., 2014; Thabet et al., 2015), field observations are fundamental to improve the current knowledge on their vulnerability to climate change and to provide key data on their ecological preferences.

Thecosome pteropods are shelled holoplanktic molluscs found in all major world oceans (Lalli and Gilmer, 1989; Peijnenburg et al., 2020). These pelagic snails are passive feeders, utilising large mucous webs to

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**Fig. 1.** Location map of sampled stations are indicated by dots. The numbers represent the station codes. Research cruise Leg 1: stations 1 to 13, Leg 2: stations 14 to 22. The colour scale corresponds to the satellite-derived surface chlorophyll *a* concentration (in  $\mu\text{g/L}$ ), retrieved from MODIS Aqua (L2) (NASA OB.DAAC, 2018), closest day to the start of each new sector, as indicated by each date. Stations: 1 – Atlantic; 2 – Strait of Gibraltar; 3 – Alboran Sea; 5 – Southern Alguero-Balea; 6 – Strait of Sardinia; 7a – Strait of Sicily; 9 – Ionian Sea; 10 – Southern Crete; 11 – Eastern basin; 12 – Nile Delta; 13 – Lebanon; 14 – Antikythera Strait; 15 – Eastern Ionian Sea; 16 – Otranto Strait; 17 – Adriatic Sea; “16–18” – Between Otranto Strait and Central Ionian; 19 – Tyrrhenian Sea; 20 – Northern Alguero-Balea; 21 – Central Alguero-Balea; 22 – Catalano-Balea (Ocean Data View - odv.awi.de; Schlitzer, 2021). Coloured points at each station correspond to different biogeochemical regions (Reygondeau et al., 2017).

collect food particles (Lalli and Gilmer, 1989). Pteropods play an important role in both the trophic system and biogeochemical cycling (Bednaršek et al., 2012b; Buitenhuis et al., 2019; Manno et al., 2010, 2019), linking phytoplankton and larger pelagic predators, such as carnivorous zooplankton, cephalopods (Fabry, 1989; Lalli and Gilmer, 1989), fish (Armstrong et al., 2008; Sturdevant et al., 2012), marine birds (Karnovsky et al., 2008) as well as other gymnosomes (Seibel and Dierssen, 2003).

Pteropods make up 1–6.6 % of the total zooplankton community in the Mediterranean Sea (Fernández de Puelles et al., 2007; Granata et al., 2020; Mazzocchi et al., 2011), yet there are few studies within this region that focus solely on detailed pteropod community distribution (e.g. Howes, 2015; Manno et al., 2019) and those that do are limited to restricted geographical and/or coastal regions. Further, many published studies addressing the entire zooplankton community (Batistić et al., 2004; Fernández de Puelles et al., 2007; Mazzocchi et al., 2011), or those that include both pteropods and other non-calcifying taxa (Andersen et al., 1998; Tarling et al., 2001), focus on the direct comparison of few target pteropod species only, and do not include seawater carbonate chemistry data. The thesis manuscript of Rampal (1975) was the first study investigating pteropod distribution and ecology across the Mediterranean Sea, combining samples collected with different methods and within different seasons and regions. More recently, Bednaršek et al., 2012b; Buitenhuis et al., 2013, and Buitenhuis et al. (2019) estimated the global distribution of pteropods and their importance as  $\text{CaCO}_3$  producers by merging a large number of existing and diverse datasets collected globally, as well as in several Mediterranean regions (Bednaršek et al., 2012b). To our knowledge, there is no published peer reviewed study on pteropod abundance and distribution across the whole Mediterranean basin, covering relatively large biogeochemical gradients and using a consistent sampling and processing methodology.

We explore shelled pteropod ecological preferences by investigating their distribution across the Mediterranean Sea at a large spatial scale, spanning the east–west environmental gradient from the Atlantic surface water influx in the Gibraltar Strait, to the Levantine basin in the Eastern Mediterranean Sea, and to the North Western Mediterranean Sea during the spring season. We also compare our results with a previous study by Mallo et al. (2017) which presented the distribution of planktic foraminifera collected during the same research cruise and in the same sampling nets as the pteropods of this study. Planktic foraminifera are calcifying single-celled protists with a calcite shell, and together with shelled pteropods, constitute the main marine calcifying zooplankton groups. They generally reside in the upper 100 m of the water column

(Lessa et al., 2020) and feed on bacteria, phytoplankton, and small zooplankton using their many, thin pseudopodia which extend out from apertures in their test (Anderson et al., 1979). Investigating the relationship between pteropods and foraminifera is important as the forecasted change in carbonate chemistry, due to increasing surface ocean uptake of atmospheric  $\text{CO}_2$  and ocean acidification, has been shown to trigger ecosystem shifts due to altered competition between calcareous species (Kroeker et al., 2013). The direct comparison of these two major groups of calcifying zooplankton allows us to improve our understanding of their ecological niches and their sensitivities to environmental change.

## 2. Materials and methods

Samples were collected from the Mediterranean Sea during the MedSeA research cruise on R/V Angeles Alvariño from May 2nd to June 3rd, 2013 (Fig. 1; Ziveri and Grelaud, 2015). The sampling covered the majority of the Mediterranean Sea sub-basins (Fig. 1) and was part of the European project “Mediterranean Sea Acidification in a changing climate - MedSeA”. The main aim of the research cruise was to characterise the Mediterranean Sea biogeochemistry at the basin scale, focusing on the marine  $\text{CaCO}_3$  system, and to investigate target calcifying organisms due to their known vulnerability to increasing  $\text{CO}_2$  conditions (Busch et al., 2014; Fox et al., 2020; Goyet et al., 2015; Kroeker et al., 2013; Ziveri and Grelaud, 2015).

### 2.1. Study region

The Mediterranean Sea has distinct biogeochemical regions (Reygondeau et al., 2017), with the sill system of the Strait of Sicily connecting the Eastern and Western sub-basins (Rohling et al., 2009). It’s anti-estuarine circulation is characterised by surface Atlantic waters entering the Western basin through the Strait of Gibraltar, and by a net evaporation, that results in eastward increases in sea surface temperature, salinity, and alkalinity (Fedele et al., 2022; Rohling et al., 2009; Schneider et al., 2007). In general, the Western basin has higher concentrations and production of surface phosphate and nitrate compared to the Eastern basin. The Eastern basin is characterised by ultra-oligotrophic surface water conditions, including phosphorus limitation (Krom et al., 1991) and deep chlorophyll maxima. The Atlantic-Gibraltar region connects the Mediterranean Sea with the Atlantic Ocean through the Strait of Gibraltar (Fig. 1), which is comprised of cooler, less saline waters and relatively higher levels of chlorophyll *a*

