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Diel, seasonal and multiannual vertical zonation of copepod communities in the deep south Adriatic Sea under different environmental conditions

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Abstract

Abundance, diversity and vertical zonation of copepod communities were investigated in the oligotrophic southern Adriatic Sea (northeastern Mediterranean) over a broad time frame. A total of 136 depth-stratified samples (from the surface to 1200 m depth) were collected at day and night during nine cruises between June 2020 and September 2023. The highest copepod average abundance and diversity were found in the layers between 100 and 400 m depth during the day and in the upper 100 m depth at night, reflecting the patterns of diel vertical migration (DVM). Cluster analysis revealed three clearly defined groups of samples based on their depth range. Significant day – night differences were recorded in the epipelagic layer, which can be attributed to highly migratory species and the fine-scale vertical distribution of sub-surface (50-200 m) pelagic copepods. In contrast, diel and seasonal variations in the mesopelagic and deep zones were less pronounced. The vertical distribution of copepods in the upper layers correlated positively with temperature, salinity, and Chl *a* concentration. Periodic winter vertical mixing events disrupted the typical vertical structure, leading to the homogenization of the water column properties and the disappearance of the typical copepod community from the surface (0–50 m) both during the day and at night. These findings highlight the complexity of environmental processes in the southern Adriatic Sea and their role in shaping copepod community structure across spatial and temporal scales.

Keywords: marine crustaceans; copepods; vertical distribution; composition; Adriatic Sea; NE Mediterranean.

Introduction

Mesozooplankton communities in the marine environments are dominated by copepods both in terms of biomass and diversity (Mazzocchi *et al*., 2003; Siokou-Frangou *et al*., 2010; Kiørboe, 2011; Siokou *et al*., 2013). As primary consumers, copepods play a key role in marine food webs and serve as the main food source for various planktivorous fish and other predators (Bachiller & Irigoien, 2015; Hure & Mustać, 2020). Through diel vertical migration (DVM) and seasonal vertical migration (SVM), copepods play a central role in driving the biological pump by actively transporting organic material from the surface waters to deeper layers (Schnetzer & Steinberg, 2002; Jónasdóttir *et al*., 2015). This active transport of carbon varies regionally and seasonally, depending on the biomass of the migrating community (Takahashi *et al*., 2009; Isla *et al*., 2015).

In the open waters of the Mediterranean Sea, epipelagic mesozooplankton are primarily concentrated within the upper 100 m layer (Siokou-Frangou *et al*., 2010) and are predominantly composed of small copepod taxa such as *Ctenocalanus*, *Clausocalanus*, *Oithona*, Oncaeidae, and Corycaeidae. Furthermore, due to the ecological barrier of the Gibraltar Strait, the Mediterranean is characterized by scarcity of bathypelagic species and the presence of mesopelagic species in the deep layers (Scotto di Carlo *et al*., 1984; Weikert & Koppelmann, 1993).

The oligotrophic Southern Adriatic (SA) is the deepest region (up to 1270 m depth) of the semi-enclosed Adriatic Sea, which is connected to the eastern Mediterranean by the Strait of Otranto (~ 800 m depth). The SA represents a highly complex ecosystem in which a topographically enclosed, quasi-permanent cyclonic gyre prevails (Faganeli *et al*., 1989; Gačić *et al*., 1997). The more saline Levantine Intermediate Water (LIW) enters the SA on the eastern side of the Strait of Otranto and is entrained in the gyre. The northerly winds in winter create conditions that are favorable for deep convection and the formation of cold and relatively fresh (~38.6) Adriatic Dense Water (AdDW). This latter water mass becomes the main component of the Eastern Mediterranean Deep Water (EMDW), which is exported through the Strait of Otranto to the rest of the eastern Mediterranean basin (Malanotte-Rizzoli *et al*., 1996). The water masses that enter the SA during winter exhibit a decadal circulation change called the Adriatic-Ionian Bimodal Oscillating System (BIOS), which consists of the alternation of cyclonic and anticyclonic circulation regimes (Gačić *et al*., 2010) and influences the biodiversity of the Adriatic Sea (Civitarese *et al*., 2023; Batistić *et al*., 2014). In addition, the SA is one of the three main Mediterranean regions where vertical mixing (upwelling, convection in winter) plays a crucial role in homogenizing the physical and chemical properties of seawater and controlling primary production (Gačić *et al*., 2002, 2021; Ljubimir *et al*., 2017; Batistić *et al*., 2019; Civitarese *et al*., 2023). Bora-driven convective mixing in winter results from repeated sinking episodes, causing high evaporation and significant heat loss at the air-sea interface (Cardin & Gačić, 2003). Biological responses to these processes include the transport of phytoplankton to the aphotic zone (Batistić *et al*., 2012; Ljubimir *et al*., 2017), increased offshore zooplankton abundance (Batistić *et al*., 2012; Lučić *et al*., 2017; Hure *et al*., 2020), the ascent of copepods from the lower zone towards the surface (Hure *et al*., 2020; 2022), and the presence of a typical epipelagic species down to 400-600 m depth (Batistić *et al*., 2012).

The SA zooplankton community is characterized by a relatively stable assemblage of oceanic copepod species, with the dominant taxa present throughout the year but exhibiting low population densities (Hure *et al*., 1980; Hure & Kršinić, 1998). Early research on the seasonal vertical distribution of copepods in the SA dates back to the 1950s (Hure, 1955, 1961, 1964; Hure & Scotto di Carlo, 1969; Hure & Kršinić, 1998), with additional studies focusing on diel vertical migration patterns (Hure & Scotto di Carlo, 1969). The vertical zonation patterns of SA copepods are similar to those reported in other basins of the Mediterranean Sea and are divided into three depth zones: epipelagic photic zone (above 100 m), mesopelagic (up to 500 m) and deep below the depth of 500 m (Hure *et al*., 1980; Scotto di Carlo *et al*., 1984). Seasonal variations in this vertical distribution suggest that lower winter temperatures and reduced illumination promote an upward shift of deep-water species (Hure *et al*., 1980). Recent studies in the SA have described the vertical and horizontal patterns of copepod distribution during the winter mixing period or under post-winter conditions (Batistić *et al*., 2012; Hure *et al*., 2018, 2020) as well as the taxonomic composition and temporal and vertical distribution of abundances of small copepods (Kršinić *et al*., 2020). Additionally, an 11-year Acoustic Doppler Current Profiler (ADCP) dataset provided insights into the copepod diel vertical migration, but not at the species level (Ursella *et al*., 2018).

Part of the dataset on the finer temporal day-night distribution of copepods in the SA under contrasting environmental conditions, i.e. summer stratification in June 2020 and winter mixing in February 2021, has already been published by Hure *et al*. (2022), who focused on the 0-300 m depth layer. The present study expands upon this research by incorporating deeper layers (down to 1200 m) and a longer temporal dataset (June 2020 – September 2023). The main objective is to provide a detailed and updated overview of the vertical zonation of copepod communities in the highly dynamic area of the SA. To this end, discrete, stratified zooplankton samples were collected from the surface to deep waters (1200 m depth) over a three-year period. The specific objectives were to provide information on: (a) the copepod species composition, abundance and diversity, (b) their temporal variability at diel and seasonal scales, (c) the extent to which patterns in copepod communities correlate with environmental characteristics. This study tests the hypothesis that copepod communities undergo diel and seasonal shifts in their vertical positioning, driven by environmental gradients. By addressing these aspects, our findings contribute to a better understanding of how copepod communities respond to physical and chemical changes in the SA, with implications for broader Mediterranean zooplankton dynamics.

