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Spatial and temporal distribution of mesozooplankton in the coastal waters of Cyprus (Eastern Mediterranean)

Grigoria VASILOPOULOU[1], George KEHAYIAS[2] Demetris KLETOU[3,4,] Periklis KLEITOU[3], Konstantinos ANTONIADIS[5], Maria ROUSOU[5], Vassilis PAPADOPOULOS[5], Polina POLYKARPOU[5] and George TSIAMIS[1]

[1] Department of Environmental Engineering, University of Patras, 30100, Agrinio, Greece
[2] Department of Food Science & Technology, University of Patras, 30100, Agrinio, Greece
[3] Marine and Environmental Research (MER) Lab., Limassol 4533, Cyprus
[4] Department of Maritime Transport and Commerce, Frederick University, Limassol 3080, Cyprus
[5] Department of Fisheries and Marine Research, Ministry of Agriculture, Rural Development and the Environment, Republic of Cyprus, 2033, Nicosia, Cyprus

Corresponding author: George Kehayias; gkechagi@upatras.gr

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Abstract

This study provides elements on the spatial and temporal mesozooplankton variability during a three-year study, encompassing vertical hauls from 50 m deep to the surface from four coastal locations of Cyprus. The total mesozooplankton abundance fluctuated between 190.4 and 882.5 individuals m^{-3}. A total of 90 holoplanktonic and meroplanktonic taxa were recorded. Copepods dominated in the community and accounted for 71.7% of the total mesozooplankton, followed by appendicularians, molluscs, cladocerans, and siphonophores, which contributed 8.04%, 5.48%, 4.60%, and 3.31%, respectively. There were no statistically significant differences among the four sampling sites for any of the mesozooplanktonic taxa, though seasonal and interannual differences were recorded for several of them. The community composition reinforced the evidence for a higher resemblance of the Cyprus mesozooplankton to the offshore communities of the northern and central Levantine Sea and those around Rhodes Island, instead of the northeastern Mediterranean coastal areas. Comparisons of the seasonal abundance variation of the mesozooplankton taxa with other coastal areas of the Levantine Sea are provided. Considering the seasonality of the mesozooplankton, there was a separation of the taxa into distinct groups representing the summer, the winter-spring, and the autumn periods. Temperature was the most important variable that shaped the formation of the distinct seasonal groups of taxa, while chlorophyll-*α*, dissolved oxygen, and salinity contributed to a lesser extent. Chlorophyll-*α* concentrations verified the oligotrophic character of the area and seem to be unaffected by inland inputs. The mesozooplankton community showed a spatial consistency, probably as the result of the open sea influence, and seems to be regulated mainly by the properties of the central Levantine pelagic waters and less by terrestrial inputs of inland waters.

Keywords: Mesozooplankton community composition; copepods; coastal; Levantine Sea; Mediterranean Sea.

Introduction

Zooplankton is a crucial component of the energy flow in global aquatic ecosystems. In the Mediterranean Sea, the fraction of these organisms called mesozooplankton (sized between 0.2–20 mm) are the main grazers of phytoplankton and microzooplankton (Zervoudaki *et al*., 2007; Siokou-Frangou *et al*., 2010; Protopapa *et al*., 2020) and the most desirable prey of the secondary consumers and the planktivorous pelagic fish (Bachiller *et al*., 2020; Hure & Mustać, 2020). Thus, the structure of mesozooplankton communities may determine the fate of primary production, as well as the carbon transfer to the sea bottom (Saiz *et al*., 2007; Robinson *et al*., 2010). For this reason, several studies on the mesozooplankton abundance and distribution have been conducted in the Mediterranean Sea (Siokou-Frangou *et al*., 2010; Mazzocchi *et al*., 2014; Siokou *et al*., 2019). Mesozooplankton in the Mediterranean is generally affected by big-scale and local hydrological phenomena (Robinson *et al*., 2001; Schroeder *et al*., 2013) and the variation of the physical and chemical elements, some of which determine the seasonal variation of most taxa (Siokou-Frangou *et al*., 1998; Fernández de Puelles *et al*., 2003; Vidjak *et al.*, 2007).

The oligotrophic character of the eastern Mediterranean has been widely described (Azov, 1986; Yacobi *et al.*, 1995), while a west-east gradient in nutrient deficiency creates an ultra-oligotrophic environment in the easternmost part, the Levantine Sea (Siokou-Frangou *et al.*, 2010). Mesozooplankton abundance also follows this west-east gradient (Nowaczyk *et al.*, 2011) with higher values found in the upper 100 m layer (Siokou *et al.*, 2019). Coastal areas in the Mediterranean have variable hydrographic characteristics (Schroeder *et al.*, 2013; Menna *et al.*, 2021) and are seasonally exposed to different intensities of anthropogenic and terrestrial influences, which may affect the coastal marine ecosystems (Cappelletto *et al.*, 2021).

There are several mesozooplankton studies in coastal areas of the Levantine Sea (Lakkis, 1990; Zakaria, 2006; Yilmaz & Besiktepe, 2010; Uysal & Shmeleva, 2012; Terbiyik-Kurt & Polat, 2013; Besiktepe *et al.*, 2015; Aliçli & Sarihan, 2016), as well as in offshore waters of this area (Pancucci-Papadopoulou *et al.*, 1992; Mazzocchi *et al.*, 1997, 2014; Siokou-Frangou *et al.*, 1997; Pasternak *et al.*, 2005; Nowaczyk *et al.*, 2011; Protopapa *et al.*, 2020). Some of these studies provided monthly data, while the majority conducted sporadic samplings. In the only study dealing with the coastal mesozooplankton of Cyprus (Hannides *et al.*, 2015), samplings were carried out in only two seasons, providing data on the abundance and biomass of the total zooplankton and the abundance of the major zooplanktonic groups.

Following a three-year sampling survey in the coastal area of Cyprus undertaken as part of the implementation of the Marine Strategy Framework Directive (2008/56/EC), the present study aims to provide new insights about: i) the total mesozooplankton abundance and community composition of Cyprus coastal areas, ii) their seasonal and spatial variability, and iii) the relation of the mesozooplankton to environmental parameters.

Materials and Methods

Study area and sampling sites

The study was conducted on the coasts of Cyprus (Eastern Mediterranean Sea) in the Levantine Sea. Four sampling sites located at 50 m deep have been selected to be seasonally monitored for physicochemical elements and zooplankton: Latsi (LA), Amathounta (AM), Meneou (ME), and Protaras (PR) (Fig. 1). LA is located on the north coasts of Cyprus, in the Polis Chrysochou. About 3 km from the site, along the coastline, there is a fishing shelter and some touristic facilities. The area is a designated nitrate vulnerable zone (NVZ) according to the Nitrates Directive (91/676/EEC). AM is found on the south coasts of Cyprus, in the eastern part of the Limassol Bay. Several human activities are present in the area including touristic facilities (e.g., hotels, restaurants, marina), residential properties, and a sewage treatment plant about 5 km east of the site. Furthermore, the sampling site is located 500 m from the Amathus artificial reef marine protected area (MPA), in which all fishing activities are banned. ME is in the south-western edge of Larnaca Bay. On the coastline, there are residential properties, touristic facilities, the Larnaca airport, the Larnaca desalination plant, and some agricultural areas. The PR sampling site is located within the Cavo Greco MPA on the south-eastern coasts of Cyprus. The area, due to the nearby agricul-

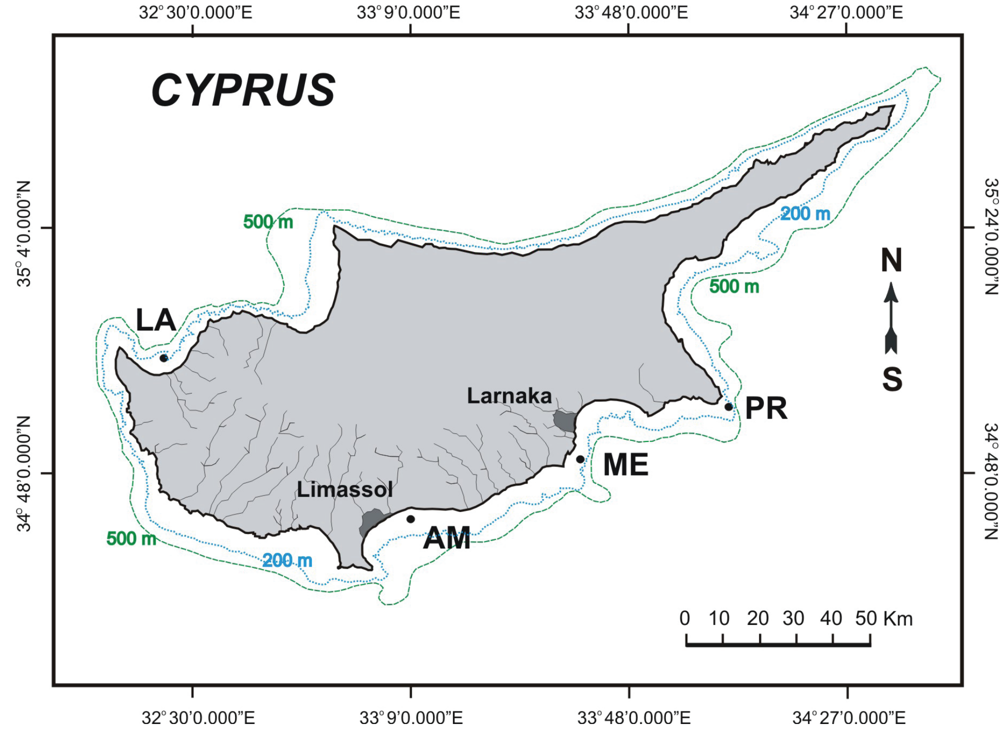

Fig. 1: Geographic location of the four sampling sites (LA: Latsi, AM: Amathounta, ME: Meneou, PR: Protaras) in the coastal area of Cyprus.

ture lands, is a designated NVZ according to the Nitrates Directive (91/676/EEC). Furthermore, in 2018, a fishing regulation for Cavo Greco was set-into-force to conserve fish stocks and marine species, according to which all fishing activities are forbidden in the marine area defined as the 'core zone'. In the 'buffer zone', professional fishermen are allowed to fish, but recreational fishing activities are not allowed. These four sites, at 50 m depth, are being monitored as part of the Water Framework Directive (WFD); for the period 2016–2019, they were found to be in good ecological status (Antoniadis *et al.*, 2020).