**Table 1**  
An overview of published pteropod studies in the Mediterranean Sea.

Region of Collection	Min-max conc. of pteropods community (ind. m <sup>-2</sup> or m <sup>-3</sup> )	x conc. (ind. m <sup>-2</sup> or m <sup>-3</sup> )	Period of sampling	Sampling depth (m)	Water column depth (m)	Most abundant species/taxa	Net/mesh size	Reference
Ligurian and Tyrrhenian Seas (NW Mediterranean)	Ind. m <sup>-2</sup> Study focuses on <i>C. inflexa</i> , <i>C. pyramidata</i> and <i>S. subula</i> . Min-max not provided	Ind. m <sup>-2</sup> Day: <i>Cavolina inflexa</i> : 4.0 ± 3.1 <i>Clio pyramidata</i> : 2.1 ± 2.6 <i>Styliola subula</i> : 0.3 ± 0.8 Night: <i>Cavolina inflexa</i> : 1.7 ± 2.7 <i>Clio pyramidata</i> : 1.6 ± 0.9 <i>Styliola subula</i> : 0.4 ± 1.5	April 1994	Various 0–350 0–450 0–550 0–700 Oblique haul	Various 700–2700	<i>Cavolina inflexa</i>	BIONESS 1 m <sup>2</sup> mouth 500 µm mesh	Andersen et al., 1998
Southern Adriatic	Ind. m <sup>-2</sup> Min: 1 Max: 2412 (0–50 m)	Not provided	April 1993 September November February June 1994	0–50 50–100 100–200 200–300 300–400 400–600 600–1000 Vertical haul	1242	<i>Heliconoides inflatus</i>	Nansen opening-closing net 113 cm diameter 380 cm length 250 µm mesh	Batistić et al., 2004
Balearic Sea	Ind. m <sup>-3</sup> Only monthly × provided. Min: 4 ± 6 Max: 11 ± 6 Not provided	Ind. m <sup>-3</sup> 5.9	1994–2003 (all year round)	75 Oblique haul	Various 78–200	<i>Creseis acicula</i>	Bongo-20 Plankton net 100 µm and 120 µm meshes	Fernández de Puelles et al., 2007
Ligurian Sea	Ind. m <sup>-2</sup> Day: <i>C. inflexa</i> : 41.2 <i>C. pyramidata</i> : 9 <i>H. inflatus</i> : 340 Night: <i>C. inflexa</i> : 31.5 <i>C. pyramidata</i> : 1.4 <i>H. inflatus</i> : 9.6	Ind. m <sup>-2</sup> Day: <i>C. inflexa</i> : 41.2 <i>C. pyramidata</i> : 9 <i>H. inflatus</i> : 340 Night: <i>C. inflexa</i> : 31.5 <i>C. pyramidata</i> : 1.4 <i>H. inflatus</i> : 9.6	April-May 2013	0–60 60–100 100–600 600–1300 Oblique haul	Various 1400–1639	<i>Heliconoides inflatus</i>	BIONESS multinet 1 m <sup>2</sup> mouth 230 µm mesh	Granata et al., 2020
NW Ligurian Sea	Ind. m <sup>-3</sup> Creseidae: ~630 Cavoliniidae: ~790 Limacinidae (incl. <i>H. inflatus</i> ): max 60.8	Ind. m <sup>-3</sup> Creseidae: 15.7 Cavoliniidae: 13.8 Limacinidae: 5.5	1967–2003 (all year round)	0–75 Vertical haul	~80	Creseidae	Juday Bogorov net 330 µm mesh 50 cm diameter	Howes et al. (2015)
Tyrrhenian Sea	Ind. m <sup>-3</sup> Min: 0.00 Max: 4.02	Ind. m <sup>-3</sup> <i>C. acicula</i> : 1.48 <i>C. conica</i> : 1.11 <i>H. inflatus</i> : 1.03 <i>L. trochiformis</i> : 0.64 <i>L. bulimoides</i> : 0.33	August 2015	Various 0–65 to 0–170	Various (73–185)	<i>Creseis acicula</i>	Bongo-40 200 µm mesh	(Manno et al., 2019)
Eastern Mediterranean	Ind. m <sup>-3</sup> Sicilian Channel: Max. 120 ind. m <sup>-3</sup>	Not provided	October - November 1991	0–50 50–100 100–200 200–300 Vertical haul	Various: 449–4359	N/A	WP-3 net 113 cm diameter 200 µm mesh	Mazzocchi et al., 1997
Ligurian Sea	Ind. m <sup>-3</sup> Study focuses solely on <i>Cavolina inflexa</i> Max: x 1.64 (0–200 m)	Not provided	September 1997	0–25 25–50 50–75 75–100 100–125 125–150 150–200 Oblique haul	Not provided	<i>Cavolina inflexa</i>	MOCNESS 1 m <sup>2</sup> mouth 300 µm and 2000 µm meshes	Tarling et al., 2001

due to the influx of water from the Atlantic and Alboran gyre dynamics (Oguz et al., 2014). The northwest Mediterranean region combines the Central and Northern Alguero-Balear basin and Tyrrhenian Sea, and is comprised of warmer and more saline modified Atlantic surface waters compared to the Atlantic-Gibraltar region. The southwest Mediterranean, made up of the Southern Alguero-Balear basin and the shallow Strait of Sicily, is comprised of modified Atlantic surface water moving eastward along the weakening Algerian current (Rohling et al., 2009), resulting in a lower chlorophyll *a* content than other regions in the Western basin, as well as warmer and more saline waters. The Ionian-Adriatic waters in the Eastern Mediterranean basin are 3–4 °C warmer here than the southwest Mediterranean and are distinctly ultra-oligotrophic. The eastern Mediterranean regions, including the Levantine and Cretan basins, remain ultra-oligotrophic throughout, with waters gradually increasing in temperature and salinity moving further east. The Adriatic Sea stands apart and is characterized by cooler surface waters than the southern Mediterranean Sea and has a higher chlorophyll *a* content. It is connected to the eastern Mediterranean through the Strait of Otranto into the Ionian Sea.

## 2.2. Hydrological and chemical collection analyses

Temperature, salinity, oxygen and fluorescence (proxy for phytoplankton biomass and therefore food availability) for the upper 200 m of the plankton tow stations were obtained from the corresponding conductivity-temperature-depth (CTD) stations using an ITS-90 and an oxygen sensor SBE 43. The overall accuracy for temperature was  $\pm 0.001$  °C and  $\pm 0.0003$  for salinity. Oxygen concentrations were measured using Winkler iodometric titration (Hansen, 1999) with a Mettler-Toledo with a Platinum ring redox electrode, with an overall accuracy of  $\pm 1.5$   $\mu\text{mol kg}^{-1}$ . Samples for phosphate ( $\text{PO}_4$ ) and nitrate ( $\text{NO}_3$ ) were filtered using a Whatman glass fibre filter (0.7  $\mu\text{m}$ ) after collection, then stored at  $-20$  °C. The final nutrient concentrations were obtained using a Bran + Luebbe3 AutoAnalyzer (detection limits were 0.01 and 0.02  $\mu\text{M}$  for  $\text{PO}_4$  and  $\text{NO}_3$  respectively; see Grasshoff and Kremling, 1999; D'Amario et al., 2017 for a detailed methodology of the nutrient analysis). Methods for the analysis of water chemistry (based on collected samples for total alkalinity and dissolved inorganic carbon) have been described in Goyet et al. (2015) and Gemayel et al. (2015). Ocean chemistry data were input into the software CO2sys v2.1 (van Heuven et al., 2009) for carbonate system calculation of  $\text{pH}_{\text{Total}}$ , aragonite saturation ( $\Omega_{\text{ar}}$ ) and  $[\text{CO}_3^{2-}]$  using dissolved inorganic carbon (DIC) and total alkalinity (TA) and applying the equilibrium constants of Mehrbach et al. (1973) refitted by Dickson and Millero (1987). Satellite-derived surface chlorophyll *a* concentration during the sampling period was obtained from Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua L2. We used these data to illustrate the Mediterranean-wide surface distribution of primary production (NASA OB.DAAC, 2018; Fig. 1).

## 2.3. Pteropod sample collection and analyses

Oblique plankton tow sampling for this pteropod study was conducted using BONGO nets (mesh size 150  $\mu\text{m}$ , 40 cm diameter), integrating the upper 200 m water depth. The net mesh size in this study targets the majority of the pteropod community in the upper 200 m of the water column (Bednarssek et al., 2012b), including different life stages (Howes et al., 2014) and therefore allowed for the quantification of most of the pteropod community standing stock. Based on a study investigating the global distribution of pteropods, which utilised a very large dataset (25939 data points) that included 41 scientific studies (Bednarssek et al., 2012a), it was found that most of the species live in the photic zone. In the Mediterranean Sea specifically, Bednarssek et al. (2012b) showed that pteropod abundance from depths deeper than 200 m is one order of magnitude lower (mean  $0.07 \pm 0.89$  ind.  $\text{m}^{-3}$ ) compared to the upper 200 m community (mean  $0.98 \pm 2.77$  ind.  $\text{m}^{-3}$ ).

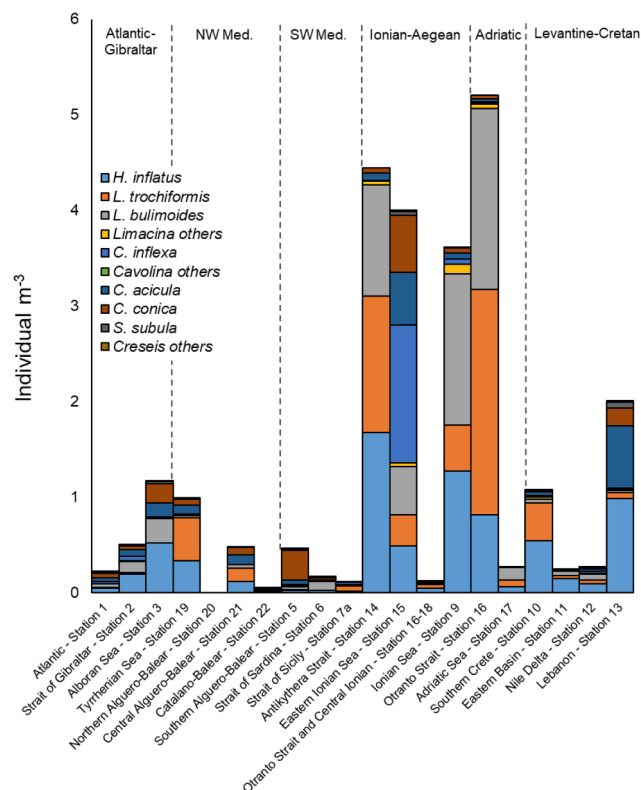


Fig. 2. Pteropod standing stocks from stations 1–22 from the western to the eastern Mediterranean Sea. Stations are organized according to their respective biogeochemical region: Atlantic Gibraltar; North-western Mediterranean; South-western Mediterranean; Ionian-Aegean; Adriatic; Levantine-Cretan.

Using the dataset in Bednarssek et al. (2012b), we calculated that our sampling allows us to characterise approximately 93 % of the total pteropod abundance (Supplementary Table 1 and Supplementary Fig. 1). However, a small number of species with deeper distribution might be underestimated in this study and this limitation is considered (see below).