Material and Methods

Sampling procedure

The research was conducted on nine seasonal cruises that took place from June 2020 to September 2023 at a fixed station (1240 m depth) in the middle of the southern Adriatic Sea (Fig. 1). To describe the environmental properties and relate them to the zooplankton distribution, temperature, salinity, chlorophyll-a fluorescence (Chl *a*) and dissolved oxygen (DO) concentration (averaged over 1 m intervals) were measured through the water column using a multiparametric CTD (Conductivity-Temperature-Depth) probe SBE 19 plus (Sea Bird Electronics INC., USA) equipped with a WETLabs fluorimeter and an SBE43 oxygen sensor. Due to a probe failure, part of the DO data for the year 2021 (March, September, December) is not available.

A total of 136 zooplankton samples were collected from the surface to a depth of 1200 m using an opening and closing Nansen net with a 250 µm mesh size (113 cm diameter, 380 cm length) equipped with a flow meter. Stratified vertical tows were conducted in full daylight and in the middle of the night at eight depth layers: 0-50, 50-100, 100-200, 200-300, 300-400, 400-600, 600-800, 800-1200 meters. Detailed information on the sampling dates and local time for each depth layer are given in Table 1. The average towing speed was 1 m/s. On board, the samples were fixed and preserved in a seawater-formalin solution containing 4% formaldehyde buffered with $CaCO_3$. Due to the poor weather conditions in March 2022, only night samples were taken. In the laboratory, a qualitative-quantitative analysis of the mesozooplankton was carried out under an Olympus SZX16 stereomicroscope on subsamples ranging from 1/7 to 1/10 of the original sample, depending on the total abundance. Whole samples were analyzed to assess the abundance of rare taxa. Copepods were identified at species level, except for the *Oithona setigera*-group (*O. setigera*, *O. longispina* and *O. atlantica*) as well as the genera *Vet-*

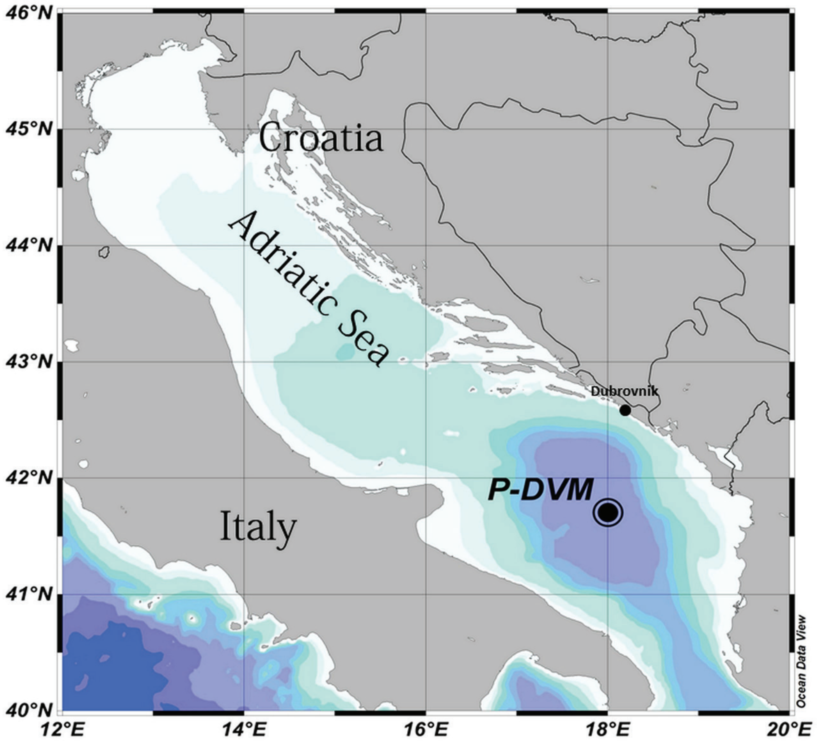


Fig. 1: Study area with the sampling station.

Table 1. Sampling dates and hours for each depth layer. Night samples are labelled with *.

	Sampling time			
Date	**Epipelagic (0-100 m)**	**Upper mesopelagic (100-400 m)**	**Lower mesopelagic (400-600 m)**	**Deep (>600 m)**
25.06.2020.	13:00; 01:00*	13:30; 00:30*	14:00; 00:00*	15:00; 23:00*
17.02.2021.	12:00; 22:30*	12:30; 23:00*	13:00; 00:00*	14:00; 01:00*
10.09.2021.	12:30; 01:00*	13:00; 00:30*	13:30; 23:30*	14:30; 22:30*
23.12.2021.	13:00; 00:30*	13:30; 00:00*	14:00; 23:30*	12:00; 22:30*
03.03.2022.	23:00*	23:30*	00:00*	01:00*
24.10.2022.	14:00; 22:00*	13:30; 22:30	13:00; 23:30*	12:00; 00:30*
17.02.2023.	13:00; 23:30*	13:30; 00:00*	12:00; 00:30*	11:00; 01:00*
09.05.2023.	13:00; 22:00*	13:30; 22:30*	14:00; 23:00*	15:00; 00:00*
19.09.2023.	14:00; 00:00*	13:30; 00:30*	13:00; 23:30*	12:00; 22:30*

toria, *Copilia* and *Sapphirina*. All copepod stages were considered to represent the total abundance of copepods. The family Oncaeidae, which is mainly represented by small species (Böttger-Schnack & Schnack, 2009) was not considered in our quantitative dataset because the relatively large mesh size of the net does not collect them efficiently. Abundance was expressed as individuals per cubic meter (Ind. m^{-3}).