Sampling surveys

Twenty-five mesozooplankton samples were collected from the above four sampling sites, using a WP2 plankton net (57 cm in diameter, mesh size 200 μm), conducting vertical hauls from 50 m to the surface. The samples were collected during daytime, between July 2017 and September 2019. Seven samples were collected in summer, autumn and winter of 2017, ten samples were taken in 2018 (spring, summer, autumn) and eight samples in 2019 in all seasons (Table 1). A flowmeter was used to estimate the volume of the filtered water. After each haul, the zooplankton samples were kept in 250 ml plastic jars and preserved in 4% borax-buffered formalin. At each sampling site, *in situ* measurements of the surface temperature and dissolved oxygen (oxyGuard probe), pH and salinity were conducted. Surface water samples were collected for the laboratory analysis of chlorophyll-*α* using a Trilogy Fluorometer (Turner Designs, USA) following the methodology of Arar & Collins (1997).

Table 1. Date of samplings and volume of filtered water of the 25 samples taken between 2017 and 2019 from the four sampling areas of Cyprus (Latsi, Amathounta, Meneou and Protaras). Surface *in situ* measurements of temperature, dissolved oxygen, pH and salinity, and concentrations of chlorophyll-*α* are also provided.

			Water			**Dissolved**		
AREA	**DATE**	**Sample's ID**	**volume (m^3)**	**Temp. (^{o}C)**	**Salinity (psu)**	**Oxygen (mg L^{-1})**	**pH**	**Chl-a (mg L^{-1})**
Latsi	30/8/2017	LA8-17	28.98	27.1	38.1	8.9	8.09	0.01
	12/3/2018	LA3-18	14.82	19.3	38.0	8.9	7.78	0.03
	12/7/2018	LA7-18	19.44	28.0	38.1	8.0	8.21	0.04
	13/11/2018	LA11-18	25.40	24.3	38.4	8.3	7.86	0.03
	14/3/2019	LA3-19	9.70	18.1	38.0	9.3	8.10	0.06
	29/7/2019	LA7-19	13.20	23.9	38.3	8.7	7.72	0.02
Amathounta	5/7/2017	AM7-17	20.07	26.2	38.1	9.1	8.17	0.03
	3/12/2017	AM12-17	9.46	17.5	38.2	8.6	7.81	0.11
	14/3/2018	AM3-18	20.94	19.0	38.0	9.2	7.78	0.03
	22/8/2018	AM8-18	11.6	25.5	38.0	8.7	7.72	0.02
	21/11/2018	AM11-18	12.00	22.6	38.8	8.2	8.00	0.05
	4/4/2019	AM4-19	27.1	18.5	38.6	9.1	8.05	0.11
Meneou	24/7/2017	ME7-17	12.54	25.1	38.2	8.4	7.96	0.03
	2/11/2017	ME11-17	8.50	23.3	38.8	8.7	8.70	0.03
	28/3/2018	ME3-18	14.25	19.5	37.9	8.4	7.57	0.03
	19/7/2018	ME7-18	15.86	26.5	37.8	7.9	8.20	0.01
	21/2/2019	ME2-19	9.20	16.7	39.2	9.3	7.71	0.08
	21/5/2019	ME5-19	10.40	20.6	38.1	9.0	7.45	0.03
	3/9/2019	ME9-19	14.30	25.9	38.7	8.2	7.40	0.03
Protaras	12/7/2017	PR7-17	8.10	24.1	38.0	8.0	7.99	0.03
	23/10/2017	PR10-17	9.98	25.2	38.4	8.1	8.07	0.06
	19/4/2018	PR4-18	10.28	20.6	38.2	8.7	7.75	0.01
	30/8/2018	PR8-18	11.40	29.1	38.1	7.5	7.61	0.02
	11/2/2019	PR2-19	8.90	17.4	38.7	9.3	7.49	0.07
	12/6/2019	PR6-19	9.60	22.8	38.2	8.6	7.92	0.04

Zooplankton analysis

In the laboratory, all samples were examined under an Olympus CH-20 stereoscope or/and an inverted Leica DMIL microscope, following the standard protocol of HELCOM Programme (HELCOM, 2017). The identification of the mesozooplankton organisms was carried-out to the lower taxonomic level possible using the most recent identification keys (e.g. Al-Yamani *et al*., 2011a, b; Bowman, 1973; Conway, 2012a, b; Conway, 2015; Dos Santos & Gonzalez-Gordillo, 2004; Gravili *et al*., 2015; Grossmann *et al*., 2014; Guglielmo *et al*., 2015; Kehayias *et al*., 1999; Kramp, 1961; Lacuna *et al*., 2016; Martel *et al*., 2014; Mills *et al*., 2007; Naomi *et al*., 2006; Plate & Husemann, 1994; Pohle & Santana, 2014; Prusova *et al*., 2012; Semenikhina *et al*., 2008; Tregouboff & Rose, 1978). The abundance of each taxon was estimated and presented as individuals m^{-3}.

Three ecological indices were estimated from the abundance data of only the copepods and cladocerans, which are the most commonly studied taxa in the Mediterranean Sea. Specifically, the Species Richness (S), Shannon-Wiener (H) and Pielou's Evenness (J) were estimated as follows:

$$\boldsymbol{S} = {}^{s}\!/\!\sqrt{N}$$

where s is the number of species in the sample and N is the total number of specimens in the sample

$$\boldsymbol{H} = -\sum_{i=1}^{s} pi * lnpi$$

where s is the number of species in community and *pi* is the proportion of total abundance represented by *i*th species

$$\mathbf{J} = H' / Hmax$$

where H' = calculated Shannon-Wiener diversity, Hmax = ln(s) [species diversity under maximum equitability conditions.

The non-parametric Kruskal-Wallis test was used for the comparison of a) the three indices' values, b) the abundance of the total mesozooplankton, c) the number of mesozooplankton taxa and their abundance, d) the environmental parameters, among sampling sites, seasons and years. Due to the lack of replication in each sampling occasion, pooled data were used (e.g., for the sampling sites comparisons, pooled data including all seasons and years were used). All the analyses were performed using IBM SPSS 25 and the significance level was set at 5% ($p = 0.05$).

To identify the zooplanktonic species assemblages that characterize each season, the Indicator Value index (IndVal, Dufrêne and Legendre, 1997) was applied. IndVal index combines the species relative abundance (the so-called specificity, A_{jk}) with the relative frequency of occurrence of this species within a given group of observations (the so-called fidelity, B_{jk}):

$$IndVal_{jk} = A_{jk} \text{ x } B_{jk} \text{ x } 100$$

where, A_{jk} is the ratio between the mean abundance of the species *j* in the observations of the season *k* and the sum of the mean abundance of the species *j* in all seasons:

$$A_{jk} = Nsp_{jk} / Nsp_{+k}$$

where, B_{jk} is the ratio between the number of observations in the season *k* where the species *j* is present and the total number of observations in *k* season:

$$Bjk = Nobs_{jk} / Nobsp_{+k}$$

The IndVal analysis identifies the most characteristic species in each season not only based on their highest abundance, but also on their occurrence in the samples of that season (Mazzocchi *et al*., 2014).

Principal component analysis (PCA) was applied to examine the variability patterns of the mesozooplankton community among sites, seasons and years. Redundancy analysis (RDA) was performed to assess significant relationships between mesozooplankton and environmental data. In the case of the mesozooplankton the numerically most important taxa were used in the estimations. Both analyses were performed in log(x+1) transformed variables using the CANOCO program, version 4.5 (TerBraak & Smilauer, 2002). Significant environmental variables that explained the variability of the community structure were determined through forward-selected Monte Carlo analysis with 999 permutation tests at $p<0.05$ (TerBraak & Smilauer, 2002).

Results

Total mesozooplankton

The total mesozooplankton abundance fluctuated between 190.4 (LA, summer of 2017) and 882.5 individuals m^{-3} (PR, summer 2019) without having a constant pattern of seasonal variability (Table 2). The average value was 472.7 ± 174.8 individuals m^{-3}. The abundance values did not present any statistically significant differences among sampling areas, seasons, or years (Kruskal-Wallis test, $p > 0.05$).

Mesozooplankton composition

The analysis of the 25 zooplankton samples revealed a total number of 90 holoplanktonic and meroplanktonic taxa (Table S1). Copepods comprised the dominant group accounting for 45 taxa, followed by decapods (9 taxa) and chaetognaths (8 taxa), while a smaller number of taxa belonged to cladocerans, appendicularians, thaliaceans, siphonophores, medusae, polychaetes, euphausiids, mysids, amphipods, ostracods, cirripeds, molluscs, and echinoderms. No statistically significant differences in the number of taxa among sampling sites and seasons

Table 2. Abundance (ind. m^{-3}) of the zooplankton groups found in each of the 25 samples taken between 2017 and 2019 from the four sampling areas of Cyprus (Latsi, Amathounta, Meneou and Protaras). Abbreviations of the samples' ID as in Table 1.