The plankton towing was performed while the vessel was moving at approximately 1 nautical knot. A flow meter attached to the ring of the net was used to determine the volume filtered through the net. Please refer to Appendix Table 1 for information pertaining to the date, time, location, environmental parameters and water volume per plankton sample. From these samples, pteropod standing stocks were determined for each station. Plankton samples were preserved on board in a 4 % formaldehyde solution that was buffered with hexamethylenetetramine at pH 8.2 and were stored in 500 ml polycarbonate bottles at 4 °C in the dark. The pH of all samples was measured at the beginning, middle, and end of the storing period to ensure that the state of the pteropod shells were not affected by the preservation technique. The samples were processed within one month of collection. Pteropod standing stocks were determined for each station and species were identified and counted using a Leica z16 APO binocular light microscope. Standing stocks were calculated as absolute abundance (ind.  $\text{m}^{-3}$ ) and integrated abundance 0–200 m (ind.  $\text{m}^2$ ; Table A2). Here, findings are reported as ind.  $\text{m}^{-3}$  (unless for the purpose of comparison with other studies). We identified four target families (Limaciniidae, Heliconoididae [both in the limacinid super family Limacinoidea] and Creseidae) and seven species (*Heliconoides inflatus*, *Limacina trochiformis*, *Limacina bulimoides*, *Cavolina inflexa*, *Creseis acicula*, *Creseis conica* and *Styliola subula*). The online plankton portal (<https://www.planktonportal.org>) was used to aid in the identification of pteropods to species level.

*Limacina bulimoides*, *L. trochiformis*, *C. acicula* and *C. conica* are classified as surface and subsurface species (Rampal, 1975). *Heliconoides*



*inflatus* and *S. subula* can be found at depths larger than 200 m and are classified as mesopelagic by Rampal (1975), however recent studies show that *H. inflatus* primarily occurs in the upper water column (Batistić et al., 2004; Granata et al., 2020; Juranek et al., 2003; Schiebel et al., 2002) while *S. subula* is more abundant below 150 m (Andersen et al., 1998). *Cavolina inflexa* is classified by Rampal (1975) as a bathypelagic species with a distribution extending below 1000 m, and this preference for deeper water has been corroborated by more recent studies in the Ligurian Sea (Granata et al., 2020; Sardou et al., 1996; Tarling et al., 2001). Due to the strong diel and seasonal variations in the depth distribution habitat of some species (Andersen et al., 1998; Rampal, 1975; Tarling et al., 2001), we do not incorporate *S. subula* and *C. inflexa* into our statistical analyses of species distribution to discuss their ecological preferences. This conservative methodological approach is to prevent any artefact related to species depth preferences versus sampling depth.

## 2.4. Statistical methods

*Heliconoides inflatus*, *L. trochiformis*, *L. bulimoides*, *C. acicula* and *C. conica* were investigated in relation to the environmental conditions at the time of sampling. All environmental parameters used in the analyses were averaged from 5 to 200 m. A parsimonious Canonical Correspondence Analysis (CCA) was used to explore the species environmental preferences using the standing stock data. It should be noted that due to the high collinearity among several environmental variables (Supplementary Fig. 2), the variability of the coefficients could be overestimated (Alves et al., 2017). However, to prevent bias to individual parameters, we have included all parameters in the statistical analysis to widen our power of explanation and to provide as much information as possible about the relationship of species with all the measured environmental variables.

To investigate species groupings across all stations, a K-means cluster analysis was conducted until all species significantly contributed to the cluster formation (ANOVA;  $< p = 0.5$ ; standing stock values standardised between  $-3$  to  $3$ ; 10 iterations). The CCA and correlation matrix were analysed using R version 3.6.0 (R Core Team, 2020) and the K-means cluster analysis was performed using IBM SPSS v23. To run the environmental parsimonious CCA, the functions *cca* and *ordistep* from the “vegan” package were used for the CCA and the permutation test, respectively (Oksanen et al., 2019).

## 3. Results and discussion

### 3.1. Mediterranean Sea pteropod distribution

In our Mediterranean basin-wide study, we found the mean standing stock was  $1.27 \pm 1.62$  (SD) ind.  $m^{-3}$  (Supplementary Table 2) which was approximately-five times greater in the Eastern basin ( $2.13$  ind.  $m^{-3}$ ; SD =  $0.4$  ind.  $m^{-3}$ ) compared to the Western basin ( $0.42$  ind.  $m^{-3}$ ; SD =  $2.0$  ind.  $m^{-3}$ ). Mean pteropod standing stocks are comparable to reported records in studies investigating pteropod communities in different Mediterranean Sea regions (e.g. Ligurian Sea, Balearic Sea, Adriatic Sea, Tyrrhenian Sea; Batistić et al., 2004; Fernández de Puelles et al., 2007; Howes et al., 2015; Fernández de Puelles et al., 2007; Manno et al., 2019; Table 1). However, all the previous investigations mentioned here (Table 1) differed in sampling methodology (including different net sizes and sampling depths), in sampling seasons and in oceanographic settings (mainly from coastal systems rather than open sea), making a direct comparison between the studies and regions difficult.

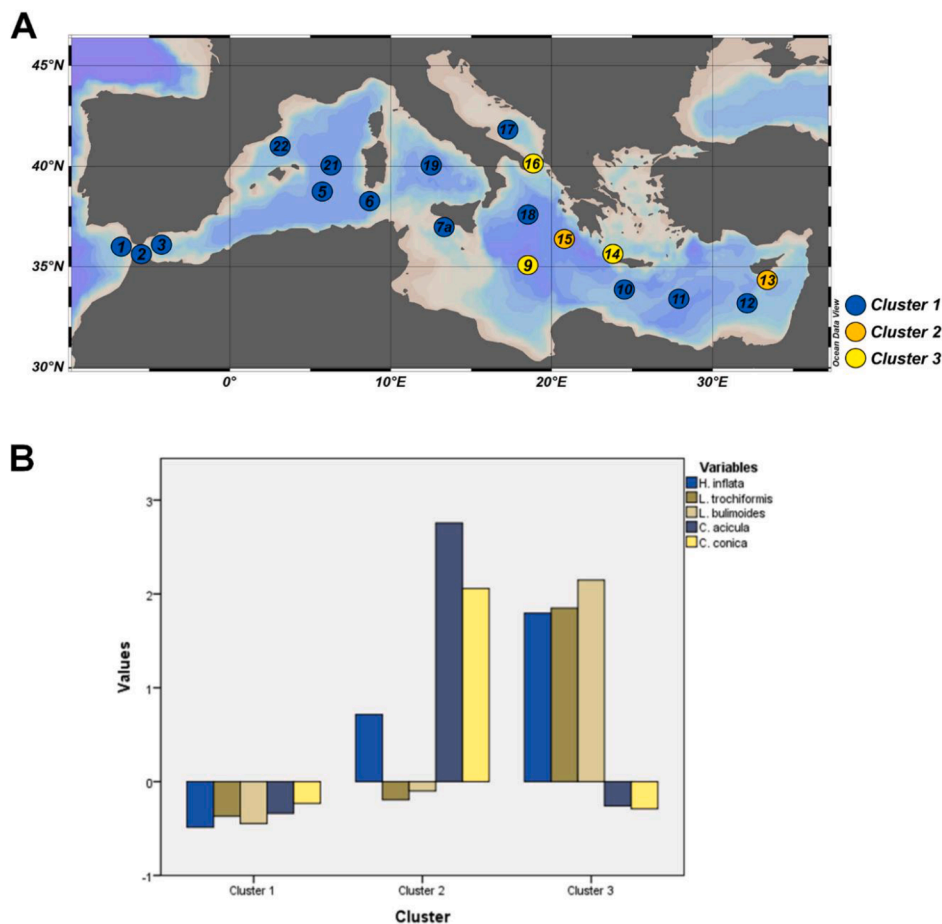
The highest standing stock was recorded in the Otranto Strait (station 16) toward the southern end of the Adriatic Sea with  $5.21$  ind.  $m^{-3}/1041.04$  ind.  $m^2$  (Supplementary Table 2, Fig. 2). High pteropod abundances have previously been reported in the Adriatic Sea ( $2412$  ind.  $m^2$  0–50 m; Batistić et al., 2004; Table 1). The lowest standing stock of

$0.02$  ind.  $m^{-3}$  was at the Catalan-Balearic Station (station 22) off the coast of Spain (Supplementary Table 2, Fig. 2). A long-term zooplankton study reported average pteropod abundances of  $5.9$  ind.  $m^{-3}$  in the Balearic Sea, however this was for a coastal site with a relatively shallow water depth of 78 – 200 m (Fernández de Puelles et al., 2007; Table 1). Coastal systems are complex and highly dynamic, and likely not representative of the open sea where the samples from this study were collected. A low standing stock was also recorded in the Strait of Sicily ( $0.11$  ind.  $m^2$ ), however a very high density ( $120$  ind.  $m^{-3}$ ) has been previously noted (Mazzocchi et al., 1997). In terms of biogeochemical regions (as identified by Reygondeau et al., 2017, Fig. 1), the Ionian-Aegean region had the highest average abundance in the Eastern basin ( $3.05$  ind.  $m^{-3}$ ; SD =  $1.98$  ind.  $m^{-3}$ ), followed by the Adriatic Sea ( $2.74$  ind.  $m^{-3}$ ; SD =  $3.49$  ind.  $m^{-3}$ ), which also has the greatest variance between stations, and then the Levantine-Cretan basins ( $0.90$  ind.  $m^{-3}$ ; SD =  $0.83$  ind.  $m^{-3}$ ). A large range in abundance has previously been noted in the Adriatic Sea (Batistić et al., 2004; Table 1).