Data analysis

Aspects of biodiversity were assessed using the Shannon-Wiener index (H') (Shannon & Weaver, 1963), which was calculated for each sample using the untransformed adult copepod abundance data. The Shannon-Wiener diversity index was calculated as follows: $H' = -\sum pi * \ln (pi)$, where pi is the proportion of species i in the total sample. Indicator species analysis (ISA) was applied to determine the species/taxa representative of each depth layer, during the day and night (Dufrêne & Legendre 1997). The Indicator values (IndVal) are the product of the relative abundance values and the frequency of occurrence of a given taxon in each group. The significance of these values was assessed using a Monte Carlo test of 1000 randomizations to determine reliable significance levels (IV, % of perfect indication, p<0.05). Copepod taxa with an occurrence greater than 0.1% (58 taxa in total; 56 species plus copepodite stages of *Pleuromamma* and *Heterorhabdus*), were further analyzed using cluster analysis, non-metric multidimensional scaling (NMDS), SIMPER (similarity percentages) test and multi-response permutation procedure (MRPP). The abundance data expressed as abundance per square meter (Ind. m^{-2}) were fourth root transformed. First, hierarchical agglomerative clustering was performed, using the Bray-Curtis similarity matrix (Bray & Curtis, 1957) coupled with group-average linkage to create dendrograms representing clusters of samples based on their biological composition. SIMPER analysis was applied to determine the species that contributed most to the similarities between the groups of samples identified by the cluster analysis. To determine the relationships between copepod communities (clusters) and environmental variables (temperature, salinity and Chl *a*), multivariate analysis was performed with a non-metric, multidimensional scaling (NMDS) procedure using the Bray-Curtis distance measure. For ordination, the final stress (a measure of goodness of fit between the data and the final ordination) was examined in terms of dimensionality to determine the minimum number of dimensions required to adequately describe the data. The results are presented in the form of biplot diagrams (the first two ordination axes), with the environmental variables represented as vectors and the cluster groups as points in the ordination space (McCune & Grace, 2002). After identifying the main environmental variables affecting the vertical and seasonal distribution of copepods, we used the multi-response permutation procedure (MRPP), a multivariate test developed for species data (Zimmerman *et al*., 1985), to test several null hypotheses (Ho) that copepod community structure differs significantly among different sample groups: cluster groups, time of day, season, and among sampling depth strata. We also tested for differences in copepod communities considering each depth layer (photic epipelagic: 0-100 m; upper mesopelagic: 100-400 m; lower mesopelagic: 400-600 m; and deep: >600 m) to determine if there were differences between sampling times, seasons, and the depth layers sampled for each zone (0-50 m and 50-100 m; 100-200 m, 200-300 m and 300-400 m; 600-800 m and 800-1200 m). The separation between the groups is determined by the Pearson type III distribution (T): the more negative the T value, the stronger the separation. The MRPP also calculates the chance-corrected for within-group agreement (A). A is calculated as: $A = 1 - \delta/m_\delta = 1$ - observed δ/expected δ, where the test statistic (delta: δ) is the mean distance among sample unit within groups and m_δ is the random expectation (i.e., the value of δ if the plots were the randomly assigned groups). When A = 1, all items within groups are identical (delta = 0); when A = 0, within-group heterogeneity is expected by chance, and when $A < 0$, within-group heterogeneity is greater than expected by chance (McCune & Grace, 2002). The Shannon-Wiener index, SIMPER and cluster analysis were conducted using PRIMER v.7. (Clarke & Gorley, 2015), while ISA, NMDS and MRPP were performed in PC-ORD for Windows 5.10 (McCune & Mefford, 2006).

Results

Environmental conditions

The vertical distribution patterns of temperature, salinity, Chl *a* and DO separately from the surface to 100 m depth (A) and from 100 m to 1200 m depth (B) during the study period are shown in Figure 2. The data reveal a clear seasonal cycle, primarily determined by winter mixing and summer warming, with the greatest variability occurring in the surface layers down to 80 m depth. The highest temperature (25.43 °C) was measured at the surface in September 2021, while the lowest tempera-

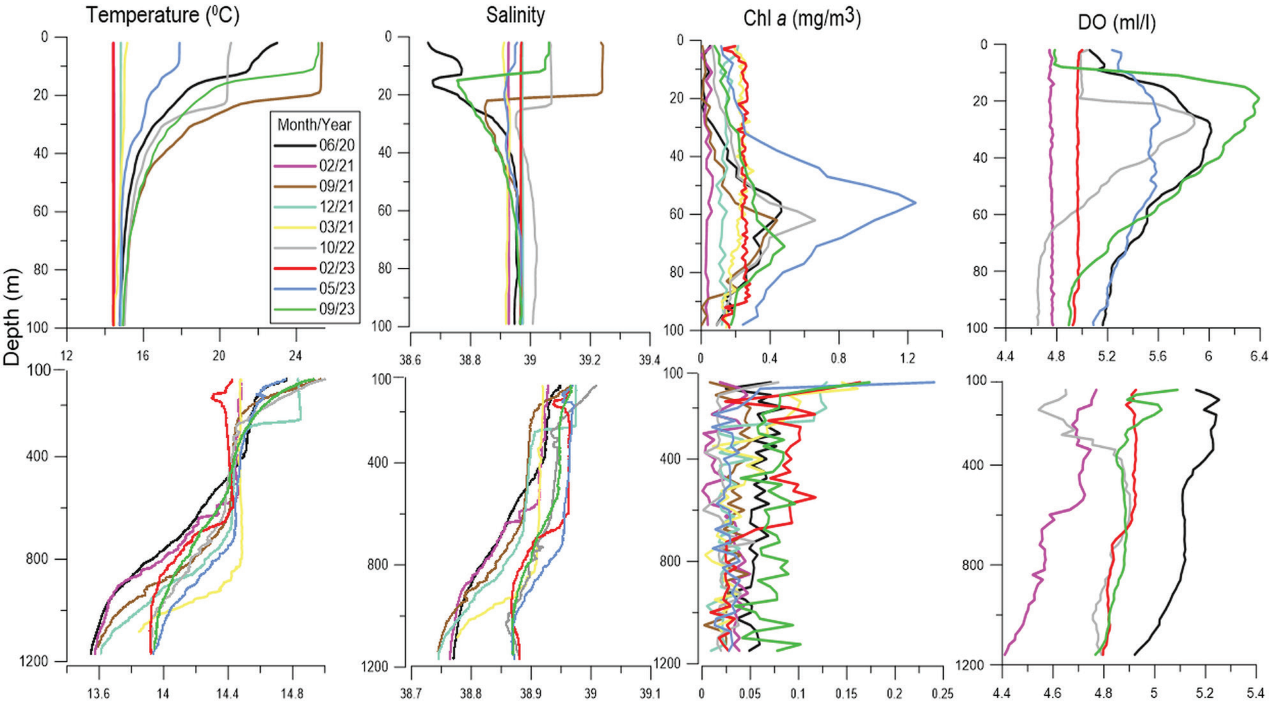


Fig. 2: Environmental variables at the sampling station over the investigated time in the upper 100 m depth (A) and below 100 m depth (B).

ture (13.55 °C) was recorded in the lower layers in June 2020. Below 100 m, the temperature profiles were similar throughout seasons and years with an average value of 14.27 ± 0.34 °C. The largest fluctuations in salinity occurred in the surface layers, from 38.66 in June 2020 to 39.33 in September 2021. Below 20 m, the salinity remained rather constant with values between 38.74 and 39.07. The profiles showed good aeration throughout the season with a mean DO concentration of 4.90 ml/l and a maximum value of 6.39 ml/l at 20 m depth in September 2023. In general, concentrations were higher in the upper 60 m. Chl *a* was low in the surface layers, with distinct peaks in the deep chlorophyll maximum (DCM) occurring between 40 and 80 meters. The highest Chl *a* value (1.24 mg m^{-3}) was measured at a depth of 56 m in May 2023. During the winter cruise in February 2021, a strong Bora wind event (NE direction) with a maximum wind speed of 19.54 m/s and wind gusts of over 50 m/s was recorded from February 11 to 14 (just three days before sampling) and was accompanied by a drop in air temperature of -2 °C (Ivančan-Picek, 2021; Hure *et al*., 2022). In 2003, from February 5 to 8, there was a strong Bora with a maximum wind speed of 20.57 m/s, combined with a low air temperature (-1 °C), and the cruise was conducted ten days later (Ivančan-Picek, 2023).