SAMPLING AREAS	Latsi						Amathounta						Meneou							Protaras					
ZOOPLANKTON GROUP	**LA8-17**	**LA3-18**	**LA7-18**	**LA11-18**	**LA3-19**	**LA7-19**	**AM7-17**	**AM12-17**	**AM3-18**	**AM8-18**	**AM11-18**	**AM4-19**	**ME7-17**	**ME11-17**	**ME3-18**	**ME7-18**	**ME2-19**	**ME5-19**	**ME9-19**	**PR7-17**	**PR10-17**	**PR4-18**	**PR8-18**	**PR2-19**	**PR6-19**
HOLOPLANKTON																									
COPEPODS	121.4	391.1	246.3	167.4	603.9	410.2	430.4	322.1	221.3	378.3	348.3	143.3	253.2	481.4	145.7	482.4	393.3	299.9	392.7	410.2	588.4	266.1	317.5	241.0	338.3
CLADOCERANS	42.52	0.13	10.70	99.17	0.00	59.39	7.18	1.69	6.06	43.46	0.08	0.00	18.50	12.47	5.05	17.15	0.00	0.00	103.50	38.50	16.03	2.33	42.67	0.00	3.96
CHAETOGNATHS	3.66	1.08	7.46	0.63	16.08	22.95	2.24	7.40	1.10	2.76	0.67	4.50	2.31	2.24	0.63	2.21	5.54	8.56	4.55	6.79	5.01	3.50	2.19	2.81	154.69
APPENDICULARIANS	1.38	11.88	7.41	7.36	157.94	4.24	29.50	24.52	164.27	47.60	20.25	28.78	24.88	22.59	78.04	5.55	36.52	13.08	8.95	9.87	25.65	25.68	12.59	134.27	24.27
THALIACEANS	0.24	0.00	0.41	1.42	18.14	0.00	0.25	4.23	0.43	1.47	0.25	14.54	0.16	2.82	0.84	0.00	4.89	2.98	1.33	2.96	0.50	2.04	0.61	2.25	1.46
EUPHAUSIIDS	0.10	0.61	0.31	0.12	2.06	0.30	0.15	1.27	0.00	0.43	0.25	0.15	0.00	0.59	0.00	0.00	0.00	0.29	0.28	0.25	0.30	1.36	0.26	0.56	1.04
MYSIDS	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.06	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
AMPHIPODS	0.00	0.00	0.10	0.08	0.21	0.15	0.05	0.00	0.05	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.11	0.10	0.00	0.00	0.00	0.10	0.00	0.11	0.00
OSTRACODS	0.55	1.55	0.82	0.63	12.37	1.21	0.80	5.92	0.00	1.38	1.00	0.15	0.40	3.76	0.56	0.32	6.09	1.54	4.55	0.99	3.21	1.56	0.00	3.93	1.04
SIPHONOPHORES	4.07	7.15	15.63	13.19	19.18	13.18	2.64	35.51	31.33	15.87	0.08	18.23	11.72	19.77	14.60	8.51	33.80	20.48	5.03	25.91	7.21	17.90	31.39	6.29	2.29
MEDUSAE	0.21	4.32	0.15	0.28	2.27	0.83	0.00	1.69	4.58	2.07	0.00	0.81	0.00	1.88	5.61	0.44	7.07	0.48	0.56	1.97	0.00	1.56	2.62	8.20	2.29
DECAPODS	0.00	0.00	0.00	0.35	0.31	0.45	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.12	0.00	0.00	0.00	0.29	0.00	0.00	0.00	0.00	0.61	0.00	2.92
MOLLUSKS	6.35	0.00	0.05	0.28	6.08	9.02	0.25	1.69	0.24	0.00	0.58	0.30	0.48	1.88	1.12	0.00	1.09	0.67	0.56	0.86	0.80	0.00	0.70	1.46	26.35
POLYCHAETS	0.24	0.54	0.05	0.12	1.96	1.06	0.30	1.48	0.10	0.69	0.00	0.33	0.00	0.00	0.56	0.00	0.76	0.19	0.21	0.00	0.00	0.58	0.26	2.02	0.52
MEROPLANKTON																									
DECAPODS (larvae)	4.59	4.72	4.11	1.89	1.13	4.55	9.77	1.80	2.34	5.09	3.42	17.05	1.36	5.65	8.98	3.34	0.54	3.75	8.32	1.73	10.42	2.33	10.49	6.18	19.58
MOLLUSKS (larvae)	4.97	8.64	4.94	3.15	24.95	7.27	3.19	3.28	0.76	2.07	10.92	0.26	79.76	16.94	0.56	0.50	3.59	2.98	29.86	24.68	6.41	3.89	4.90	20.00	302.50
ECHINODERMS (larvae)	0.00	0.00	0.00	2.95	7.63	0.53	0.00	0.42	0.33	0.00	0.00	0.00	0.00	0.00	1.68	0.00	20.00	0.58	0.00	0.00	0.00	0.78	0.00	0.45	1.04
POLYCHAETS (larve)	0.14	0.07	0.05	0.16	1.65	0.53	0.05	0.42	0.00	0.26	0.08	0.26	0.00	0.00	0.28	0.00	0.22	0.00	0.00	0.00	0.00	0.19	0.09	0.56	0.21
CIRRIPEDS (larvae)	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.28	0.00	0.00	2.72	0.00	0.00	0.00
TOTAL	190.4	431.8	298.5	299.1	875.9	536.2	486.8	414.5	432.9	501.5	386.4	229.0	392.8	572.1	264.2	520.4	513.5	355.9	561.0	524.7	663.9	335.4	426.9	430.1	882.5

were found (Kruskal-Wallis test, $p = 0.654$ and $p = 0.545$, respectively). Instead, a significantly higher number of taxa were recorded on the third year (2019) of sampling (Kruskal-Wallis test, $p = 0.001$) with the addition of 12 taxa, which included 7 copepod species (*Candacia armata*, *Euchirella messinensis*, *Euterpina acutifrons*, *Isias clavipes*, *Lucicutia ovalis*, *Pareucalanus attenuatus*, and *Pontella mediterranea*), one species of cladocerans (*Penillia avirostris*), chaetognaths (*Decipisagitta decipiens*), and decapods (*Squilla mantis*), one mollusc (cephalopod larvae), and cirriped larvae. For most of them, only a few specimens were found in one or two occasions during 2019, except for *I. clavipes* which was present on four occasions.

The three ecological indices, calculated using the abundance data set for the copepods and cladocerans, presented generally low variability (Fig. 2). Species richness (S) fluctuated between 0.236 and 0.611, the Shannon-Wiener (H) values ranged between 1.633 and 2.733, and the values of Pielou's evenness (J) ranged from 0.565 to 0.849. Comparison of the three indices' values among sampling areas, seasons, and years revealed no statistically significant differences (Kruskal-Wallis test, $p > 0.05$).

Temporal abundance variation

Copepods dominated the samples with abundance values between 121.4 and 603.9 individuals m^{-3} and an average contribution of 71.7% to the total mesozooplankton abundance. Appendicularians ranked second in abundance, accounting for 8.04% of the total mesozooplankton abundance, followed by molluscs, cladocerans, and siphonophores which contributed 5.48%, 4.60%, and 3.31%, respectively (Table 2). No statistically significant differences of abundance were found for any of the mesozooplankton taxa among the four sampling locations (Kruskal-Wallis test, $p > 0.05$).

The copepodites of the genus *Clausocalanus* (not identified down to the species level), along with the adults of *Clausocalanus furcatus* and *Clausocalanus arcuicornis*, accounted for nearly the 25% of the total copepod abundance. The above taxa were present in all seasons and sampling sites, with the abundance of *C. furcatus* being higher in summer and that of *C. arcuicornis* being higher in winter and spring (Table 3). *Paracalanus parvus* and *Oithona plumifera* contributed 10.39% and 10.36% of the total copepods, respectively. The abundance variation of *P. parvus* showed a remarkable stability among seasons, while *O. plumifera* was more abundant in autumn without any statistical significance. In contrast, the genus *Calocalanus*, especially the species *Calocalanus pavo* (accounting for 8.32% in the total mesozooplankton along with the copepodites *Calocalanus* sp.), was among the few species, together with *Centropages kroyeri*, *Centropages typicus*, Oncaeidae, *Pleuromamma gracilis,* and *Temora stylifera*, that presented statistically significant seasonal differences (Kruskal-Wallis test, $p < 0.05$). In particular, *C. kroyeri*, *C. typicus*, and *T. stylifera* presented greater abundance in summer, *C. pavo* and *P. gracilis* in autumn, and Oncaeidae in spring (Table 3). Considering the seasonal comparisons, it must be pointed out that the sample taken on the 3rd of September 2019 in the ME area (ME9-19) is considered a summer sample.

Appendicularians were ranked second in terms of abundance among the mesozooplankton groups, with *Oikopleura dioica* reaching 37.82% of the total zooplankton in one sample taken on the 14th of March 2018 (AM3-18). This species was more abundant in winter and spring and lower in summer (Kruskal-Wallis test, $p = 0.024$). Several other taxa presented seasonal differences (Fig. 3), such as the cladocerans *Evadne spinifera* and *Pseudevadne tergestina*, which were more abundant in summer ($p = 0.018$ and $p = 0.001$, respectively). The medusa *Sarsia* sp. was the most abundant cnidarian during winter ($p = 0.025$), along with the polychaete family Tomopteridae ($p = 0.007$), while the salp *Thalia democratica* was more abundant in spring ($p = 0.048$). Among the meroplanktonic taxa, gastropod larvae dominated the mollusc community having an average proportion of 4.62% of the

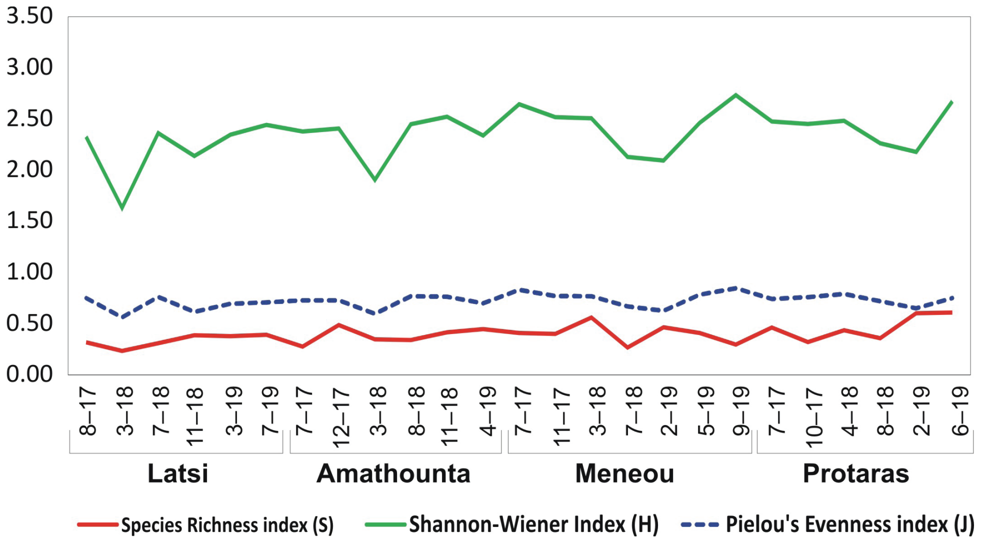

Fig. 2: Variability of the three ecological indices (S: species richness, H: Shannon-Wiener, J: Pielou's evenness) during the entire sampling period of 2017-2019.