The Western basin had consistently lower standing stocks when compared to the Eastern basin, with an average of  $0.63$  ind.  $m^{-3}$  (SD =  $0.49$  ind.  $m^{-3}$ ) in the Atlantic-Gibraltar region,  $0.25$  ind.  $m^{-3}$  (SD =  $0.19$  ind.  $m^{-3}$ ) in the south western Mediterranean, and  $0.51$  ind.  $m^{-3}$  (SD =  $0.47$  ind.  $m^{-3}$ ) in the north western Mediterranean (Fig. 2). Similar average abundances were recorded in the Tyrrhenian Sea (*C. acicula* –  $1.48$  ind.  $m^{-3}$ ; *C. conica* –  $1.11$  ind.  $m^{-3}$ ; *H. inflatus* –  $1.03$  ind.  $m^{-3}$ ; *L. trochiformis* –  $0.64$  ind.  $m^{-3}$ ; *L. bulimoides* –  $0.33$  ind.  $m^{-3}$ ), albeit in shallower waters (73 – 185 m; Manno et al., 2019; Table 1).

The super family Limacinoidea made up 76.4 % of the total pteropod abundance. Limaciniidae was the most abundant family (47.0 %), which dominated the eastern part of the Mediterranean Sea, followed by Heliconiidae (29.4 %), Creseidae (15.4 %) and then Cavoliniidae (6.8 %). Specimens within the target families that were unidentifiable to species level made up 1.4 % of the total abundance. A previous study based on pteropod distribution is the seminal work of Rampal (1975) who performed a comparative analysis of abundances within the different Mediterranean sectors. Unfortunately, the heterogeneity of the presented studies (no standardized sampling strategy; samples collected using different methods) limited the quantitative approach of this work and the results are not presented in terms of pteropod concentration. Howes et al. (2015) is the only study investigating pteropod abundance in the Mediterranean Sea from a time-series over a long-term scale (1957–2003). This study is solely focused in a shallow water coastal site of the Ligurian Sea (water depth approximately 80 m), and contrary to our results, Limaciniidae was the least abundant family, which the authors attributed to a sampling bias. In our study, *H. inflatus* was the most abundant species in the Mediterranean Sea (29.4 %) and recorded at all stations, followed by *L. bulimoides* (23.8 %) and *L. trochiformis* (23.2 %). *H. inflatus* has previously been reported as the most common species in specific regions in the Mediterranean Sea (Batistić et al., 2004 – Southern Adriatic Sea; Granata et al., 2020 - Ligurian Sea). Species belonging to the super family Limacinoidea, included *H. inflatus*, *L. bulimoides* and *L. trochiformis*, and followed a similar distribution pattern with high standing stocks in the Ionian Sea (station 9) and the Antikythera Strait (station 14) and the Otranto Strait (station 16), while there were lower standing stocks in the southwest Mediterranean. *C. inflexa* (6.8 %), *C. acicula* (7.7 %) and *C. conica* (6.8 %) all presented the highest standing stocks in the Eastern Ionian Sea (station 15), while *S. subula* (0.63 %) was most abundant at the easternmost station of the Levantine basin (Station 13 Supplementary Table 2). Howes et al. (2015), indicated that the dominant species in each family were *C. acicula* and *H. inflatus* (previously *Limacina inflata*), corroborating our overall findings.

A global study showed that pteropod biomass generally peak in the spring in both hemispheres (Bednaršek et al., 2012b), suggesting that total pteropod community abundances reported here may be at their peak. This seasonal pattern has also been reported from a long-term (1994 – 2003) zooplankton time-series study in the Balearic Sea,



**Fig. 3.** The results of a K-means cluster based on species standing stocks split the 20 stations within the Mediterranean into 3 clusters. **A** Cluster distribution according to the sampling stations, each cluster is characterized by a colour. In this figure, we can see more homogenous communities in the Western Mediterranean and more heterogeneity in the Eastern Mediterranean. Blue circles = cluster 1; orange circles = cluster 2; yellow circles = cluster 3. **B** Column graph indicating the relative contribution of each species to each cluster. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

where pteropod abundance was highest during late spring (Fernández de Puelles et al., 2007). In addition, in a coastal region of the Ligurian Sea, a distinct Mediterranean biogeochemical region (Reygondeau et al., 2017), Howes et al. (2015) observed a species-specific seasonal pattern, with blooms for Limacinid pteropods in both the spring and early autumn, while Cresidae bloomed during summer and winter, suggesting that different species groups could experience different peaks throughout the year. In contrast, an inter-comparison of long-term zooplankton studies in the Mediterranean Sea shows that peaks in abundance during spring may not be uniform across the region, and that overall, late summer to autumn experience the highest annual maxima (Berline et al., 2012; Skjoldal et al., 2013). Pteropod biomass also experiences seasonal oscillations corresponding to their various life-history stages, therefore further Mediterranean-wide investigations over different seasons would be important in determining temporal differences in pteropod abundance and distribution.

### 3.2. Species groupings in the Mediterranean

We found that mean pteropod standing stocks were not only greater in the Eastern Mediterranean, but this basin also presented high variability in pteropod distribution between, and within, the distinct biogeochemical regions. The pteropod populations, when abundant, were generally made up of family groups. The Western basin was typified by low standing stocks of both the super family Limacinoidea and family Cresidae, as was the central Levantine basin in the easternmost Mediterranean Sea (stations 10–12). High numbers of the super family Limacinoidea were associated with lower standing stocks of Cresidae (Fig. 3). Where Cresidae was more abundant however, *H. inflatus* was also present in higher numbers (Fig. 3). Notably, the pteropod

communities in the Western Mediterranean Sea were more homogenous, while there was more variability in community groupings in the Eastern Mediterranean Sea. Cluster analysis on species standing stocks (Fig. 3) shows that cluster 1 makes up the entirety of the Western basin and the central Levantine basin, with overall lower species standing stocks. Cluster 2 is comprised of only 2 stations (stations 13 and 15) and dominated by family Cresidae. The dominant taxa in cluster 3 belong to the super family Limacinoidea, and is mainly found in the Ionian Sea (stations 9, 14 and 16).

A recent study investigating pteropod trophic dynamics in the Southern Ocean suggested that the niche partitioning for groups of species (between thecosomes and gymnosomes) was likely associated with anatomical differences, particularly those used for feeding (Weldrick et al., 2019). The super family Limacinoidea (*H. inflatus* and *Limacina* species) and the super family Cavoliniidae (*Creseis* species) are evolutionarily and anatomically distinct (Burrige et al., 2017a). Limacinoidea are characterised by a coiled shell and Cavoliniidae are characterised by a bilaterally symmetrical conical shell. While these taxa have similar feeding structures, their anatomical differences may lead to one group being more successful or favouring a particular environment over another, which may in part explain some of the taxonomic clustering that we see in the Eastern Mediterranean Sea. While we did not investigate what specific taxonomic differences have led to the clustering in this study, taxonomic clustering was also observed in the Atlantic Ocean between uncoiled and coiled pteropods (Burrige et al., 2017b).

### 3.3. Environmental drivers of pteropod distribution

The CCA that includes all variables explains 90.8 % (CCA1 – 67.6 %;