Day-night vertical distribution of copepod abundance, species composition and diversity

The highest total number of individuals was recorded in the surface layer at night time in March 2022 (457.9 ind. m^{-3}), while the lowest number of 3.5 ind. m^{-3} was recorded in the deepest layer sampled at night time in June 2020. In general, the total copepod abundance below 400 m decreases with depth. Periodically (especially from February 2023), a reverse situation was observed, with higher total copepod numbers (up to 22 ind. m^{-3}) found in the bottom layers than in the 300-600 m layer, which was due to the increased populations of *Subeucalanus monachus* and *Calanus helgolandicus*. The relative abundances of copepodite stages of Calanoida and Oithonidae in the total copepod assemblage in the entire water column averaged 23.1 ± 8% and 21.4 ± 8%, respectively. The proportion of copepodites increased to 43.2% (Calanoida) during the night at 300-400 m depth in September 2021 and to 77.6% (Oithonidae) during the day in the surface layer in September 2023. The vertical day and night distribution of copepod order abundance is shown in Figure 3 and Table 2. The dominant order was Calanoida, accounting on average for 63 ± 17% of total copepod abundance. During the day, the Calanoida were concentrated at 200-300 m depth, while at night they were most abundant in the upper 100 m of the water column. The cyclopoid family Oithonidae inhabited the upper layers, especially during the day, when they outnumbered the calanoids in the subsurface zone. The order Mormonilloida showed an even vertical distribution across the water column, while the Corycaeidae were more abundant in the upper layers. The order Harpacticoida, and the less abundant cyclopoid families Lubbockiidae and Sapphirinidae contributed minimally to the total abundance of copepods.

The complete list of copepod taxa detected during the day and night in the investigated depth layers is reported in Table 3. A total of 104 copepod taxa were identified, with the order Calanoida (81 species) showing the greatest richness. The order Cyclopoida was represented by the families Oithonidae (5 taxa), Lubbockiidae (one species - *Lubbockia squillimana*), Corycaeidae (9 species) and Sapphirinidae (genera *Copilia*, *Sapphirina* and *Vettoria*). The Harpacticoida included four species (*Goniopsyllus clausi*, *Microsetella norvegica*, *Macrosetella gracilis* and *Euterpina acutifrons*), while the order

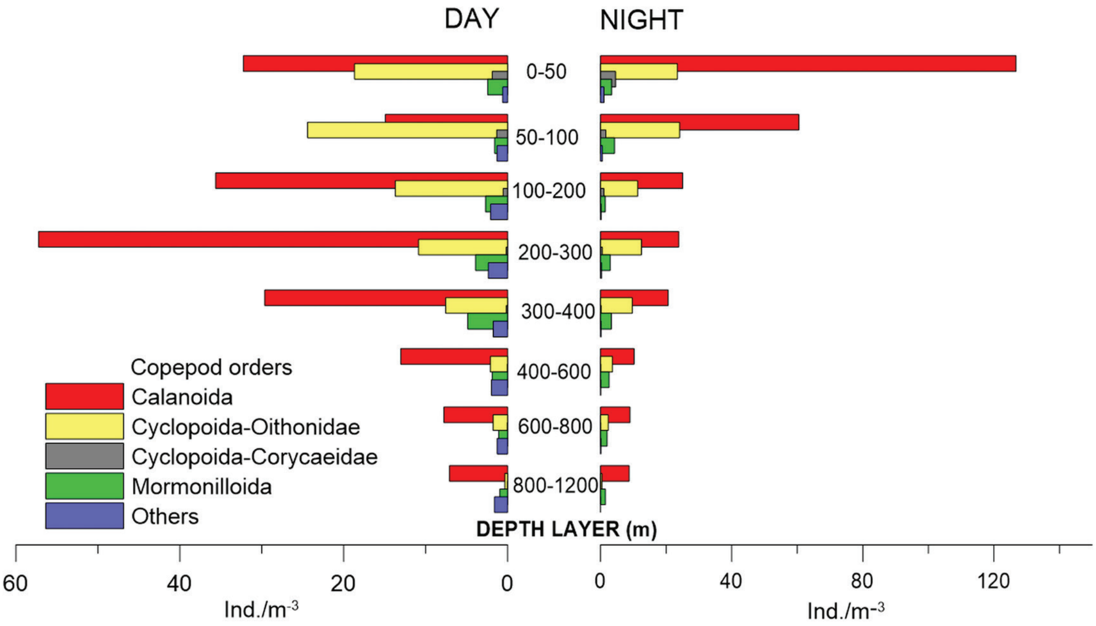


Fig. 3: Vertical distribution of average copepod abundances during the day and night per sampling layer. Standard deviations are reported in Table 2.

Table 2. Averages and standard deviations of abundance (Ind./m^{-3}) and diversity index (H') for each sampling layer during day and night.

		Abundance		Diversity (H')	
Layer		**DAY**	**NIGHT**	**DAY**	**NIGHT**
0-50 m	Total copepods	55.80±30.41	159.12±140.11	2.16±0.45	2.56±0.39
Copepod orders	Calanoida	32.24±21.59	126.75±110.62		
	Cyclopoida-Oithonidae	18.67±11.14	23.44±20.03		
	Cyclopoida - Corycaeidae	1.86±1.42	4.54±5.78		
	Mormonilloida	2.43±2.16	3.38±3.11		
	Others	0.58±0.62	1.02±1.03		
50-100 m	Total copepods	43.49±26.77	90.13±83.89	2.12±0.47	2.72±0.14
Copepod orders	Calanoida	14.91±12.29	60.46±55.01		
	Cyclopoida-Oithonidae	24.41±20.56	24.09±21.23		
	Cyclopoida - Corycaeidae	1.32±1.48	1.59±2.56		
	Mormonilloida	1.58±1.59	4.24±4.15		
	Others	1.28±1.19	0.56±0.45		
100-200 m	Total copepods	53.18±34.31	38.24±37.42	2.52±0.20	2.59±0.26
Copepod orders	Calanoida	35.62±22.23	25.06±28.28		
	Cyclopoida-Oithonidae	13.71±9.61	11.29±8.01		
	Cyclopoida - Corycaeidae	0.54±0.47	0.99±1.81		
	Mormonilloida	2.69±4.00	1.43±0.94		
	Others	2.07±2.14	1.53±0.22		
200-300 m	Total copepods	74.24±67.56	39.92±28.69	2.46±0.31	2.53±0.32
Copepod orders	Calanoida	57.22±56.01	23.84±17.82		
	Cyclopoida-Oithonidae	10.87±6.51	12.46±10.74		
	Cyclopoida - Corycaeidae	0.17±0.39	0.54±0.91		
	Mormonilloida	3.91±2.34	2.91±1.98		
	Others	2.35±2.49	0.30±0.32		
300-400 m	Total copepods	42.91±19.44	33.88±30.24	2.52±0.19	2.57±0.28
Copepod orders	Calanoida	29.62±14.21	20.63±15.88		
	Cyclopoida-Oithonidae	7.55±5.40	9.67±12.42		
	Cyclopoida - Corycaeidae	0.16±0.42	0.16±0.30		
	Mormonilloida	4.86±3.76	3.30±1.8		
	Others	1.74±1.08	0.14±0.21		
400-600 m	Total copepods	19.01±10.31	16.49±6.76	2.51±0.35	2.34±0.38
Copepod orders	Calanoida	13.04±8.72	10.21±4.32		
	Cyclopoida-Oithonidae	2.11±1.25	3.63±2.13		
	Cyclopoida - Corycaeidae	0.02±0.03	0.04±0.08		
	Mormonilloida	1.87±1.47	2.57±1.04		
	Others	1.97±1.83	0.04±0.06		
600-800 m	Total copepods	11.90±4.05	13.84±5.68	2.22±0.30	2.29±0.19
Copepod orders	Calanoida	7.76±3.87	8.95±3.41		
	Cyclopoida-Oithonidae	1.77±0.69	2.32±1.11		
	Cyclopoida - Corycaeidae	0.02±0.06	0		
	Mormonilloida	1.09±0.65	1.99±1.73		
	Others	1.255±0.71	0.08±0.10		
800-1200 m	Total copepods	9.93±6.62	10.59±5.94	1.77±0.38	1.81±0.23
Copepod orders	Calanoida	7.08±6.35	8.71±5.56		
	Cyclopoida-Oithonidae	0.34±0.26	0.42±0.37		
	Cyclopoida - Corycaeidae	0	0		
	Mormonilloida	0.93±0.44	1.46±0.58		
	Others	1.59±0.67	0		

Table 3. List of copepod taxa found in each sampling layer during day (D) and night (N).