Table 3. Abundance (ind. m^{-3}) of the numerically most important copepod species (> 5 ind. m^{-3}) found in each of the 25 samples taken between 2017 and 2019 from the four sampling areas of Cyprus (Latsi, Amathounta, Meneou and Protaras). Abbreviations of the samples' ID as in Table 1.

SAMPLING AREAS	**Latsi**						**Amathounta**						**Meneou**							**Protaras**					
COPEPODS	**LA8-17**	**LA3-18**	**LA7-18**	**LA11-18**	**LA3-19**	**LA7-19**	**AM7-17**	**AM12-17**	**AM3-18**	**AM8-18**	**AM11-18**	**AM4-19**	**ME7-17**	**ME11-17**	**ME3-18**	**ME7-18**	**ME2-19**	**ME5-19**	**ME9-19**	**PR7-17**	**PR10-17**	**PR4-18**	**PR8-18**	**PR2-19**	**PR6-19**
Acartia clausi	1.10	5.13	4.11	1.85	0.41	0.00	6.58	4.23	0.33	4.83	2.50	3.54	4.63	1.88	0.21	9.08	1.85	2.31	3.92	11.84	2.40	4.47	7.69	2.70	2.60
Acartia negligens	0.00	0.27	1.23	3.19	1.65	0.91	0.65	0.00	0.00	0.00	0.00	0.00	3.03	0.00	0.00	2.02	0.87	0.48	2.24	22.70	0.00	0.19	12.59	0.00	1.56
Calocalanus pavo	6.49	10.80	16.87	8.43	7.63	15.91	5.98	16.49	3.34	11.73	34.17	1.18	14.99	65.88	8.42	19.67	7.07	3.85	26.85	15.79	54.10	9.34	31.48	0.90	20.00
Calocalanus pavoninus	0.28	2.16	1.65	1.02	1.75	2.88	0.00	4.23	0.29	1.38	15.83	1.11	4.47	8.47	3.37	6.05	0.98	0.77	2.94	3.95	3.21	3.11	0.70	0.00	2.19
Calocalanus spp. (copep.)	11.73	18.36	20.98	7.56	16.49	19.70	11.56	39.31	4.78	7.59	42.50	8.86	20.74	60.24	12.91	17.65	14.78	20.00	32.52	34.55	84.55	18.68	9.09	3.48	19.17
Centropages kroyeri	2.21	0.00	8.64	0.00	0.00	0.00	84.56	1.16	0.57	55.19	0.00	0.00	8.29	0.00	3.30	11.60	0.00	3.08	23.08	0.74	0.00	3.11	0.70	0.00	0.21
Centropages typicus	0.55	0.00	2.06	0.20	0.00	0.76	16.69	1.06	0.24	37.25	0.00	1.22	13.32	0.00	1.12	15.63	0.00	9.13	43.64	1.97	0.00	0.78	0.70	0.00	0.21
Clausocalanus arcuicornis	3.87	7.56	16.87	3.74	66.19	3.26	12.76	12.68	38.97	8.97	8.33	28.93	10.21	21.65	4.49	9.58	13.91	9.81	6.01	20.73	33.26	6.23	23.78	38.43	29.17
Clausocalanus furcatus	13.25	21.60	18.51	25.20	63.09	38.94	31.89	10.15	33.62	24.15	15.83	7.68	30.63	14.12	3.93	33.79	33.04	13.85	23.78	108.58	8.82	4.67	50.36	11.69	18.75
Clausocalanus parapergens	0.00	1.08	0.82	0.94	10.41	15.23	2.39	0.63	0.48	0.00	0.00	1.33	1.91	0.00	0.56	0.13	3.37	2.50	6.57	0.49	0.90	1.56	0.00	0.79	14.17
Clausocalanus spp. (copep.)	27.61	221.36	53.49	58.27	187.01	151.82	33.49	50.73	93.21	84.17	59.58	43.69	38.28	28.24	22.46	227.95	180.00	47.50	79.44	76.99	58.10	42.80	39.17	83.15	57.50
Corycaeus crassiusculus	0.83	0.00	1.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.47	0.00	0.00	0.00	0.00	0.00	0.74	20.44	0.00	2.10	0.00	0.00
Corycaeus lubbocki	0.00	0.00	0.00	6.93	24.74	3.48	0.00	0.00	0.00	0.00	15.42	0.00	0.00	0.00	0.00	0.00	6.09	1.44	0.98	0.00	0.00	0.00	0.00	0.00	0.42
Corycaeus typicus	1.38	12.15	4.94	4.41	51.96	7.88	28.70	16.91	17.00	15.87	2.50	11.22	12.76	22.59	8.42	14.62	23.37	8.56	10.07	15.79	18.03	19.46	8.39	36.85	20.00
Farranula rostrata	1.38	42.92	1.23	0.71	6.60	5.45	0.80	6.76	6.69	0.00	1.67	1.77	0.64	5.65	3.37	0.00	6.30	6.54	25.24	1.97	6.41	16.34	0.70	8.09	28.13
Isias clavipes	0.00	0.00	0.00	0.00	0.00	12.88	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00	14.06	0.00	0.00	0.00	0.00	0.00	0.63
Lucicutia flavicornis	0.24	3.24	0.82	0.24	11.55	16.67	0.35	0.53	0.19	5.52	21.33	0.00	1.91	8.47	1.12	9.08	7.07	4.04	0.98	2.96	14.43	9.34	3.50	0.90	2.60
Lucicutia spp. (copep.)	0.00	0.00	0.00	0.00	0.00	0.00	7.97	0.00	0.00	0.26	0.00	0.00	0.64	0.00	0.00	0.00	0.00	0.00	0.35	0.00	0.00	0.00	0.00	0.22	0.00
Mecynocera clausii	0.21	0.00	0.41	0.87	1.24	4.92	1.59	0.00	0.38	0.69	2.50	1.11	1.60	7.53	0.00	7.56	3.26	1.63	1.05	3.95	9.62	0.00	0.00	3.60	3.44
Mesocalanus tenuicornis	0.00	0.00	0.00	0.47	5.36	3.33	0.00	1.69	0.00	0.00	0.75	1.03	0.00	0.00	2.25	0.00	3.04	2.12	2.10	0.00	0.00	6.23	0.00	0.90	1.04
Nannocalanus minor	4.14	0.00	0.00	0.28	1.13	0.38	1.59	0.00	0.00	0.00	0.17	0.55	0.48	18.82	0.35	0.00	1.09	0.38	0.84	0.99	14.43	0.00	0.00	0.00	1.77
Oithona plumifera	5.52	6.48	9.87	12.28	14.85	18.11	27.90	33.82	11.46	40.01	25.17	5.35	22.97	122.36	22.46	35.30	9.24	16.15	38.60	38.50	168.30	40.47	108.42	7.30	28.33
Oithona setigera	0.00	0.00	0.00	5.35	2.47	2.42	0.00	3.59	0.57	0.00	2.92	0.00	0.00	1.88	1.68	0.00	1.63	9.33	2.66	0.00	0.00	4.67	0.00	1.01	3.13
Oncaeidae	0.00	2.16	0.00	0.00	21.03	3.64	3.19	3.38	1.34	1.38	11.67	3.51	0.00	6.59	5.61	2.02	20.00	1.63	2.87	0.99	6.41	13.23	1.40	6.52	3.75
Paracalanus parvus	8.28	34.42	23.45	21.10	80.93	53.94	112.37	69.75	2.29	14.49	49.58	9.45	31.90	47.06	35.09	25.22	44.57	16.73	15.24	23.69	48.09	58.37	15.39	15.28	15.42
Temora stylifera	31.75	0.00	58.42	2.13	13.20	23.64	36.68	39.74	4.58	60.71	32.00	7.08	29.35	24.47	2.25	34.80	6.52	7.50	18.95	19.74	28.85	1.56	0.00	11.69	55.00

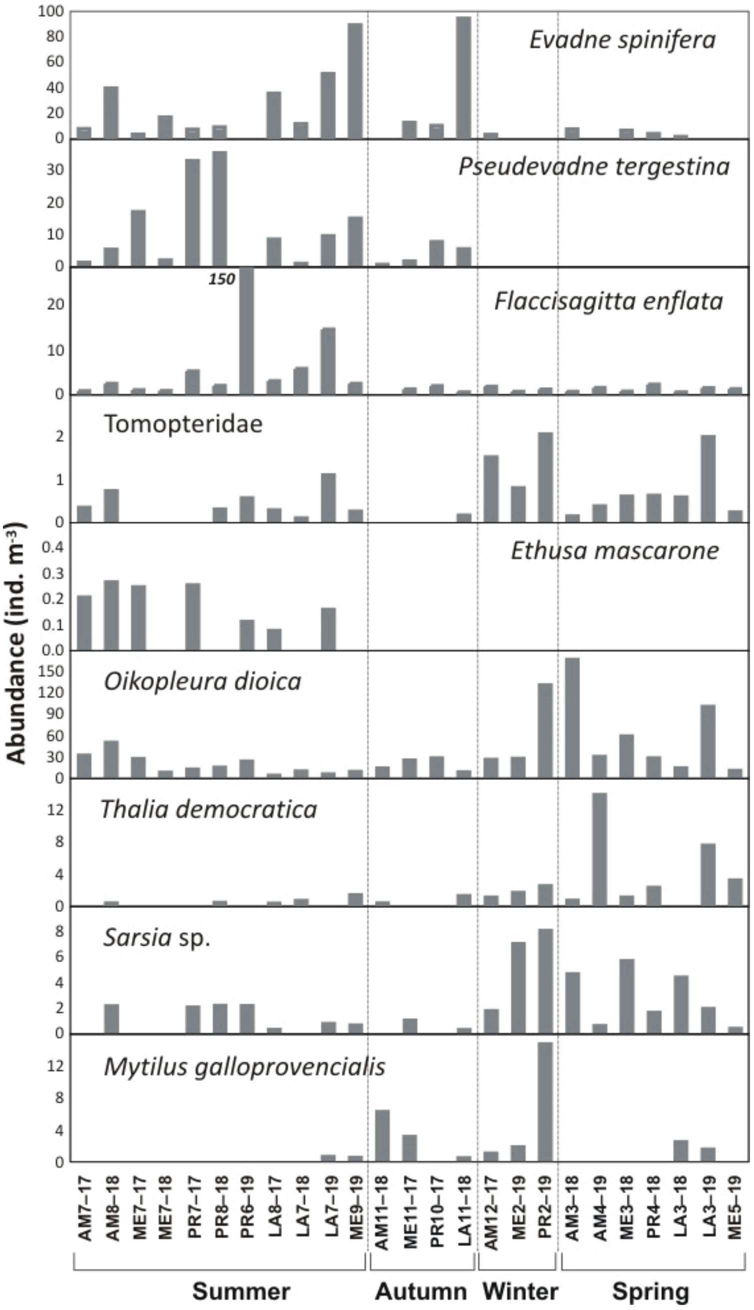

Fig. 3: Seasonal variability of abundance (ind. m^{-3}) of some important mesozooplanktonic taxa that presented clear seasonality. Abbreviations of the samples' IDs are listed in Table 1.

total zooplankton and presented peaks during the summer period; this was also the case for the decapod larvae of *Ethusa mascarone*, which was found only in the summer samples ($p = 0.021$). In contrast, the larvae of the mollusc *Mytilus galloprovincialis* displayed greater abundances in winter ($p = 0.013$). Some taxa were found extremely abundant only in certain locations, like the chaetognath *Flaccisagitta enflata* and the larvae of gastropods on the 12th of June 2019 (PR6-19 (Fig. 3).