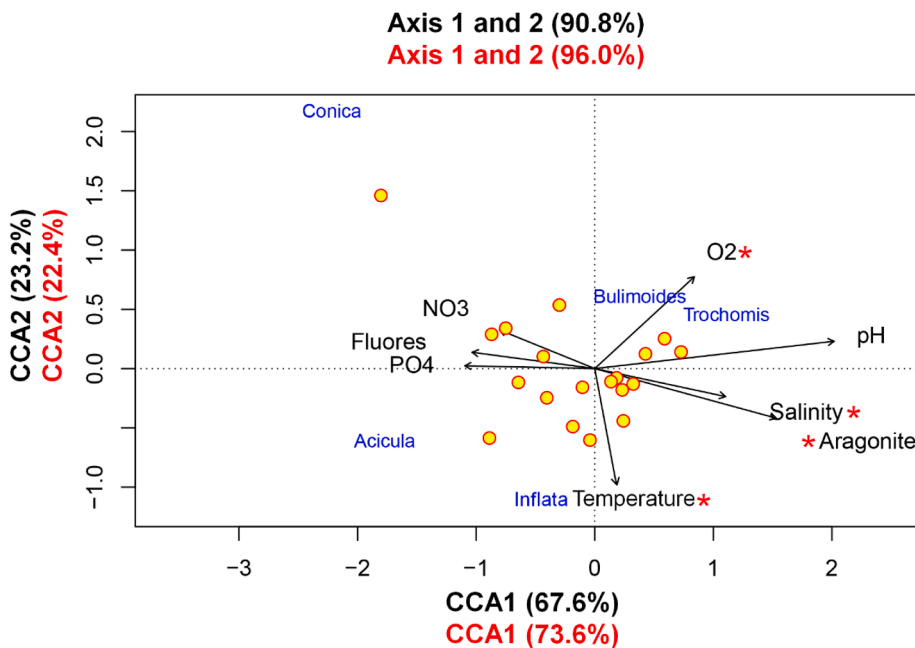


Fig. 4. Triplot of the CCA indicating the relationship between pteropod species (as indicated by species name only) in the Mediterranean Sea and the environmental variables. The first CCA (black) shows that  $\text{NO}_3$  ( $\text{NO}_3$ ),  $\text{PO}_4$  ( $\text{PO}_4$ ), fluorescence (Fluores), temperature, salinity, pH,  $\text{O}_2$  ( $\text{O}_2$ ), and  $\Omega_{\text{ar}}$  (Aragonite) are affecting 90.8 % (CCA1 – 67.6 %; CCA2 – 23.2 %) of the structure of the observed community at the time of sampling (adj.  $r^2 = 0.32$ ,  $F = 1.99$ ,  $p = <0.06$ ). The red text and asterisks indicate the results of parsimonious CCA showing the relationship between pteropod species in the Mediterranean and the significant environmental variables. Temperature,  $\text{O}_2$ , salinity and  $\Omega_{\text{ar}}$  are significantly affecting 96.0 % (CCA1 – 73.6 %; CCA2 – 22.4 %) of the structure of the observed community at the time of sampling (adj.  $r^2 = 0.51$ ,  $F = 4.14$ ,  $p = <0.001$ ). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

CCA2 – 23.2 %) of the observed community structure at the time of sampling. CCA1 exhibits positive loadings for  $\text{O}_2$ , pH, salinity and  $\Omega_{\text{ar}}$ , and negative loadings for fluorescence,  $\text{PO}_4$  and  $\text{NO}_3$  (Fig. 4). CCA2 exhibits positive loadings for  $\text{O}_2$  and negative loadings for temperature (Fig. 4). Temperature,  $\text{O}_2$ , salinity and  $\Omega_{\text{ar}}$  are significantly affecting 96.0 % (CCA1 – 73.6 %; CCA2 – 22.4 %) of the structure of the observed community at the time of sampling (adj.  $r^2 = 0.51$ ,  $F = 4.14$ ,  $p = <0.001$ ; Fig. 4).

The CCA indicates that in the Mediterranean Sea, the distribution of the super family Limacinodea is predominately driven by specific environmental parameters. In particular, *H. inflatus* is mainly linked to temperature, and *L. trochiformis* and *L. bulimoides* more strongly to  $\text{O}_2$  (Fig. 4). *C. acicula* is not driven by any significant parameter, but is negatively associated with salinity,  $\Omega_{\text{ar}}$ , and  $\text{O}_2$ . *Creseis conica* does not exhibit a clear pattern, which may be because the standing stock of this species is too low to statistically identify any solid relationship with the environmental parameters. The inverse distribution of family Creseidae, and the super family Limacinodea, as indicated by the cluster analysis (Fig. 3), is reflected in the opposite relationship these groups have with the environmental variables in the Mediterranean Sea (Fig. 4).

The results indicate that temperature is one of the main factors modulating shelled pteropod distribution in the Mediterranean Sea, as observed in previous studies (Beaugrand et al., 2012, North Atlantic; Howes et al., 2015, Ligurian Sea; Kacprzak et al., 2017, Barents Sea; Thibodeau et al., 2019, Southern Ocean). Indeed, a positive correlation between pteropod respiration rates and temperature have been observed in eastern tropical North Pacific, Arctic, and Antarctic pteropods under experimental conditions (Comeau et al., 2010; Maas et al., 2012a; Thibodeau et al., 2020). For instance, in the Mediterranean, sea surface temperatures (SST) vary by about  $10^\circ\text{C}$  over the course of a year, with winter-summer averages of  $12\text{--}21^\circ\text{C}$  and  $18\text{--}28^\circ\text{C}$  in the Northwest and Southwest Mediterranean, respectively. Therefore, the temperature variability of this springtime study is by comparison relatively small ( $14.08\text{--}18.18^\circ\text{C}$ ) and are temperatures that will likely be experienced at some point over the course of the year for all pteropod populations (Rohling et al., 2009). Given the ongoing rapid warming of the Mediterranean Sea, further studies should address the potential impacts of sustained warming on pteropod distribution in this region.

We found that pteropod standing stocks are positively related to  $\Omega_{\text{ar}}$ , even in waters above critical values of aragonite saturation state for

pteropods ( $\Omega_{\text{ar}} < 1$  - Bednarssek et al., 2019). The pteropod shell is made of aragonite and therefore changes in  $\Omega_{\text{ar}}$  might modulate the net calcification process (Bednarssek et al., 2014; Mekkes et al., 2021). Further, pteropod distribution is predicted to decline as a result of the projected global decrease in  $\Omega_{\text{ar}}$  (Comeau et al., 2012b). A study in the Mediterranean Sea at  $\text{CO}_2$  vents in the Gulf of Naples investigated pteropod abundance along an  $\Omega_{\text{ar}}$  gradient ( $1.9\text{--}2.7$ ; Manno et al., 2019) and found a positive correlation between pteropod abundance and  $\Omega_{\text{ar}}$  in oversaturated conditions, similar to our study. Howes et al. (2017; Ligurian Sea) showed that shells of *S. subula* were thicker and shells of *C. inflexa* were denser under higher  $\Omega_{\text{ar}}$  conditions when comparing samples collected from 1910 ( $\Omega_{\text{ar}} = 3.97$ ) to 2012 ( $\Omega_{\text{ar}} = 3.4$ ). Similarly, a 50 year long-term Australian study (tropical waters) revealed a significant decrease in shell thickness of *C. acicula* and *Diacavolinia longirostris*, coinciding with a decrease in  $0.4 \Omega_{\text{ar}}$  in waters greater than  $3.0 \Omega_{\text{ar}}$  (averaged over 7 sites; Roger et al. 2011). An experiment using oversaturated aragonite conditions showed that with a reduction of  $\Omega_{\text{ar}}$  (control – 2.8; reduced – 2.1  $\Omega_{\text{ar}}$ ), *H. inflatus* calcification rate decreased, and metabolic rate increased (Moya et al., 2016). Overall, these studies suggest a high level of sensitivity to carbonate saturation for pteropods, and even in oversaturated conditions such as the Mediterranean Sea, variability in  $\Omega_{\text{ar}}$  ( $2.68\text{--}3.61$  here) can generate physiological stress. While pH, another key parameter of the carbonate system that was not significant here, has also been shown to induce a response in pteropods to reduced pH conditions (from pH  $8.1\text{--}7.9$  T; Moya et al., 2016). Increased gene expression involved in acid-base regulation in pteropods demonstrates that this is an important mechanism for many physiological processes, including calcification (Moya et al., 2016), and shows that impacts on internal pH homeostasis can be costly. Due to the collinearity of carbonate chemistry parameters, including both pH and  $\Omega_{\text{ar}}$ , it is difficult to disentangle their individual effects on pteropod physiology. Nevertheless, pteropods in the Mediterranean Sea may show an ecological preference for areas (i.e., the Eastern Mediterranean Sea) with relatively high pH and  $\Omega_{\text{ar}}$ , where they will likely devote less energy to maintaining physiological processes.

We observed a positive correlation between  $\text{O}_2$  concentration and *L. bulimoides* and *L. trochiformis* distribution. Oxygen is an important driver of pteropod biology and ecology (Bednarssek et al., 2016). The Mediterranean is in general a well oxygenated sea (Powley et al., 2016), and the  $\text{O}_2$  measurements collected in this study are within the normal

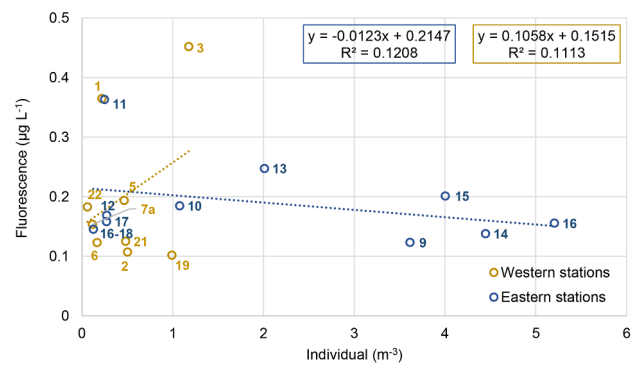


range for pteropods (191–233  $\mu\text{mol O}_2 \text{ kg}^{-1}$  – well above hypoxic conditions for pteropods characterised as  $< 20 \mu\text{mol O}_2 \text{ kg}^{-1}$  in Manno et al., 2017). However, different pteropod species have different  $\text{O}_2$  requirements (Maas et al., 2012a), and the positive correlation between *L. bulimoides* and *L. trochiformis*, both shallow water species, could reflect higher oxygen requirements for these limacinid species, and therefore an ecological preference for areas with higher  $\text{O}_2$  concentration compared to other species, such as *Clio pyramidata* and *Creseis virgula* (Maas et al., 2012b), which may be better adapted to experience lower  $\text{O}_2$  levels during their vertical migration.