	0-50 m		**50-100 m**		**100-200 m**		**200-300 m**		**300-400 m**		**400-600 m**		**600-800 m**		**800-1200 m**	
	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N
Calanus helgolandicus	x	x	x	x		x		x	x	x	x	x	x	x	x	x
Mesocalanus tenuicornis	x	x	x	x	x	x	x	x	x	x	x	x				
Nannocalanus minor	x	x	x		x	x	x		x	x						
Neocalanus gracilis		x	x	x	x	x	x	x	x	x	x	x				
Eucalanus elongatus					x	x	x	x	x	x	x	x	x	x	x	x
Pareucalanus attenuatus	x	x	x	x			x			x						
Subeucalanus monachus					x	x	x	x	x	x	x	x	x	x	x	x
Calocalanus contractus	x	x	x	x	x	x	x	x		x						
Calocalanus pavo	x	x	x			x										
Calocalanus styliremis	x	x	x	x	x	x	x	x		x						
Paracalanus denudatus	x		x		x											
Paracalanus nanus		x	x	x	x			x								
Paracalanus parvus	x	x	x	x	x	x	x	x								
Mecynocera clausi	x	x	x	x	x	x	x	x	x	x						
Clausocalanus arcuicornis	x	x	x		x		x									
Clausocalanus furcatus	x	x	x	x	x	x	x	x								
Clausocalanus jobei	x	x	x		x		x									
Clausocalanus mastigophorus	x	x	x	x	x	x	x	x	x	x	x	x	x			
Clausocalanus lividus	x	x	x	x	x	x	x	x	x	x	x	x	x			
Clausocalanus parapergens	x	x	x	x	x	x	x	x	x	x	x	x	x	x		
Clausocalanus paululus	x	x	x	x	x	x	x	x	x	x	x	x	x	x		
Clausocalanus pergens	x	x	x	x	x	x	x	x	x	x	x	x	x	x		
Ctenocalanus vanus	x	x	x	x	x	x	x	x	x	x		x				
Spinocalanus longicornis						x	x	x	x	x	x	x	x	x	x	x
Spinocalanus magnus										x		x	x	x	x	x
Spinocalanus oligospinosus						x	x	x	x	x	x	x	x	x	x	x
Monacilla typica				x				x		x	x	x	x	x	x	x
Aetideus armatus		x	x	x	x	x	x	x	x	x	x	x				
Aetideus giesbrechti		x	x	x	x	x	x	x	x	x	x	x		x		x
Chiridius poppei				x		x	x	x	x	x	x	x	x	x	x	x
Euchirella messinensis		x		x		x		x	x	x	x	x	x	x	x	x
Euchaeta acuta		x		x		x	x	x	x	x	x	x	x	x		
Euchaeta marina									x	x						
Paraeuchaeta hebes		x		x				x	x							
Onchocalanus trigoniceps												x	x	x		
Phaenna spinifera				x	x	x	x	x	x		x					
Xanthocalanus agilis									x						x	x
Scaphocalanus curtus						x	x	x	x	x	x	x	x	x		x
Scolecithricella abyssalis									x		x	x	x			
Scolecithricella dentata	x	x	x	x	x	x	x	x	x	x	x	x	x	x		
Scolecithricella vittata				x	x	x	x	x	x	x	x	x		x		
Scolecithrix brady		x	x	x	x	x	x	x	x	x		x				
Diaixis pygmaea	x	x	x													
Centropages typicus	x	x					x									
Centropages violaceus	x	x	x	x	x											
Temora longicornis	x															
Temora stylifera	x	x	x	x		x										
Temoropia mayumbaensis						x	x	x	x	x	x	x	x	x	x	x
Temorides brevis												x	x		x	x
Pleuromamma abdominalis		x		x		x	x	x	x	x	x		x		x	x
Pleuromamma gracilis		x		x	x	x	x	x	x	x	x	x	x	x	x	x
Lucicutia clausi		x	x	x	x	x	x	x	x	x	x	x				
Lucicutia curta															x	
Lucicutia flavicornis	x	x	x	x	x	x	x	x	x	x	x	x				

Continued

Table 3 continued

	0-50 m		**50-100 m**		**100-200 m**		**200-300 m**		**300-400 m**		**400-600 m**		**600-800 m**		**800-1200 m**	
	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N
Lucicutia gemina		x		x	x	x	x	x	x	x		x				
Lucicutia ovalis			x	x	x		x	x	x		x	x		x		x
Lucicutia pera											x		x	x	x	x
Heterorhabdus abyssalis														x	x	x
Heterorhabdus spinifrons		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Heterorhabdus papilliger		x	x	x	x	x	x	x	x	x	x	x	x	x		
Euaugaptilus filiger					x		x									
Euaugaptilus hecticus					x	x	x	x	x	x	x	x	x			
Haloptilus acutifrons					x		x	x				x				
Haloptilus angusticeps							x	x	x	x	x	x	x	x	x	
Haloptilus fertilis					x	x	x	x								
Haloptilus longicornis	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Haloptilus ornatus					x	x	x	x	x	x	x	x	x			
Arietellus pavoninus														x		
Disco minutus							x									
Candacia bispinosa					x											
Candacia elongata												x		x	x	x
Candacia giesbrechti		x														
Candacia longimana		x		x					x	x	x					
Candacia simplex				x	x	x	x	x								x
Candacia tenuimana								x		x	x	x	x	x	x	x
Candacia varicans				x	x	x		x	x	x	x	x				x
Anomalocera patersoni		x														
Pontellopsis regalis	x						x									
Acartia (Acartiura) clausi	x	x	x	x	x	x	x	x	x	x						
Acartia (Acartiura) longiremis	x	x	x		x	x										
Acartia (Acartia) negligens	x	x			x	x		x								
Neomormonilla minor	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Oithona nana		x														
Oithona plumifera	x	x	x	x	x	x										
Oithona setigera-group	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Oithona similis	x	x	x	x	x	x	x	x	x	x	x	x				
Oithona tenuis		x	x		x	x										
Microsetella norvegica	x			x			x	x					x			
Macrosetella gracilis	x	x	x	x	x	x		x	x	x	x	x	x	x		
Euterpina acutifrons		x														
Goniopsyllus clausi	x	x	x	x	x	x	x	x	x	x	x	x	x	x		
Lubbockia squillimana	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x
Saphirina spp.	x	x	x	x		x		x	x	x	x				x	
Vettoria spp.	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x
Copilia spp.		x							x	x	x	x		x		
Corycaeus (Agetus) flaccus	x	x	x	x	x	x	x	x	x	x						
Corycaeus (Agetus) typicus	x	x	x	x	x	x	x	x		x		x				
Corycaeus (Corycaeus) clausi	x	x	x	x	x	x	x		x	x						
Corycaeus (Corycaeus) speciosus			x													
Corycaeus (Ditrichocoryceaus) anglicus			x			x		x	x							
Corycaeus (Ditrichocoryceaus) brehmi	x	x	x	x	x	x	x	x	x							
Corycaeus (Onychocorycaeus) giesbrechti	x	x	x		x		x	x	x							
Corycaeus (Urocorycaeus) furcifer		x	x	x	x	x	x	x	x	x		x		x		
Farranula rostrata	x	x	x	x	x	x	x	x	x	x						