Significant differences in the abundance between the three years were also observed in the cases of taxa found mainly or only in 2019, such as *Centropages violaceus*, *Corycaeus lubbocki*, *Haloptilus longicornis*, and *I. clavipes* (Kruskal-Wallis test, $p < 0.05$). In addition, abundance differences were noticed for *Clausocalanus parapergens*, *Mesocalanus tenuicornis*, and *Scolecitrichella tenuiserrata*, which displayed the highest values in 2019, while *Nannocalanus minor* displayed the highest values in 2017. The appendicularian *Fritillaria borealis,* the chaetognaths *Sagitta bipunctata* and *Serratosagitta serratodentata*, the amphipod *Hyperia* sp, and the meroplanktonic larvae of the polychaetes Amphiodititidae, of the decapod *Upogebia* sp., and of the pteropods were more abundant in 2019 than in 2017–18 (Kruskal-Wallis test, $p < 0.05$).

In the PCA plot, the samples collected during the summer months are clearly discriminated along the first axis by those collected in the winter-spring (Fig. 4, Table S2). The summer samples are placed close to taxa being more abundant in summer, like *C. kroyeri*, *C. typicus*, *E. spinifera, P. tergestina*, and *T. stylifera,* as well as the copepods *Acartia clausi*, *Acartia negligens*, *C. furcatus*, and

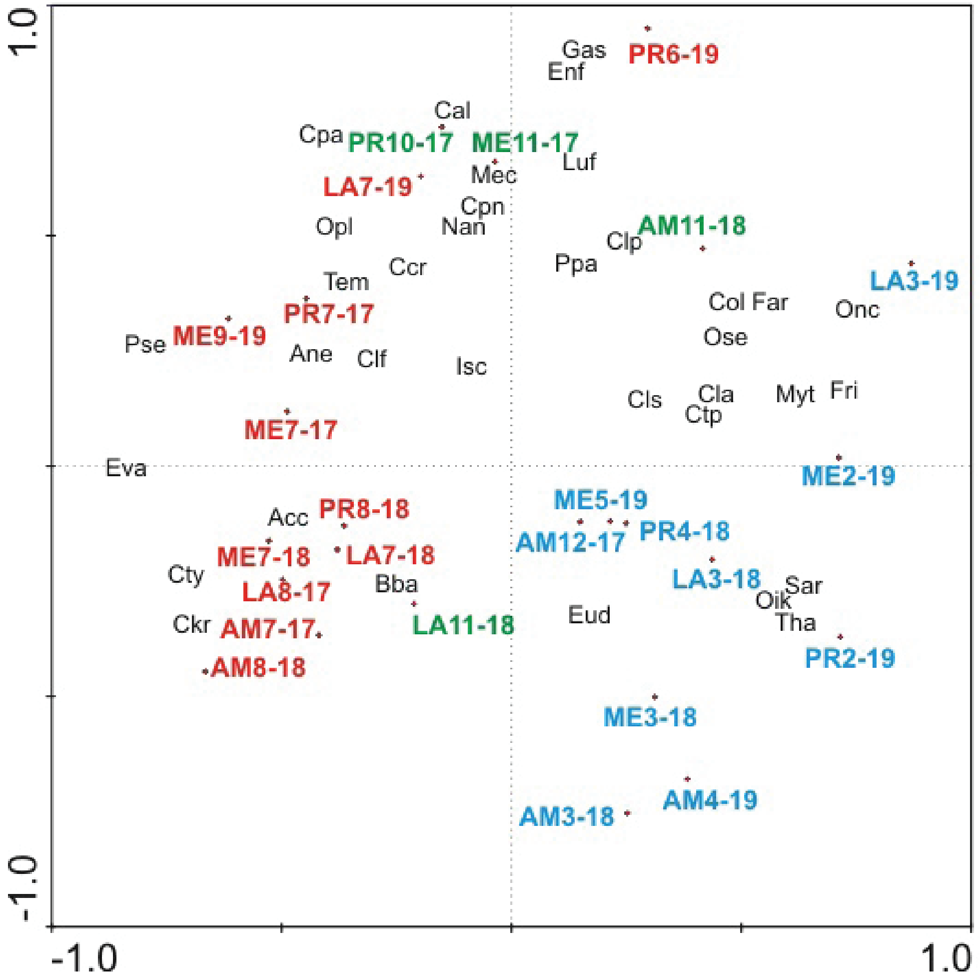

Fig. 4: PCA plot of the 25 samples and the numerically most important mesozooplankton taxa recorded in the four sampling sites during the entire sampling period of 2017–2019. The codes of samples are the same as in Table 1. The taxa abbreviations are as follows: Acc: *Acartia clausi,* Ane: *A. negligens*, Cpa: *Calocalanus pavo*, Cpn: *Calocalanus pavoninus*, Cal: *Calocalanus* spp., Ckr: *Centropages kroyeri*, Cty: *Centropages typicus*, Cla: *Clausocalanus arcuicornis*, Clf: *Clausocalanus furcatus*, Clp: *Clausocalanus parapergens*, Cls: *Clausocalanus* spp., Ccr: *Corycaeus crassiusculus*, Ctp: *Corycaeus typicus*, Col: *Corycaeus lubbocki*, Far: *Farranula rostrata*, Isc: *Isias clavipes*, Luf: *Lucicutia flavicornis*, Mec: *Mecynocera clausii*, Nan: *Nannocalanus minor*, Opl: *Oithona plumifera*, Ose: *Oithona setigera*, Onc: Oncaeidae Ppa: *Paracalanus parvus*, Tem: *Temora stylifera*, Eva: *Evadne spinifera*, Pse: *Pseudevadne tergestina*, Enf: *Flaccisagitta enflata*, Bba: *Bassia bassensis*, Eud: *Eudoxoides* sp., Fri: *Fritillaria borealis*, Oik: *Oikopleura dioica*, Tha: *Thalia democratica*, Sar: *Sarsia* sp., Gas: Gastropod larvae, Myt: *Mytilus galloprovencialis*. (With red, green and blue colours are the samples taken in the summer, the autumn and the winter-spring seasons, respectively).

I. clavipes, and the siphonophore *Bassia bassensis*. These taxa could be considered as the ‘summer group’. On the other hand, samples collected in the winter and spring are closely projected at the opposite side of the first axis forming the ‘winter-spring group’ and are associated with several taxa, such as the copepods *C. arcuicornis*, *Clausocalanus* sp., *C. lubbocki*, *Corycaeus typicus*, *Farranula rostrata*, *Oithona setigera*, and Oncaeidae, the appendicularians *F. borealis* and *O. dioica*, the siphonophore *Eudoxoides* sp., the thaliacean *T. democratica*, the medusa *Sarsia* sp., and the larvae of *M. galloprovencialis*. Samples collected in the autumn are projected between the summer and the winter-spring samples; the autumn samples are closely projected and associated with some taxa that presented abundance peaks in autumn, such as the copepods *C. pavo*, *Calocalanus pavoninus*, *Calocalanus* sp., *Corycaeus crassiusculus*, *Lucicutia flavicornis*, *Mecynocera clausii*, *N. minor*, and *O. plumifera*. This could account for a smaller third party considered as the ‘autumn group’. Apart from these formations, there are species like *P. parvus* and *C. parapergens*, which had uniform seasonal abundance variation and were plotted outside of the three groups. The single sample collected in June (PR6-19) is projected close to the autumn samples; *F. enflata* and gastropod larvae, which were extremely abundant in this sample, are projected closely in the PCA plot. Considering the distinction of the summer samples from those collected in winter-spring along the first axis, it is evident that temperature variability accounts for the formation of this axis.

Table 4 presents the values of the indicator value index (IndVal) estimated for the three periods. In summer, *C. kroyeri*, *P. tergestina*, *C. typicus*, and *A. negligens* presented higher values (60.45, 54.93, 51.74, and 44.72, respectively) and were the most characteristic species of this period. *F. enflata* and the gastropod larvae also presented

Table 4. The values of Indicator Value Index (IndVal) estimated for the 35 most important zooplanktonic taxa in each season, and the average abundance (ind. m^{-3}) of these taxa in all samples collected from the four sampling sites (Latsi, Amathounta. Meneou and Protaras) during 2017-2019.