The results indicate that salinity significantly affected pteropod distribution in the Mediterranean Sea. Only relatively low salinities ( $< 33$  PSU) have been shown to negatively impact pteropod abundance (Pasternak et al., 2020) and the range of salinity in this study (36.2 – 39.1 PSU) is within the normal range for most pteropods. For *C. acicula* however, their preferred salinity is between 28 and 33 ppt based on physiological responses such as oxygen consumption and calcification rate (Han et al., 2022), and here this species does exhibit a negative relationship with salinity. However, a study investigating the impacts of ocean acidification and sea water freshening on *Limacina retroversa* found that mortality significantly increased only with a combined decrease in pH and salinity, and it was suggested that high salinities may be energetically favourable to pteropods as they are benefited by increased buoyancy (Manno et al., 2012).

Fluorescence (as indicative of food availability) was not a significant parameter affecting pteropod distribution in this study. Fluorescence has a weak and slightly negative relationship with the super family Limacinodea (76.4 % of total pteropod abundance), which is unexpected as pteropod distribution has been previously correlated with high productivity (Bednaršek et al., 2012b; Burridge et al., 2017b; Fig. 4). There is an east–west gradient of oligotrophy in the Mediterranean Sea that does not have much seasonal variability (Pasqueron de Fommervault et al., 2015) and in our study, pteropod abundance was higher in the ultra-oligotrophic eastern Mediterranean, which accounts for the weak negative correlation to fluorescence. An intercomparison of long-term studies in the Mediterranean also showed an overall negative correlation between abundance and chlorophyll *a* (Berline et al., 2012). However, the quality of food (in terms of energy), rather than quantity, might be an important factor driving distribution, and further analysis of gut contents would be required to investigate this aspect. Further, the majority of shelled pteropods have a unique feeding behaviour 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). This feeding method may allow them to overcome low food conditions due to their ability to capture and filter through relatively large amounts of organic matter (Hamner et al., 1975).

Other factors outside of those measured in this study may affect pteropod community composition. For instance, lateral advection is one of the major physical forcings experienced by marine life and plankton. In the Mediterranean Sea, however, the large-scale surface circulation in the Mediterranean has been described as sub-basin-scale, with meso-scale gyres interconnected and bounded by currents and jets (Millot and Taupier-Letage, 2012; Rohling et al., 2009). The general circulation flow can impact coastal regions and heavily influence local current dynamics. Mediterranean shelf areas are relatively small and are separated from deeper regions by steep continental shelf breaks. While lateral advection may play a role in pteropod distribution, it is more likely that the coastal pteropod populations in the Mediterranean Sea are influenced by coastal currents and local dynamics rather than the deeper, ocean-like stations of this study. We also investigated the effect of day/night on pteropod standing stocks (ANOVA – day/night fixed factor; IBM SPSS v23) and found there was no significant effect of day/night on total and individual species abundances (Supplementary Table 2). Given that these species primarily occur in the upper water column (above 200 m depth), we suggest that the time of day did not play a major role in pteropod species



**Fig. 5.** Box plot comparing the abundance distribution of pteropods (blue) and foraminifera (orange) (ind.  $\text{m}^{-3}$ ) between the east and west of the Mediterranean Sea. Pteropods and foraminifera are inversely distributed within the two major sub-basins of the Mediterranean Sea. The results of the Generalized Linear Mixed Model indicate that there are significant differences between the abundance of both taxa (chisq = 29.27,  $p < 0.05$ ) including between the Eastern and Western Mediterranean basins (chisq = 5.57,  $p < 0.05$ ), and also in their interaction (chisq = 4.97,  $p < 0.05$ ). Note that the scale of foraminiferal abundance is distinctly lower than pteropod abundance. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

distribution here.

#### 3.4. Pteropod and foraminiferal interaction

Planktic foraminiferal standing stocks and distribution data presented in Mallo et al. (2017) were compared to the pteropod data from this study. Pteropod samples from this study and foraminiferal samples from Mallo et al. (2017) came from the same plankton tow samples and stations, and were preserved using the same methodology. For a more detailed description of the foraminiferal collection, preservation and taxonomic identification methods, please refer to Mallo et al. (2017). To compare the standing stocks of pteropods and foraminifera within specific regions of the Mediterranean Sea, we used a generalized linear mixed model (GLMM) with a gamma distribution. As the magnitude of the count data is very different between pteropods and foraminifera (almost one order of magnitude), it was transformed to logarithmic scale to make standing stocks from both groups comparable. For this analysis, the Mediterranean Sea was split into two main sub-basins: “Western” stations (1, 2, 3, 5, 6, 7, 19, 20, 21, 22) and “Eastern” stations (11, 12, 13, 14, 15, 16, 17, 16–18). The GLMM was conducted with R version 3.6.0 (R Core Team, 2020) using functions “glm” in the glmmTMB package (Brooks et al., 2017).

The results from the GLMM, comparing the standing stocks of pteropods and foraminifera between the two basins (Eastern and Western basins), indicates that there are significant differences between the abundance of both taxa (chisq = 29.27,  $p < 0.05$ ) between the Eastern and Western Mediterranean basins (chisq = 5.57,  $p < 0.05$ ), and also in their interaction (chisq = 4.97,  $p < 0.05$ ). These results indicate that an inverse relationship between taxa distribution and the Mediterranean Sea sub-basins is present (Fig. 5). Pteropod abundance is distinctly greater in the Eastern Mediterranean Sea than in the Western Mediterranean Sea. Foraminifera showed a contrasting abundance distribution (Fig. 5) with higher abundances in the Western Mediterranean Sea than in the Eastern Mediterranean Sea.

There have been only a handful of studies that investigate the relationship between pteropod and foraminiferal distribution. In the Western Arabian Sea (January – September 1993), the ratio between pteropod and foraminifera abundance shifted throughout the year, indicating an opposing temporal distribution (Mohan et al., 2006). A multi-decadal study at two sites off the coast of Southern California and



Central California showed no relationship between foraminifera or pteropod abundances (Ohman et al., 2009). In the Gulf Stream, Sargasso Sea and the Gulf of Mexico, pteropod and foraminifera distribution followed a similar pattern, with abundance decreasing closer to oligotrophic conditions (Casey et al., 1979). In Schiebel et al. (2001), foraminiferal and pteropod abundance in the North Atlantic was positively correlated with chlorophyll-a. In the Arctic Ocean, there was no clear trend between foraminifera and pteropod abundances along a longitudinal transect (Zamelczyk et al., 2021). The results of these studies indicate that the environmental factors that impact pteropod and foraminiferal abundance and distribution might be distinct.

In the Mediterranean Sea, Mallo et al. (2017) found that foraminiferal distribution is not strongly linked to carbonate saturation levels as observed for pteropod distribution in this study (see section 3.3), but instead links more to trophic complexity.

Mallo et al. (2017) found that foraminifera distribution was strongly dependent on food availability, and suggested that the lower foraminiferal abundance in the Eastern Mediterranean Sea (ultra-oligotrophic sector) results from reduced reproduction due to limiting resources. Planktic foraminifera have lifespans on the scale of weeks to months, and their production is often seasonal, thus peaks and troughs in foraminiferal abundance are often in line with peaks and troughs in phytoplankton biomass (Hernández-Almeida et al., 2011), their main food source. In contrast to foraminifera, pteropod feeding behaviour allows them to capture large amounts of organic matter (see prg.3.3) and they are also able to actively swim (Hammer et al., 1975; Lalli and Gilmer, 1989) and potentially search for more favourable food conditions. These different feeding strategies indicate that foraminifera are more reliant on sustenance in their immediate surroundings, whereas pteropods may not be as restricted. Holocene downcore samples from the North Aegean Sea also indicated that pteropod and foraminifera distribution did not respond similarly to changes in productivity (Giamali et al., 2021). Further, results from incubation experiments show that the survival of pteropods does not appear to be affected when experiencing prolonged starvation (i.e. Busch et al., 2014; Lischka et al., 2011).

Our results show a relationship between pteropod distribution and several environmental parameters, however it is difficult to determine if there is a single main driver or a combination of drivers. Overall, we suggest that the Eastern Mediterranean basin is more energetically favourable for pteropods due to more favourable environmental conditions (i.e., low energetic physiological demand due to higher  $\Omega_{ar}$ ), and that pteropods may be able to adapt better to the low food availability than foraminifera, which could be due to a combination of both their feeding behaviour, a greater capability to actively move along the water column, and their ability to withstand starvation.