Mormonilloida was only represented by *Neomormonilla minor*. The highest number of taxa (50) was found in the surface layer during the day in June 2020, while the lowest number (12) was recorded in the bottom layers in September 2023. On average, the vertical distribution of the diversity index during the day followed the number of taxa, which increased between 100 and 600 m (Fig. 4; Table 2). During the day, the highest Shannon-Wiener diversity index (3.10, February 2021) was in the 400-600 m layer. Low species diversity was observed below 600 m depth, in the layers where the gradual disappearance of some mesopelagic species was evident. During the night, the average number of taxa gradually decreased from the surface to the deeper layers, while the highest diversity was noted in the subsurface layer at 50-100 m depth.

The results of the ISA analysis (Table 4) show that *Mecynocera clausi*, *Temora stylifera*, *Centropages typicus* and *Clausocalanus furcatus* were tipically found in the surface layer both during the day and at night. At night, the upper layer was enriched by migrating copepods (*Euchaeta acuta*, genus *Pleuromamma*), which inhabit deeper layers during the day (i.e. 300-400 m layer for the genus *Pleuromamma* and 400-600 m layer for *E. acuta*). Good indicators for the upper mesopelagic layer (200-300 m) during the day were subsurface species of the genus *Clausocalanus* (*C. pergens* and *C. parapergens*) and typical mesopelagic taxa of the Adriatic Sea (genera *Heterorhabdus*, *Aetidaeus*, *Scolecithricella* and *Haloptilus longicornis*). Below 600 m, the indicator species were the same both during the day and at night.

Multivariate analyses of copepod community

In the cluster analysis, the copepod community was divided into three main groups of samples with a 45% similarity (Fig. 5), which were grouped according to sampling depth: surface (most samples collected during the day from the surface to 100 m, group 1), middle layers (100 – 600 m), which included the nocturnal surface samples (group 2), and the deep layers, (mainly samples collected in waters deeper than 600 m, group 3). A further division resulted in subgroups of samples, with two subgroups for surface and deep samples and three subgroups for the middle layer samples. The number of samples in each subgroup ranged from 3 to 40. The vertical distribution of each cluster subgroup, separated by day and night, is shown in Figure 6, while Table 5 provides information on the average abundance, diversity and results of the SIMPER analysis, which lists the species that mainly contribute to the similarity of each group.

Cluster 1 consisted of daytime surface samples (with the exception of February 2021) and to a depth of 100 m, with the most abundant species in both subgroups being *Oithona similis*. Only in September 2023 was the surface community found deeper, down to a layer of 100-200 m. In the upper 100 m depth, a subgroup of samples (1a) was characterized by low abundances, fewer species and low diversity values, as well as quite high contribution of *Acartia negligens* and *Nannocalanus minor*. The same subgroup only occurred in the surface layer during the day in October. Compared to subgroup 1a, subgroup 1b contained a higher number of representative species, including small taxa such as *C.pergens*, *Calocalanus styliremis* and the genus *Oithona*.

Cluster 2 was the most numerous sample group, comprising three subgroups: 2a - nocturnal surface community, 2b - upper mesopelagic community and 2c - deep mesopelagic copepod community. The average abun-

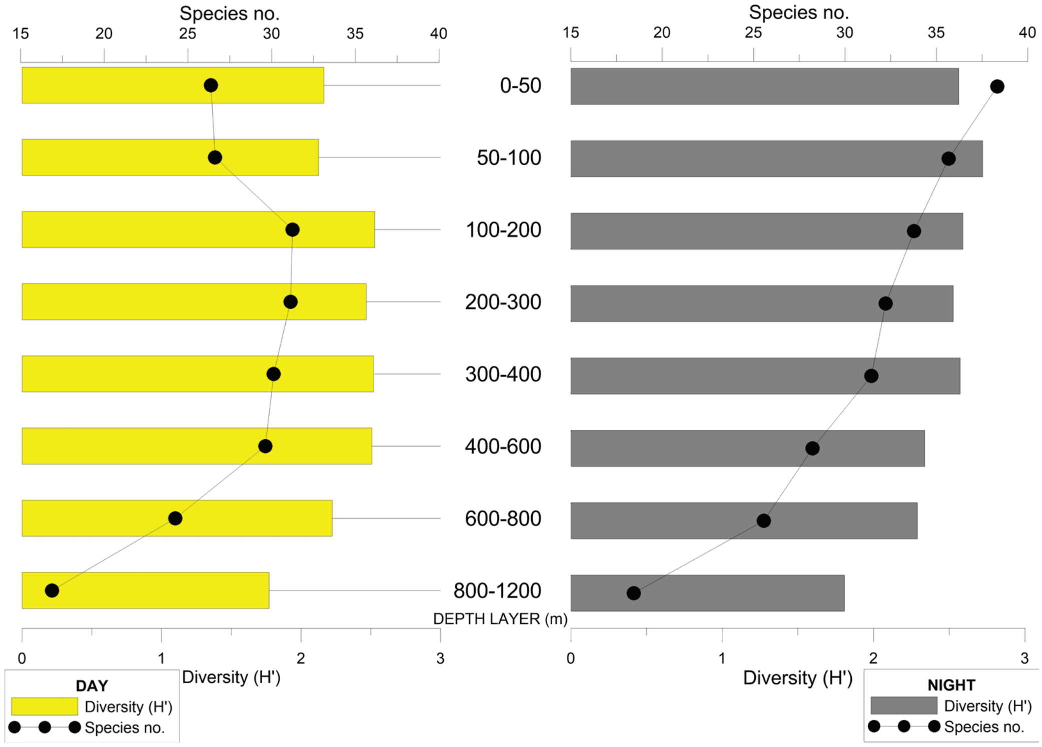


Fig. 4: Vertical distribution of the temporally averaged numbers of taxa and Shannon-Wiener index (H') during the day and night per sampling layer. Standard deviations are reported in Table 2.

Table 4. Results of Indicator Species Analysis (ISA) performed on copepod taxa in the SA according to the sampling layer and separated by day and night. Only taxa whose IndVal was significant (p <0.05) are shown in the table.