Code	Zooplankton taxa	Summer	Autumn	Win.-Spr.	Avg
Acc	*Acartia clausi*	17.01	2.87	8.36	3.61
Ane	*Acartia negligens*	44.72	0.93	2.02	2.14
Bba	*Bassia bassensis*	15.98	1.54	11.35	4.41
Cpa	*Calocalanus pavo*	10.31	9.03	3.83	16.69
Cpn	*Calocalanus pavoninus*	8.01	9.49	5.32	2.91
Cal	*Calocalanus* sp.	8.14	7.73	6.25	22.31
Ckr	*Centropages kroyeri*	60.45	0.00	1.91	8.26
Cty	*Centropages typicus*	51.74	0.02	3.17	5.86
Cla	*Clausocalanus arcuicornis*	7.77	3.58	12.15	17.57
Clf	*Clausocalanus furcatus*	17.22	2.81	8.92	26.40
Clp	*Clausocalanus parapergens*	18.04	0.55	13.50	2.65
Cls	*Clausocalanus* sp.	10.58	2.48	11.83	81.84
Ccr	*Corycaeus crassiusculus*	4.18	31.25	0.00	1.37
Col	*Corycaeus lubbocki*	1.41	11.84	10.26	2.38
Ctp	*Corycaeus typicus*	8.17	2.77	11.98	15.75
Eud	*Eudoxoides* sp.	6.10	2.43	12.54	9.16
Eva	*Evadne spinifera*	24.01	8.70	0.78	15.59
Far	*Farranula rostrata*	8.14	2.19	15.99	7.41
Enf	*Flaccisagitta enflata*	40.42	0.41	1.78	7.89
Fri	*Fritillaria borealis*	0.63	2.71	26.27	4.87
Gas	Gastropod larvae	31.89	1.96	3.35	21.66
Isc	*Isias clavipes*	11.19	0.00	14.89	5.10
Luf	*Lucicutia flavicornis*	8.37	8.34	6.41	5.08
Mec	*Mecynocera clausii*	11.17	9.91	3.25	2.29
Myt	*Mytilus galloprovencialis*	0.08	8.64	12.97	1.18
Nan	*Nannocalanus minor*	4.03	20.94	1.09	1.90
Oik	*Oikopleura dioica*	4.62	1.79	15.50	32.22
Opl	*Oithona plumifera*	9.99	8.78	4.48	34.77
Ose	*Oithona setigera*	1.99	6.77	17.75	1.73
Onc	Oncaeidae	2.68	3.55	15.05	4.89
Ppa	*Paracalanus parvus*	9.09	4.44	9.82	34.88
Pse	*Pseudevadne tergestina*	54.93	6.60	0.00	5.47
Sar	*Sarsia* sp.	3.45	0.32	19.84	1.85
Tem	*Temora stylifera*	18.26	4.76	4.61	22.02
Tha	*Thalia democratica*	0.90	0.59	30.59	1.39

very high values during this period (40.42 and 31.89, respectively). In autumn, the copepods *C. crassiusculus* and *N. minor* presented the highest IndVal values (31.25 and 20.94, respectively). Finally, in the winter-spring period, *T. democratica* and *F. borealis* presented the highest IndVal values (30.59 and 26.27, respectively), while other taxa, such as *O. setigera*, *F. rostrata*, *O. dioica*, and the Oncaeidae, presented values greater than 15 and could be considered as characteristic species of the latter season (Table 4).

Influence of the environmental parameters

During 2017–2019, data concerning five environmental parameters were measured in the surface water of the sampling sites (Table 1). There were no statistically significant differences among the four sampling locations for any of the five parameters (Kruskal-Wallis test, $p < 0.05$). The *in-situ* measurements of the water temperature revealed a fluctuation due to seasonality (between 16.70 °C in February 2019 in ME and 29.10 °C in August 2018 in PR). Salinity varied between 37.8 and 39.2, presenting differences among seasons with the highest mean value in autumn (38.60 ± 0.23). The concentration of dissolved oxygen (DO) ranged between 7.50 and 9.3 mg L^{-1} with greater values in winter, and the chlorophyll-*α* (Chl-*α*) concentration ranged between 0.01 and 0.11 μg L^{-1} with greater values in winter-spring. The seasonal differences of temperature, salinity, DO, and Chl-*α* were statistically significant (Kruskal-Wallis test, $p < 0.05$). Greater values of Chl-*α* were recorded in the winter to early spring of 2019 in the areas of LA, ME, and PR, although there were no statistically significant differences among the three years. The pH fluctuated between 7.40 and 8.70 without any significant seasonal variation but with lower values in 2019 (Kruskal-Wallis test, $p < 0.05$).

In order to reveal the influence of the five environmental parameters on the abundance variation of the mesozooplankton taxa, the RDA analysis was applied, and the results are shown in Figure 5 and Table S3. The numerical elements revealed that there was a significant proportion of the total variability (34.0%), with axes 1 and 2 representing the greatest proportion of explanatory values (18.6% and 7.4%, respectively). Based on the first two axes, RDA analysis explains the 26.0% of the variance of species data and the 76.4% of the variance in the weighted averages of the species with respect to the environmental variables (Table S3). The environmental variables in the plot are represented by arrows, the length of which is proportional to the rate of change into the direction of the maximum change of these variables across the diagram. Temperature holds the longest arrow along the first axis and this parameter explains 63% of the species composition, while DO and Chl-*α* accounted for 44% and 36%, respectively, and pH had the smaller contribution (16%). Along the second axis, 66%, 43%, and 39% of the species composition are explained by pH, salinity, and DO, respectively. Temperature positively affected several taxa, mostly those that are plotted towards the direction of the arrow and are more remote from the central of the axes, such as *E. spinifera, P. tergestina,* and *A. negligens,* as well as *C. kroyeri* and *C. typicus*, which are the characteristic species of the summer samples. At the same time, temperature negatively affected the taxa projected at the exact opposite side of the vector, like Oncaeidae, *O. dioica*, *Corycaeus typicus*, and *O. setigera*, but also *T. democratica*, *F. rostrata,* and *F. borealis*, all being characteristic species of the winter-spring samples. Additionally, according to the RDA plot, temperature is

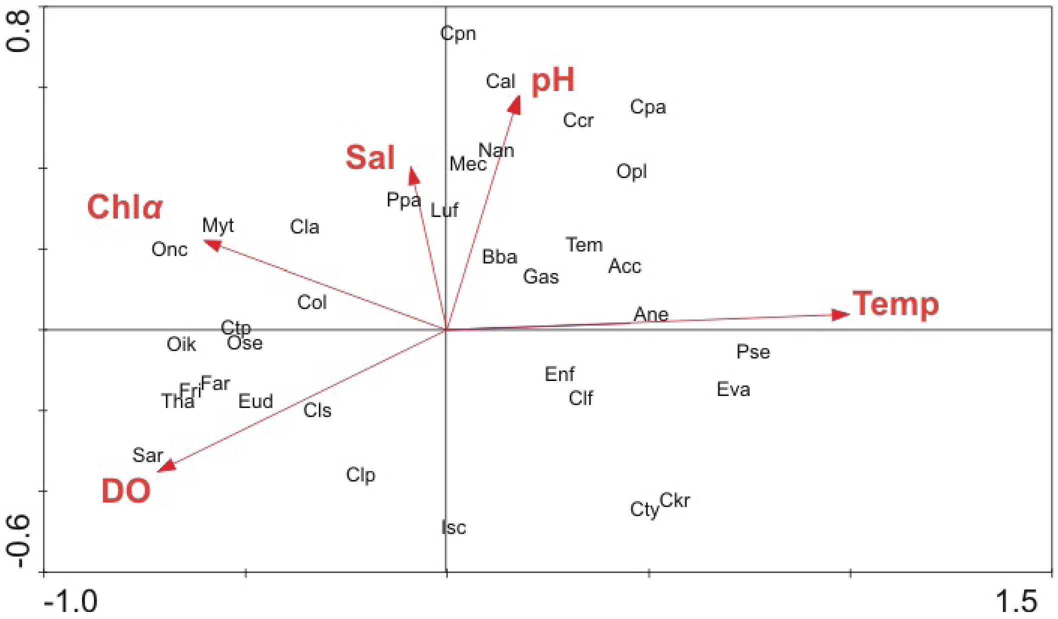

Fig. 5: RDA plot of the environmental parameters and the mesozooplankton taxa recorded in the four sampling sites during the entire sampling period of 2017–2019. The taxa abbreviations are the same as in Figure 4. Temp: temperature; Chl*α*: chlorophyll-*α*; DO: dissolved oxygen; Sal: salinity.

opposed to Chl-*α* and DO along the first axis, thus all three parameters contribute to the distinction of samples collected during the warm period (summer), which was the period of low Chl-*α* and DO values, from those of the cold period (winter-spring) with rather high Chl-*α* and DO values. However, the Monte Carlo test revealed that temperature was the only statistically significant parameter contributing to this variability ($p = 0.002$). The copepods *C. crassiusculus* and *N. minor,* characteristic species of the autumn samples, are projected on the positive side of the second axis, which is explained by pH and salinity. Indeed, high salinity and pH values were recorded during autumn, except at the LA site (sample LA11-18).

Discussion

Total mesozooplankton

The present abundance values for the total mesozooplankton present certain similarities with the reports of Hannides *et al*. (2015) for the same area, though the elevated abundance in spring that was found by the latter was not recorded in the samples from this season in any of the three years. In contrast to the present investigation, where the vertical zooplankton tows were conducted in the 0–50 m depth range, the average tow depth was about 100 m in the study of Hannides *et al*. (2015). Considering these differences in the sampling depths and that in the oligotrophic area of the eastern Mediterranean the mesozooplankton abundance decreases under the 0–50 m depth stratum (Mazzocchi *et al*., 1997; Ramfos *et al*., 2006), direct comparisons between the present study and that of Hannides *et al.* (2015) must be taken with caution. The present abundance values were considerably lower compared with other neritic areas of the eastern Levantine, such as Iskenderun Bay (Terbiyik-Kurt & Polat, 2013, 2015; Terbiyik-Kurt *et al*., 2022) and the Egyptian coasts (Zakaria, 2006), and more closely resemble the values of the Lebanese coasts (Lakkis, 1990) and the coastal area of Rhodes Island (Siokou-Frangou & Papathanassiou, 1989), as well as the values recorded at the surface 0–50 m depth strata in offshore sites of the central Levantine Sea (Mazzocchi *et al*., 1997; Nowaczyk *et al*., 2011) and in pelagic areas of the Ionian Sea (Ramfos *et al*., 2006). Moreover, the lack of abundance differences among the sampling sites, for the total mesozooplankton and for all of the taxa, could be related to the open sea influence, considering the narrow continental shelf of the island and the absence of gulfs or other enclosures where the sampling sites are situated. Hannides *et al*. (2015) reached the same conclusion, as they also reported the lack of significant spatial differences in the abundance of the mesozooplankton on the coasts of Cyprus.