#### 4. Conclusions

Our results provide new insights into pteropod distribution during spring across diverse biogeochemical regions of the Mediterranean Sea, with particular focus on the two largest Mediterranean basins (Western and Eastern). Spring pteropod standing stocks in the Eastern, and largely ultra-oligotrophic sector of the Mediterranean Sea, were 5x greater than in the Western basin. The natural environmental longitudinal gradient across the Mediterranean Sea influences pteropod distribution, and they may be exhibiting a preference for environments with a lower energy demand, such as regions with higher aragonite saturation levels. During the sampling period, foraminifera and pteropods were inversely distributed in the Mediterranean, with greater foraminiferal abundance in the Western Mediterranean Sea, a region of greater nutrients and surface food availability. We speculate that feeding behaviour, alongside swimming capability, may be factors promoting the observed inverse distribution. While our findings provide only a snapshot during the spring season, the paucity of pteropod studies in the Mediterranean Sea makes this work important in providing ecological data on pteropod

**Table A1** Location and environmental parameters for each station of the cruise. All the parameters are averaged from 5 to 200 m depth. The table includes: Station code, Station name, day (day/month/year), location time (LT), latitude (Lat.), longitude (Long.), bottom depth (m), volume ( $m^3$ ), temperature (Temp. °C), salinity (PSU), fluorescence (Fluor.), pH, aragonite saturation ( $\Omega_{ar}$ ), nitrate ( $NO_3$ ), phosphate ( $PO_4$ ), and oxygen ( $O_2$ ).  $\Omega_{ar}$  is a calculated parameter.

Station name	Station	Day (dd/mm/yyyy)	Time (LT)	Latitude	Longitude	Bottom depth (m)	Volume ( $m^3$ )	Temp. (°C)	Salinity PSU	Fluor. ( $\mu g L^{-1}$ )	pH	$\Omega_{ar}$ ( $kg^{-1}$ )	$NO_3$ ( $\mu mol L^{-1}$ )	$PO_4$ ( $\mu mol L^{-1}$ )	$O_2$ ( $\mu mol kg^{-1}$ )
Atlantic	1	5/2/2013	00:03	36°03'	-6°64'	557	1016	16.39	36.19	0.36	8.06	2.70	1.92	0.13	226.03
Gibraltar	2	5/3/2013	12:47	35°95'	-5°56'	557	537	14.68	37.20	0.11	8.06	2.68	4.18	0.22	191.05
Alboran Sea	3	5/4/2013	20:55	36°12'	-4°19'	1337	1403	15.43	36.97	0.45	8.09	2.87	2.08	0.13	214.19
Southern Alguero-Balear	5	5/8/2013	10:44	38°52'	5°55'	2844	459	14.60	37.89	0.18	8.10	2.97	1.22	0.05	224.38
Strait of Sardinia	6	5/9/2013	20:34	38°27'	8°69'	2237	423	14.60	38.13	0.19	8.08	2.96	2.30	0.15	212.38
Strait of Sicily	7a	5/11/2013	00:20	37°04'	13°19'	469	447	15.40	38.09	0.23	8.09	3.07	1.35	0.06	216.91
Ionian Sea	9	5/12/2013	11:31	35°11'	18°29'	3775	425	16.64	38.75	0.13	8.12	3.44	0.41	0.02	227.67
Southern Crete	10	5/14/2013	14:40	33°81'	24°27'	1845	320	16.70	39.04	0.12	8.11	3.43	1.03	0.03	211.61
Eastern Basin	11	5/15/2013	13:01	33°50'	28°00'	2865	372	17.73	38.85	0.10	8.12	3.61	0.58	0.02	224.16
Nile Delta	12	5/17/2013	03:14	33°21'	32°00'	1648	364	18.18	39.06	0.15	8.11	3.56	0.50	0.03	225.32
Lebanon	13	5/17/2013	16:15	34°22'	33°23'	2043	397	17.80	38.96	0.16	8.11	3.53	0.40	0.03	222.81
Antikythera Strait	14	5/21/2013	6:06	35°70'	23°42'	619	334	16.90	39.06	0.12	8.13	3.57	0.37	0.03	229.53
Eastern Ionian Sea	15	5/21/2013	21:25	36°40'	20°81'	2897	391	16.52	39.05	0.15	8.12	3.40	1.08	0.04	228.12
Otranto Strait	16	5/24/2013	23:49	40°23'	18°84'	808	385	15.14	38.81	0.20	8.10	3.22	1.70	0.05	229.39
Adriatic Sea	17	5/23/2013	21:09	41°84'	17°25'	970	440	16.34	38.82	0.16	8.13	3.50	0.90	0.03	231.22
Between Otranto Strait and Central Ionian	16-18	5/25/2013	09:30	37°71'	18°52'	3069	426	16.15	38.88	0.14	8.11	3.40	1.97	0.06	216.01
Tyrrhenian Sea	19	5/27/2013	12:30	39°83'	12°52'	3165	391	15.05	38.29	0.18	8.12	3.21	1.60	0.07	212.45
Northern Alguero-Balear	20	5/29/2013	20:00	41°32'	5°67'	2561	356	14.08	38.39	0.36	8.14	3.24	4.01	0.20	208.91
Central Alguero-Balear	21	5/30/2013	10:30	40°07'	5°95'	2834	392	14.51	37.88	0.17	8.11	3.03	0.81	0.04	233.14
Catalano-Balear	22	5/31/2013	13:55	40°95'	3°32'	2275	339	14.62	38.39	0.25	8.13	3.23	3.55	0.17	210.47

Table A2

Absolute (ind. m<sup>-3</sup>), integrated abundance 0–200 m (ind. m<sup>2</sup>), and relative abundance (%) of pteropods collected from BONGO nets. Western stations are 1-7a, 19–22 and Eastern stations are 9-16-18'.