LAYER	**DAY SAMPLES**			**NIGHT SAMPLES**		
	Copepod taxa	**IndVal**	**p**	**Copepod taxa**	**IndVal**	**p**
0-50 m	*Mecynocera clausi*	72.1	0.0002	*Mecynocera clausi*	71.1	0.0002
	Temora stylifera	49.2	0.0002	*Clausocalanus pergens*	67.6	0.0002
	Centropages typicus	37.0	0.0052	*Clausocalanu furcatus*	49.9	0.0002
	Paracalanus parvus	35.5	0.0072	*Pleuromamma gracilis*	43.4	0.0008
	Clausocalanus furcatus	27.5	0.0100	*Pleuromamma* juv.	42.1	0.0052
				Lucicutia flavicornis	41.8	0.0028
				Neocalanus gracilis	41.3	0.0006
				Nannocalanus minor	38.3	0.0008
				Pleuromamma abdominalis	37.1	0.0338
				Temora stylifera	37.1	0.0012
				Clausocalanus parapergens	36.5	0.0042
				Clausocalanus paululus	32.9	0.0126
				Calocalanus styliremis	32.3	0.0058
				Ctenocalanus vanus	32.2	0.0172
				Euchaeta acuta	31.9	0.0280
				Clausocalanus mastigophorus	30.5	0.0086
				Centropages typicus	23.4	0.0142
50-100 m						
	Calocalanus styliremis	48.7	0.0004	*Heterorhabdus* juv.	28.4	0.0304
	Nannocalanus minor	35.5	0.0042	*Scolecithrix bradyi*	22.5	0.0432
	Lucicutia ovalis	20.5	0.0450			
100-200 m	*Mesocalanus tenuicornis*	44.2	0.0012			
	Ctenocalanus vanus	32.3	0.0114			
	Lucicutia flavicornis	29.9	0.0248			
200-300 m						
	Clausocalanus pergens	55.5	0.0014	*Scolecithricella vittata*	47.1	0.0004
	Neocalanus gracilis	47.8	0.0002	*Haloptilus longicornis*	28.5	0.0162
	Clausocalanus paululus	41.5	0.0020			
	Pleuromamma juv.	39.2	0.0026			
	Heterorhabdus juv.	37.9	0.0030			
	Heterorhabdus papilliger	35.2	0.0022			
	Haloptilus longicornis	35.0	0.0022			
	Clausocalanus parapergens	33.9	0.0054			
	Aetideus giesbrechti	33.7	0.0034			

Continued

Table 4 continued

LAYER	DAY SAMPLES			NIGHT SAMPLES		
	Copepod taxa	**IndVal**	**p**	**Copepod taxa**	**IndVal**	**p**
	Aetidaeus armatus	32.0	0.0048			
	Scolecithricella vittata	29.6	0.0098			
300-400 m						
	Pleuromamma abdominalis	87.2	0.0002			
	Pleuromamma gracilis	61.3	0.0002			
	Scolecithricella dentata	44.7	0.0016			
	Spinocalanus longicornis	28.4	0.0268			
400-600 m						
	Euchirella messinensis	58.3	0.0002	*Spinocalanus longicornis*	36.5	0.0030
	Euchaeta acuta	51.2	0.0002			
	Spinocalanus oligospinosus	29.6	0.0080			
600-800 m						
	Eucalanus elongatus	34.8	0.0230	*Eucalanus elongatus*	36.2	0.0054
	Subeucalanus monachus	28.0	0.0508	*Subeucalanus monachus*	31.1	0.0152
				Spinocalanus oligospinosus	29.9	0.0034
800-1200 m						
	Monacilla typica	77.0	0.0002	*Monacilla typica*	74.0	0.0002
	Calanus helgolandicus	68.2	0.0002	*Calanus helgolandicus*	61.8	0.0008
	Temoropia mayumbaensis	49.0	0.0008	*Temoropia mayumbaensis*	45.8	0.0004
	Lucicutia pera	31.5	0.0176			

dance and diversity decreased with increasing depth. The community of nocturnal surface copepods (cluster 2a) was characterized by the greatest diversity and abundance, which included different species according to their diel vertical positioning: typical migratory species (genus *Pleuromamma, E. acuta*), surface species that remain in these layers throughout the 24-hour cycle (*O. similis*, *M. clausi*), and copepods that are distributed not only in the surface but also in some deeper layers (*C. pergens*, *C. paululus*). Subgroups 2b and 2c are typical mesopelagic copepod communities of the Adriatic Sea, which are generally distributed below 100 m (especially during the day) and whose lower limit was between 400 and 800 m depth. Therefore, the vertical position of the mesopelagic copepod community varied throughout the year and day-night conditions. In February 2021, the upper mesopelagic community (cluster 2b) occupied the vertical column from the surface to the deep layers both during the day and at night, while in June 2020 and May 2023 it was absent at night. The copepod taxa that contributed most to subgroup 2b were similar to those of subgroup 2a, with the exception of migratory taxa and the presence of the common mesopelagic copepod *H. longicornis*.

Finally, the strong grouping of the deep samples (cluster 3) indicates a specific community characterized by low abundances and the presence of a specific deep community. This was also confirmed by a high degree of similarity with SIMPER. The upper cluster (3a) was characterized by the still significant presence of the genus *Spinocalanus*, while the deepest cluster was more uniform and numerically dominated by *Temoropia mayumbaensis*, *N. minor*, *Monacylla typica* and *C. helgolandicus* (Table 5).

These groupings separated along two axes of NMDS ordination with a final stress of 12.8 (p = 0.00001). (Fig. 7). The two axes explained 92.0% of the total variability in zooplankton community structure (r2 = 0.31 for axis 1 and r2 = 0.61 for axis 2). The environmental variables showed the highest positive correlations with the second ordination axis (Table 6), reflecting the gradients in seasonal and vertical temperature, salinity and primary pro-