The lack of a constant pattern of seasonal variation with specific abundance peaks of the total mesozooplankton contrasts with the findings of other studies in the Mediterranean and the nearby southwestern Turkish coasts (see references in Terbiyik-Kurt & Polat, 2015) and could be attributed to the lack of excessive seasonal peaks in the abundance of certain mesozooplankton groups (e.g., cladocerans). However, another reason could be the low sampling resolution and number of samples, which can also stand as an explanation for the absence of interannual abundance differences.

Mesozooplankton composition

In comparison to the study of Hannides *et al.* (2015), the present investigation provides a more comprehensive picture of the mesozooplankton community on the coasts of Cyprus, utilizing a greater number of samples collected seasonally during a three-year period. Moreover, the identification of the zooplankton organisms, especially the copepods, to the species level elevate the total number of taxa that have been reported from this area and allow comparisons with other regions of the eastern Mediterranean. The use of the three ecological indices revealed that the mesozooplankton community of copepods and cladocerans in the four coastal areas of Cyprus is characterized by low seasonal or interannual variability. Similar biodiversity estimations reported by Terbiyik-Kurt & Polat (2013) for the mesozooplankton of the Iskenderun Bay presented lower values of S, expressed as the number of the species found, in comparison to the present results. However, the other two indices presented similar range values to the present investigation. The absence of spatial differences in these three indices is an indication of a homogenous community of copepods and cladocerans in the four sampling sites.

The dominance of copepods in the total mesozooplankton abundance agrees with the previous studies conducted on the coasts of Cyprus by Hannides *et al*. (2015), as well as on the coasts of Rhodes Island (Siokou-Frangou & Papathanassiou, 1989), the Lebanese coast (Lakkis, 1990), and the coasts in southwestern Turkey (Uysal *et al*., 2002; Uysal & Shmeleva, 2012; Terbiyik-Kurt & Polat, 2013; Besiktepe *et al*., 2015; Aliçli & Sarihan, 2016).

In comparison to the copepod species found in neighbouring areas to Cyprus, like the southeastern Turkish coasts (Uysal *et al*., 2002; Uysal & Shmeleva, 2012; Terbiyik-Kurt & Polat, 2013; Besiktepe *et al*., 2015; Aliçli & Sarihan, 2016), the present taxonomic list contains a number of species that are reported only in this study, e.g., *Centropages typicus*, *C. parapergens*, *C. crassiusculus*, *C. lubbocki*, *E. messinensis*, and *I. clavipes*. Some of these species (especially *C. typicus* which is a species particularly abundant in the western Mediterranean) have been found in the northwestern Levantine Sea close to Rhodes Island (Siokou-Frangou & Papathanassiou, 1989; Siokou-Frangou *et al*., 1997) and in the central Levantine pelagic waters (Nowaczyk *et al*., 2011), and they have also been reported from the Lebanon coasts (Lakkis, 1990) but not from the southeastern Turkish coasts. Thus, the present results on the species composition concerning the copepods point out a differentiation of their community in the northern Levantine Sea than of its eastern part along the Turkish coasts.

In addition, the scarcity of the cladoceran *P. avirostris* from the study area contrasts with the reports of Terbiyik-Kurt & Polat (2013) and Aliçli & Sarihan (2016), who found that this species dominated the cladocerans on the southeastern Turkish coasts (Iskenderun Bay) during summer. Another difference with the above study is the absence of the cladoceran genus *Podon* sp. from the coasts of Cyprus. The scarcity of cladocerans could be due to the topography and bathymetry of the studied coastal area, which is an open area, in contrast to Iskenderun Bay, a more confined area. Indeed, cladocerans, especially *P. avirostris*, have been more abundant in confined areas of central Greece (Ramfos *et al.*, 2005), while this species has been associated with areas of low salinity and increased river runoffs (Christou & Stergiou, 1998; Isari *et al.*, 2007; Terbiyik-Kurt & Polat, 2015; Karagianni *et al.*, 2022). Additionally, all of the chaetognath species found in the present study have been reported from the northern Levantine Sea, close to Rhodes Island (Kehayias, 2004). On the other hand, the characteristic chaetognath species *Ferosagitta galerita* and the cladoceran *Pleopis schmackeri*, which both have introduced from the Red Sea (Lessepsian species) and have been reported from the Iskenderun Bay (Terbiyik *et al.*, 2007; Terbiyik-Kurt & Polat, 2017), were absent from the present samples. The presence or absence of an alien species depends significantly on the sampling effort, as well as on the abundance of the alien species in this area. According to Hamad *et al.* (2006), there is a predominant surface current in the eastern Levantine Sea that reaches the Turkish coast and affects the northeast coastal area of Iskenderun Bay due to the wide mouth opening of the bay. Terbiyik-Kurt & Polat (2017) suggested that this circulation pattern may be responsible for the distribution of several Lessepsian species in this region of the Anatolian coastline (Occhipinti-Ambrogi & Galil, 2010). Menna *et al*. (2021) also provided an analytical picture of the water circulation in the eastern Mediterranean, showing a water-flow along the eastern coasts of the Mediterranean Sea that runs eastern of Cyprus along the Turkish coasts. In contrast, the south and the northwest coasts of Cyprus are under the influence of the Mid-Mediterranean Jet and the Asia Minor Current, respectively, which both flow from west to east. Therefore, this complex water circulation in the Levantine Sea could have been responsible for the above differences in the species composition between the coasts of Cyprus and the southeastern Turkish coasts.

Temporal abundance variation

The use of a considerable number of samples taken in all seasons provided some new insights concerning the seasonal abundance variation of the mesozooplankton community. The studies by Terbiyik-Kurt & Polat (2013) and Besiktepe *et al*. (2015) on the Iskenderun Bay, Lakkis (1990) on the Lebanese coasts and Zakaria (2006) and Zakaria *et al.* (2016) on the Egyptian coasts provide information for the seasonal variability of species and groups and can be used comparatively with the present data (Table 5). Considering the numerically most important taxa in the present study, *P. parvus* was more abundant during winter in the Cyprus coastal waters, in contrast to the results of Terbiyik-Kurt & Polat (2013) and Lakkis (1990), who found its highest abundance in spring (Table 5). The highest abundance of *O. plumifera* was recorded in autumn, in accordance with Terbiyik-Kurt & Polat (2013) and Besiktepe *et al.* (2016) but not with Zakaria *et al.* (2016), who found its maximum abundance in spring. *C. furcatus* was more abundant in summer, which agrees with Lakkis (1990) but not with Terbiyik-Kurt & Polat (2013), who found it was more abundant in autumn. *T. stylifera* showed pronounced abundance in summer, as it was also found by Lakkis (1990), but not by Terbiyik-Kurt & Polat (2013) and Besiktepe *et al.* (2015), who found it to be more abundant in spring. *C. arcuicornis* was more abundant in winter according to Terbiyik-Kurt & Polat (2013) and Zakaria *et al.* (2016), which is in agreement with the present study. *C. pavo* was more abundant in autumn than in winter and summer, as reported by Terbiyik-Kurt & Polat (2013) and Zakaria *et al.* (2016), respectively. *Corycaeus typicus* showed higher abundance in winter as reported by Terbiyik-Kurt & Polat (2013). *C. kroyeri* was more abundant in summer in accordance with Besiktepe *et al.* (2015), while Terbiyik-Kurt & Polat (2013) found a higher abundance in the spring. The latter authors reported the highest abundance of *F. rostrata* in spring, which is in agreement with the present study but in contrast to Lakkis (1990) and Zakaria *et al.* (2016), who found this species to be more abundant in winter. *L. flavicornis* was more abundant in autumn and not in winter (Terbiyik-Kurt & Polat, 2013). Oncaeidae were more abundant in winter, which is in agreement with Terbiyik-Kurt & Polat (2013) and Lakkis (1990) but not with Besiktepe *et al.* (2015), who found them to be more abundant in summer. *A. clausi* and *C. pavoninus* were more abundant in summer and autumn, respectively, in contrast to Terbiyik-Kurt & Polat (2013) who found them more abundant in spring and winter. *M. clausii* was more abundant in autumn than in the winter (Terbiyik-Kurt & Polat, 2013). Moreover, comparisons between the study of Terbiyik-Kurt & Polat (2013) with the present data revealed similarities in the seasonal abundance maxima of certain taxa, such as the cladoceran *P. tergestina* (summer), the total siphonophores (spring), and the ostracods (winter). *E. spinifera* and *P. avirostris* were more abundant in summer, but Terbiyik-Kurt & Polat (2013) found them both more abundant in spring (Table 5). According to the latter authors, the temperature in Iskenderun Bay is higher than in other coastal Mediterranean areas during the spring, and this may favour the increased abundance of thermophilus species like *P. avirostris* and *T. stylifera* in this season (Siokou-Frangou *et al.*, 1998). The appendicularians were more abundant in spring rather than summer and winter according to Terbiyik-Kurt & Polat (2013) and Zakaria (2006), respectively. According to Terbiyik-Kurt & Polat (2013), the chaetognaths and pteropods were more abundant in winter and spring, respectively, and not in summer, agreeing with the present results. Also, the larvae of decapods and echinoderms were more abundant

Table 5. The seasonal maxima of various mesozooplanktonic taxa as reported in the present study, in comparison to other studies conducted in Levantine coastal areas.

Zooplanktonic taxon	Present study	Terbiyik-Kurt & Polat (2013)	Besiktepe *et al.* (2015)	Lakkis (1990)	Zakaria (2006)	Zakaria *et al.* (2016)
Acartia clausi	summer	spring				
Calocalanus pavo	autumn	winter				summer
Calocalanus pavoninus	autumn	winter				
Centropages kroyeri	summer	spring	summer			
Clausocalanus arcuicornis	winter	winter				winter
Clausocalanus furcatus	summer	autumn		summer		
Corycaeus typicus	winter	winter				
Farranula rostrata	spring	spring		winter		winter
Lucicutia flavicornis	autumn	winter				
Mecynocera clausii	autumn	winter				
Oithona plumifera	autumn	autumn	autumn			spring
Oncaeidae	winter	winter	summer	winter		
Paracalanus parvus	winter	spring		spring		
Temora stylifera	summer	spring	spring	summer		
Evadne spinifera	summer	spring				
Penillia avirostris	summer	spring				
Pseudevadne tergestina	summer	summer				
Appendicularians	spring	summer			winter	
Chaetognaths	summer	winter				
Ostracods	winter	winter				
Pteropods	summer	spring				
Siphonophores	spring	spring				
Echinoderm larvae	winter	summer				
Decapod larvae	summer	autumn				

in summer and winter, in contrast to autumn and summer according to Terbiyik-Kurt & Polat (2013). However, the seasonality of a taxonomic group depends on the seasonality of its dominant species.