Absolute abundance (individuals m <sup>-3</sup> )												
Station name	Station	<i>H. inflata</i>	<i>L. trochiformis</i>	<i>L. bulimoides</i>	<i>Limacinidae</i> sp.	<i>C. inflexa</i>	<i>Cavoliniidae</i> sp.	<i>C. acicula</i>	<i>C. conica</i>	<i>S. subula</i>	<i>Creseidae</i> sp.	Total
Atlantic	1	0.049	0.010	0.038	0.002	0.022	0.000	0.037	0.049	0.010	0.002	0.219
Gibraltar	2	0.196	0.019	0.119	0.006	0.047	0.002	0.065	0.039	0.007	0.002	0.501
Alboran Sea	3	0.523	0.003	0.249	0.008	0.007	0.001	0.154	0.200	0.019	0.011	1.176
S. central W. Med.	5	0.031	0.007	0.026	0.002	0.020	0.002	0.052	0.305	0.015	0.004	0.464
Str. of Sardinia	6	0.026	0.000	0.092	0.007	0.000	0.000	0.007	0.028	0.002	0.002	0.165
Str. of Sicily	7a	0.018	0.056	0.013	0.002	0.022	0.002	0.000	0.000	0.000	0.000	0.114
S. of Ionian Sea	9	1.278	0.475	1.584	0.099	0.056	0.000	0.061	0.054	0.005	0.002	3.614
Off S. Crete	10	0.550	0.394	0.034	0.025	0.019	0.000	0.034	0.013	0.003	0.003	1.075
Eastern Basin	11	0.153	0.027	0.046	0.000	0.005	0.000	0.011	0.003	0.000	0.003	0.247
Off Nile delta	12	0.093	0.038	0.069	0.003	0.025	0.000	0.025	0.014	0.003	0.003	0.272
Off Lebanon	13	0.987	0.063	0.020	0.013	0.018	0.000	0.645	0.191	0.063	0.010	2.010
Antikythera Str.	14	1.677	1.428	1.162	0.042	0.009	0.000	0.072	0.057	0.000	0.000	4.446
E. Ionian Sea	15	0.488	0.327	0.504	0.041	1.440	0.000	0.552	0.601	0.036	0.013	4.003
Otranto Str.	16	0.818	2.353	1.894	0.002	0.016	0.000	0.036	0.034	0.000	0.000	0.270
Adriatic Sea	17	0.066	0.070	0.132	0.052	0.000	0.003	0.000	0.000	0.000	0.000	5.205
N. Ionian Sea	16–18	0.049	0.040	0.019	0.002	0.005	0.000	0.002	0.005	0.002	0.000	0.124
Tyrrhenian Sea	19	0.340	0.445	0.023	0.000	0.018	0.000	0.090	0.064	0.008	0.003	0.990
N-central W. Med.	20	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Central W. Med.	21	0.120	0.138	0.041	0.000	0.000	0.000	0.102	0.077	0.000	0.003	0.480
Catalano-Balear	22	0.018	0.015	0.000	0.000	0.015	0.000	0.012	0.000	0.000	0.000	0.059
Avg. Western Stations	1-7a, 19–22	0.132	0.069	0.060	0.003	0.015	0.001	0.052	0.076	0.006	0.003	0.417
Avg. Eastern Stations	9-16-18'	0.616	0.522	0.546	0.028	0.159	0.000	0.144	0.097	0.011	0.003	2.127
Avg. All Stations	1–22	0.374	0.295	0.303	0.015	0.087	0.000	0.098	0.087	0.009	0.003	1.272
Integrated abundance 0–200 m (individuals m <sup>2</sup> )												
Station	Station	<i>H. inflata</i>	<i>L. trochiformis</i>	<i>L. bulimoides</i>	<i>Limacinidae</i> sp.	<i>C. inflexa</i>	<i>Cavoliniidae</i> sp.	<i>C. acicula</i>	<i>C. conica</i>	<i>S. subula</i>	<i>Creseidae</i> sp.	Total
Atlantic	1	9.843	1.969	7.677	0.394	4.331	0.000	7.480	9.843	1.969	0.394	43.898
Gibraltar	2	39.106	3.724	23.836	1.117	9.311	0.372	13.035	7.821	1.490	0.372	100.186
Alboran Sea	3	104.633	0.570	49.893	1.568	1.426	0.143	30.791	40.057	3.849	2.281	235.210
S. central W. Med.	5	6.100	1.307	5.229	0.436	3.922	0.436	10.458	61.002	3.050	0.871	92.810
Str. of Sardinia	6	5.201	0.000	18.440	1.418	0.000	0.000	1.418	5.674	0.473	0.473	33.097
Str. of Sicily	7a	3.579	11.186	2.685	0.447	4.474	0.447	0.000	0.000	0.000	0.000	22.819
S. of Ionian Sea	9	255.529	95.059	316.706	19.765	11.294	0.000	12.235	10.824	0.941	0.471	722.824
Off S. Crete	10	110.000	78.750	6.875	5.000	3.750	0.000	6.875	2.500	0.625	0.625	215.000
Eastern Basin	11	30.645	5.376	9.140	0.000	1.075	0.000	2.151	0.538	0.000	0.538	49.462
Off Nile delta	12	18.681	7.692	13.736	0.549	4.945	0.000	4.945	2.747	0.549	0.549	54.396
Off Lebanon	13	197.481	12.594	4.030	2.519	3.526	0.000	128.967	38.287	12.594	2.015	402.015
Antikythera Str.	14	335.329	285.629	232.335	8.383	1.796	0.000	14.371	11.377	0.000	0.000	889.222
E. Ionian Sea	15	97.698	65.473	100.767	8.184	287.980	0.000	110.486	120.205	7.161	2.558	800.512
Otranto Str.	16	163.636	470.649	378.701	10.390	3.117	0.519	7.273	6.753	0.000	0.000	1041.039
Adriatic Sea	17	13.182	14.091	26.364	0.455	0.000	0.000	0.000	0.000	0.000	0.000	54.091
N. Ionian Sea	16–18	9.859	7.981	3.756	0.469	0.939	0.000	0.469	0.939	0.469	0.000	24.883
Tyrrhenian Sea	19	68.031	89.003	4.604	0.000	3.581	0.000	17.903	12.788	1.535	0.512	197.954
N-central W. Med.	20	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Central W. Med.	21	23.980	27.551	8.163	0.000	0.000	0.000	20.408	15.306	0.000	0.510	95.918
Catalano-Balear	22	3.540	2.950	0.000	0.000	2.950	0.000	2.360	0.000	0.000	0.000	11.799
Western Stations	1-7a, 19–22	26.401	13.826	12.053	0.538	2.999	0.140	10.385	15.249	1.236	0.541	83.369
Eastern Stations	9-16-18'	123.204	104.330	109.241	5.571	31.842	0.052	28.777	19.417	2.234	0.676	425.344
All Stations	1–22	74.803	59.078	60.647	3.055	17.421	0.096	19.581	17.333	1.735	0.608	254.357
Relative abundance (%)												
Station	Station	<i>H. inflata</i>	<i>L. trochiformis</i>	<i>L. bulimoides</i>	<i>Limacinidae</i> sp.	<i>C. inflexa</i>	<i>Cavoliniidae</i> sp.	<i>C. acicula</i>	<i>C. conica</i>	<i>S. subula</i>	<i>Creseidae</i> sp.	Total
Atlantic	1	22.4	4.5	17.5	0.9	9.9	0.0	17.0	22.4	4.5	0.9	0.9
Gibraltar	2	39.0	3.7	23.8	1.1	9.3	0.4	13.0	7.8	1.5	0.4	2.0
Alboran Sea	3	44.5	0.2	21.2	0.7	0.6	0.1	13.1	17.0	1.6	1.0	4.6

(continued on next page)

**Table A2 (continued)**

Station name	Station	<i>H. inflata</i>	<i>L. trochiformis</i>	<i>L. bulimoides</i>	<i>Limacina</i> sp.	<i>C. inflexa</i>	<i>Cavoliniidae</i> sp.	<i>C. acicula</i>	<i>C. conica</i>	<i>S. subula</i>	<i>Creseidae</i> sp.	Total
S. central W. Med.	5	6.6	1.4	5.6	0.5	4.2	0.5	11.3	65.7	3.3	0.9	1.8
Str. of Sardinia	6	15.7	0.0	55.7	4.3	0.0	0.0	4.3	17.1	1.4	1.4	0.7
Str. of Sicily	7a	15.7	49.0	11.8	2.0	19.6	2.0	0.0	0.0	0.0	0.0	0.4
S. of Ionian Sea	9	35.4	13.2	43.8	2.7	1.6	0.0	1.7	1.5	0.1	0.1	14.2
Off S. Crete	10	51.2	36.6	3.2	2.3	1.7	0.0	3.2	1.2	0.3	0.3	4.2
Eastern Basin	11	62.0	10.9	18.5	0.0	2.2	0.0	4.3	1.1	0.0	1.1	1.0
Off Nile delta	12	34.3	14.1	25.3	1.0	9.1	0.0	9.1	5.1	1.0	1.0	1.1
Off Lebanon	13	49.1	3.1	1.0	0.6	0.9	0.0	32.1	9.5	3.1	0.5	7.9
Antikythera Str.	14	37.7	32.1	26.1	0.9	0.9	0.0	1.6	1.3	0.0	0.0	17.5
E. Ionian Sea	15	12.2	8.2	12.6	1.0	36.0	0.0	13.8	15.0	0.9	0.3	15.7
Otranto Str.	16	15.7	45.2	36.4	1.0	0.3	0.0	0.7	0.6	0.0	0.0	20.5
Adriatic Sea	17	24.4	26.1	48.7	0.8	0.0	0.0	0.0	0.0	0.0	0.0	1.1
N. Ionian Sea	16-18	39.6	32.1	15.1	1.9	3.8	0.0	1.9	3.8	1.9	0.0	0.5
Tyrrhenian Sea	19	34.4	45.0	2.3	0.0	1.8	0.0	9.0	6.5	0.8	0.3	3.9
N-central W. Med.	20	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Central W. Med.	21	25.0	28.7	8.5	0.0	0.0	0.0	21.3	16.0	0.0	0.5	1.9
Catalano-Balear	22	30	25	0	0	25	0	20	0	0	0	0.2
Western Stations	1-7a, 19-22	31.7	16.6	14.5	0.6	3.6	0.2	12.5	18.3	1.5	0.6	16.4
Eastern Stations	9-16-18'	29.0	24.5	25.7	1.3	7.5	0.0	6.8	4.6	0.5	0.2	83.6
All Stations	1-22	29.4	23.2	23.8	1.2	6.8	0.0	7.7	6.8	0.7	0.2	100

**Table A3**

Absolute (10 ind. m<sup>-3</sup>) and relative abundance (%) of foraminifera (all species) collected from BONGO nets. Western stations are 1-7a, 19-22 and Eastern stations are 9-16-18'. For data regarding individual species of foraminifera, please refer to Mallo et al. (2017).

Station name	Station	Total abundance (10 ind. m <sup>-3</sup> )	Relative abundance (%)
Atlantic	1	0.985	3.476
Gibraltar	2	5.120	18.070
Alboran Sea	3	4.141	14.614
S. central W. Med.	5	1.460	5.153
Str. of Sardinia	6	0.709	2.502
Str. of Sicily	7a	1.006	3.550
S. of Ionian Sea	9	0.683	2.410
Off S. Crete	10	3.003	10.598
Eastern Basin	11	0.753	2.657
Off Nile delta	12	0.439	1.549
Off Lebanon	13	1.689	5.961
Antikythera Str.	14	0.898	3.169
E. Ionian Sea	15	0.307	1.083
Otranto Str.	16	1.482	5.230
Adriatic Sea	17	0.114	0.402
N. Ionian Sea	16-18	0.258	0.911
Tyrrhenian Sea	19	3.607	12.730
N-central W. Med.	20	0.365	1.288
Central W. Med.	21	0.638	2.252
Catalano-Balear	22	0.678	2.393
Avg. Western Stations	1-7a, 19-22	1.871	66.028
Avg. Eastern Stations	9-16-18'	0.963	33.972
Avg. All Stations	1-22	1.417	100.000

distribution across this entire region. Future studies covering other seasons, depths, and additional sites would further help to characterise the pteropod distribution across the Mediterranean Sea over large temporal scales as a function of environmental forcings, with implications for their global ecological preferences, life cycle, and impacts on ocean biogeochemistry.

**Declaration of Competing Interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

**Data availability**

All data is included in the Appendix.

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## Appendix

(Tables A1–A3).

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pocean.2022.102930>.

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