Considering the above comparisons, it is obvious that there is intense variability on the mesozooplankton seasonality among areas, while in some cases the reports provide pronounced contradictory results even for the same area of study. For instance, Aliçli & Sarihan (2016) reported the absence of cladocerans during the winter in the Iskenderun Bay in contrast to Terbiyik-Kurt & Polat (2013) and Besiktepe *et al.* (2015), who conducted similar studies in the same area but in different years. It seems that spatial and interannual distinctions in water characteristics, which may concern biological (e.g., food availability, reproduction, competition, predation) or/and physicochemical and hydrological features, may be more important than the actual dates of sampling (Calbet *et al.*, 2001; Nowaczyk *et al.*, 2011).

The main feature in the seasonality of the mesozooplankton community was the differentiation of taxa in two distinct groups structured by those having greater abundance in the warmer period, which accounts for the ‘summer group’, and the ‘winter-spring group’ with elevated abundances in the colder period. Between them, there was a third ‘autumn group’ of taxa having greatest abundance in this period. In each of these groups, there were some characteristic species having elevated abundance as well as occurrence, as they came from the estimation of the IndVal index. A distinction of the zooplankton taxa to four groups reflecting the different seasons has been reported by Terbiyik-Kurt & Polat (2013) and Aliçli & Sarihan (2016) for Iskenderun Bay, using canonical correspondence analysis (CCA) and multidimensional scaling analysis (MDS), respectively. However, in both of the above studies, the sampling had been conducted seasonally in certain sites during a year, while in the present study the samples were taken in different months during a three-year period. This has resulted in different number of samples per season with a greater number of summer samples (11), in comparison to only three samples in winter, five in spring, and six in autumn. Moreover, in certain samples, there were abundance outbursts for some taxa that gave a distinct character to this sample which was plotted away from the others in the PCA diagram. This was the case of the sample taken in PR in June 2019 (PR6-19), where the chaetognath *F. enflata* and the larvae of gastropods presented their highest density. The outburst in the number of *F. enflata* specimens (being ten times greater than the second maximum recorded abundance) was not expected in this season according to its life cycle in the Mediterranean (Kehayias, 1996). On the other hand, the simultaneous appearance of this species and the larvae of gastropods in such large numbers could not be related with preying activities of *F. enflata* upon the gastropod larvae, since there are no reports of such a trophic relation between them.

The human population and industrial establishments in the coastal areas, along with variations in terrestrial inputs due to rainfall or other factors, may have substantial impact on the abundance and diversity of zooplanktonic organisms (Terbiyik-Kurt & Polat, 2013, 2015). Two of the four sampling sites were situated relatively close to anthropogenic activities (e.g., the ports of Limassol and Larnaka); however, the mesozooplankton community in these coastal sites was not differentiated from the other sites. In addition, the freshwater runoffs in the coasts of Cyprus are restricted by dams constructed in most of the small rivers and streams. It must be pointed out that the large rainfalls in the winter of 2019 resulted in the overflow of most of these dams (Water Development Department of Cyprus, personal communication) and could explain the increased Chl-*α* concentration in late winter to early spring in the LA, ME, and PR sites. This increase of Chl-*α*, due to an elevated concentration of phytoplankton, could explain the appearance of some of the twelve new taxa in 2019. For instance, the cladoceran *P. avirostris* has been associated with mixed waters of low salinity and river runoffs in areas and seasons of high productivity (Christou & Stergiou, 1998; Ramfos *et al.*, 2005; Karagianni et al., 2022). However, *P. avirostis* was recorded in high numbers in Saronikos Gulf in 1984–85 with salinity varying between 38.5 and 39 (Siokou-Frangou *et al.*, 1996, 1998). This species was found only in the early summer of 2019 in PR, but its presence cannot be related with a decrease in the salinity in this area because of increased river inputs. *P. avirostris* is abundant in coastal and neritic areas (e.g., north Aegean Sea) but rare in offshore waters, such as the south Aegean Sea (Siokou *et al.*, 2013), as well as in coastal waters largely influenced by open sea, such as the coasts of Rhodes (Siokou & Papathanassiou, 1989). On the other hand, the chaetognath *D. decipiens*, which was also recorded only in 2019, is a pelagic species that has been related to the high salinity Levantine intermediate waters (Kehayias, 2004). Therefore, considering the small density of most of the new taxa in the samples of 2019, their presence could have been incidental.

The previously discussed influence of the open sea on the mesozooplankton community is indicated by the presence of certain copepod species; *O. setigera*, *A. negligens*, *N. minor*, and *C. arcuicornis* are abundant in Levantine and South Aegean offshore waters (Siokou-Frangou *et al.*, 1997; Siokou *et al.*, 2013), while *C. furcatus* is dominant both in coastal and offshore waters (Siokou-Frangou & Papathanassiou, 1989; Lakkis, 1990; Zakaria, 2006; Terbiyik-Kurt & Polat, 2013). The open sea influence is also verified by the presence of pelagic species like the chaetognaths *D. decipiens*, *Flaccisagitta hexaptera*, *Pseudosagitta lyra*, and *Krohnitta subtilis* (Kehayias, 2004). The prevailing open sea hydrological features affecting the four sampling locations are the Mid-Mediterranean Jet, flowing north along the western coasts, and the Asia Minor Current, flowing along the southern coasts (Zodiatis *et al.*, 2008).

Considering the lack of differences among the sampling areas, a uniform hydrological influence on the mesozooplankton community could be assumed, although there is lack of information about the seasonality in the water circulation around Cyprus. Thus, it is suggested that the open sea influence and the limited effect from the terrestrial inputs from inland waters in this region may have been the main reasons for the lack of considerable interannual variability, as well as for the absence of spatial differences regarding the abundance of the total mesozooplankton and the individual taxa.

Influence of the environmental parameters

Although surface measurements of environmental parameters do not always reflect the actual conditions in the subsurface layers from where the mesozooplankton samples were collected, they can provide a mean to investigate their relation to this biotic element. Temperature was the most important parameter affecting the seasonal dynamics of the mesozooplankton taxa in the present study. The influence of temperature to the abundance variation of several mesozooplankton taxa is in accordance with various reports for the eastern Mediterranean (Christou, 1998; Siokou-Frangou *et al.*, 1998; Terbiyik-Kurt & Polat, 2013; Besiktepe *et al.*, 2015), as well as for the western Mediterranean (Calbet *et al.*, 2001; Fernández de Puelles *et al.*, 2003). Fernández de Puelles *et al.* (2003) found that temperature was strongly correlated with *A. clausi*, *T. stylifera*, and the cladocerans, similarly to the present study. Temperature seems to have been the most important variable that shaped the formation of the distinct seasonal groups of taxa, while Chl-*α* and DO contribute in a lesser extent to this formation. The concentration of Chl-*α* verified the oligotrophic character of the coasts of Cyprus, being part of the ultra-oligotrophic central Levantine Sea (Siokou-Frangou *et al.*, 2010). This parameter has been reported as a strong biological factor in the variation of mesozooplankton taxa reflecting the food availability (Siokou-Frangou *et al*., 1998; Nowaczyk *et al*., 2011), although it was not a crucial parameter in other investigations (Terbiyik-Kurt & Polat, 2013; Besiktepe *et al*., 2015). The concentration of oxygen in the surface waters of the study area was always high, especially in winter, when the low temperature increases the solubility of this gas in the water, while the increased Chl-*α* concentrations in this period lead to a greater photosynthetic production of oxygen. Both of these variables seem to have directly or indirectly affected the abundance of several taxa, along with temperature, as was presented in the RDA plot. On the other hand, the variation of salinity was not intense and seemed unaffected by the increased river runoffs in 2019, pointing to a general stability that resembles an offshore environment. Nevertheless, RDA revealed salinity as an important factor for the autumn samples and characteristic taxa. Great salinity variations can influence the zooplankton abundance and distribution mainly in coastal areas with intense river outflows (Terbiyik-Kurt & Polat, 2013), while in other cases with narrow range of values, it is not considered a significant factor (Siokou-Frangou *et al*., 1998). Finally, the weak fluctuations of pH were not associated with other variables but may point out a divergence in 2019 with pH being significantly lower than in 2017 and 2018, which may have been the result of a larger disposition of rainwaters through the river runoffs; however, pH is rarely included among the environmental measurements conducted in marine environments (Rossano *et al*., 2020), and it is not usually related to zooplankton variations.

In conclusion, both the results on the abundance variation of the mesozooplankton taxa and the fluctuation of the environmental parameters point out the existence of a seasonality of community composition which is very common in the Mediterranean (Berline *et al*., 2012). This was characterized by three periods, one with elevated temperature (summer), the autumn period with moderate temperature and higher salinity, and the colder period of the winter and spring with increased concentrations of Chl-*α* and oxygen. The low number of winter samples (three of 25 samples) could account for the non-differentiation between winter and spring samples. The mesozooplankton community composition and abundance in the coasts of Cyprus showed a spatial and interannual consistency, probably being under the influence of the seasonal properties of the central Levantine open waters.

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Supplementary Data

The following supplementary information is available online for the article:

Table S1. List of all the zooplanktonic taxa found in the samples taken from the coasts of Cyprus during 2017-2019.

Table S2. The numerical results of the PCA analysis on the abundance (ind. m^{-3}) of the mesozooplanktonic taxa collected in the four sampling sites (Latsi, Amathounta, Meneou, and Protaras) during 2017-2019.

Table S3. The numerical results of the first two axes of the RDA analysis on the abundance (ind. m^{-3}) of the mesozooplanktonic taxa and the environmental parameters measured at the surface of the four sampling sites (Latsi, Amathounta, Meneou, and Protaras) during 2017-2019.