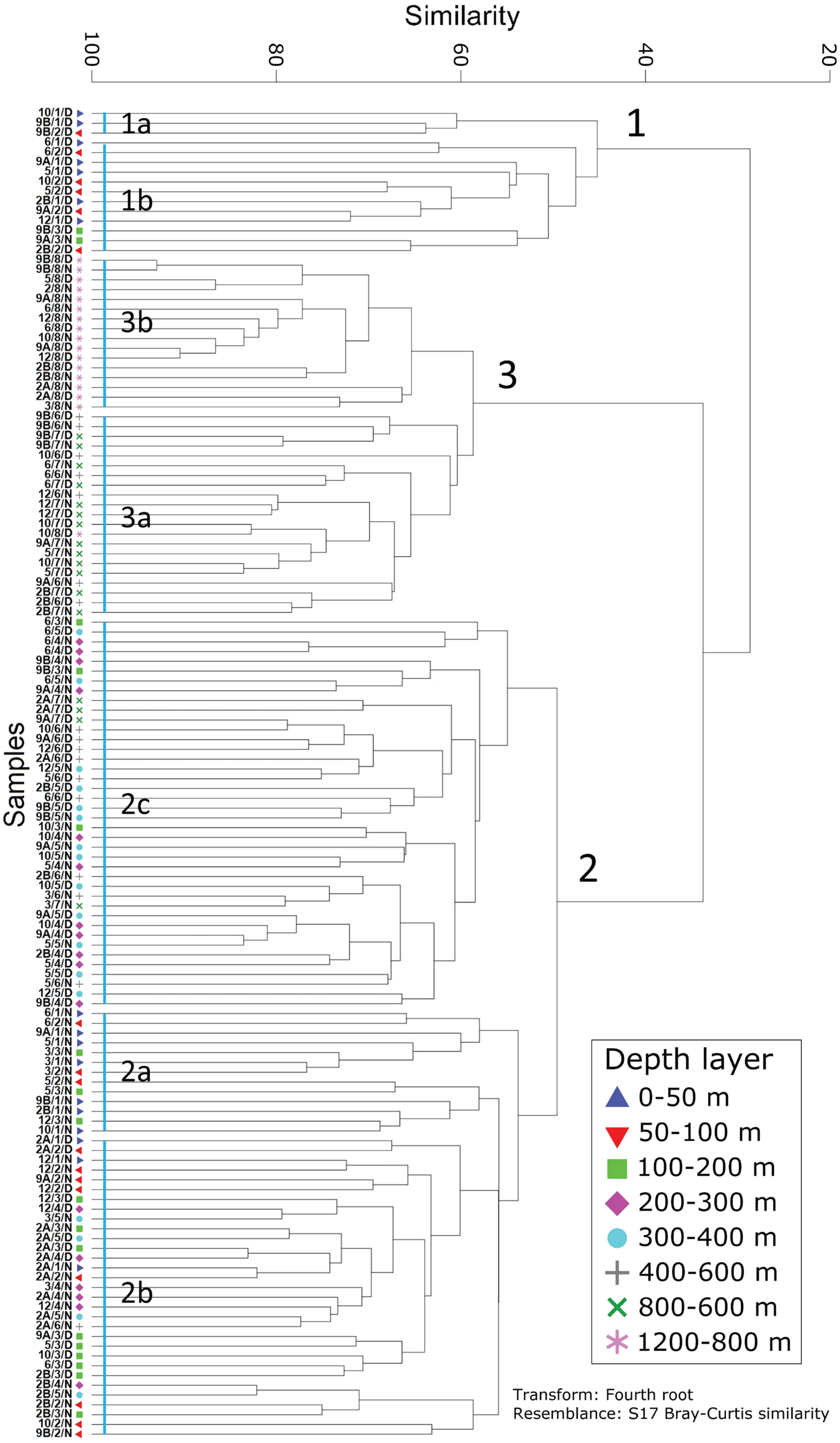
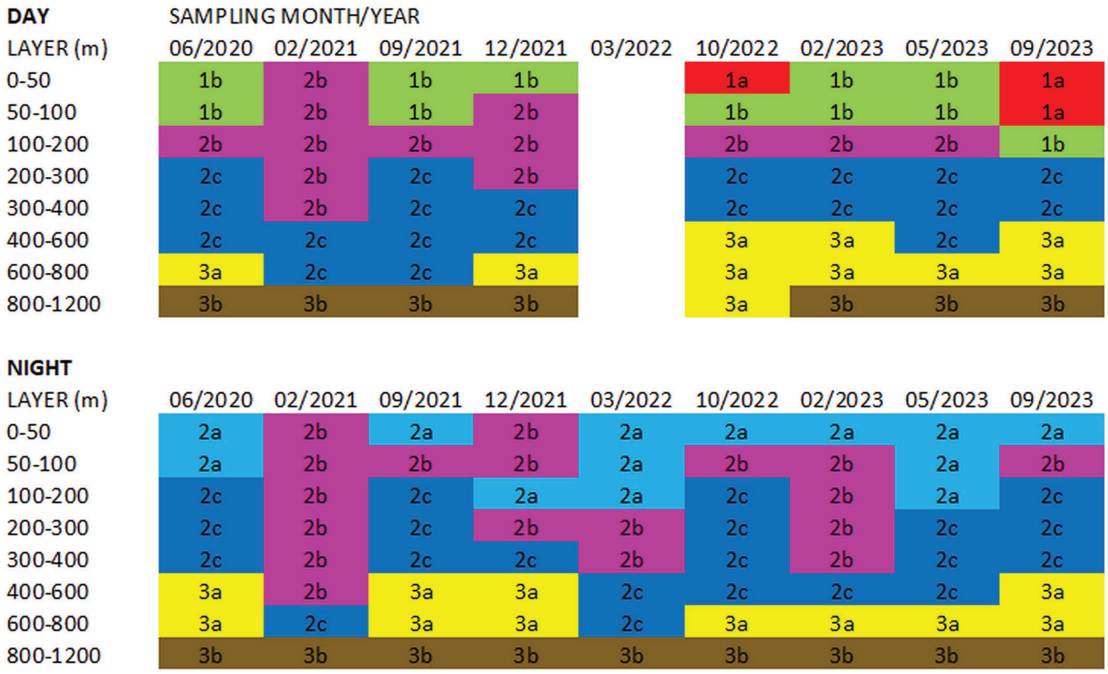


Fig. 5: Cluster dendrogram of copepod samples. Samples are indicated by sampling layer, month (capital letters indicate sampling year: A = 2021; B = 2023) and sampling time (D = day; N = night).



DAY SAMPLING MONTH/YEAR

LAYER (m)	06/2020	02/2021	09/2021	12/2021	03/2022	10/2022	02/2023	05/2023	09/2023
0-50	1b	2b	1b	1b		1a	1b	1b	1a
50-100	1b	2b	1b	2b		1b	1b	1b	1a
100-200	2b	2b	2b	2b		2b	2b	2b	1b
200-300	2c	2b	2c	2b		2c	2c	2c	2c
300-400	2c	2b	2c	2c		2c	2c	2c	2c
400-600	2c	2c	2c	2c		3a	3a	2c	3a
600-800	3a	2c	2c	3a		3a	3a	3a	3a
800-1200	3b	3b	3b	3b		3a	3b	3b	3b

NIGHT

LAYER (m)	06/2020	02/2021	09/2021	12/2021	03/2022	10/2022	02/2023	05/2023	09/2023
0-50	2a	2b	2a	2b	2a	2a	2a	2a	2a
50-100	2a	2b	2b	2b	2a	2b	2b	2a	2b
100-200	2c	2b	2c	2a	2a	2c	2b	2a	2c
200-300	2c	2b	2c	2b	2b	2c	2b	2c	2c
300-400	2c	2b	2c	2c	2b	2c	2b	2c	2c
400-600	3a	2b	3a	3a	2c	2c	2c	2c	3a
600-800	3a	2c	3a	3a	2c	3a	3a	3a	3a
800-1200	3b	3b	3b	3b	3b	3b	3b	3b	3b

Fig. 6. Vertical distribution of cluster groups showed in Figure 5 over the sampling period during the day and night.

Table 5. Information on each cluster group obtained by SIMPER: mean copepod abundance, diversity indices and list of copepod taxa mainly responsible for the similarity among groups identified by cluster analysis. Average abundance, as well as individual and cumulative contribution of key taxa to each group are also indicated.

		Av. Abundance	Contrib %	Cum.%
CLUSTER 1a				
Average abundance	14.19±6.47			
Average diversity (H')	1.59 ±0.22			
Average species number	16 ±2			
Average similarity	50.46			
Oithona similis		1.55	31.99	
Neomormonilla minor		1.40	15.86	47.85
Acartia negligens		1.40	9.49	57.34
Mecynocera clausi		0.61	9.17	66.51
Nannocalanus minor		0.42	7.93	74.44
CLUSTER 1b				
Average abundance	33.77±16.60			
Average diversity (H')	2.16 ±0.28			
Average species number	28 ±4			
Average similarity	46.94			
Oithona similis		2.94	26.06	
Mecynocera clausi		1.00	7.57	34.38
Oithona setigera-group		1.25	7.72	44.15
Clausocalanus pergens		1.05	6.80	50.95
Neomormonilla minor		1.01	6.55	57.50
Oithona plumifera		0.88	5.97	63.47
Farranula rostrata		0.64	4.64	65.46
Calocalanus styliremis		0.52	4.33	72.86
CLUSTER 2a				
Average abundance	97.22±76.66			
Average diversity (H')	2.65±0.59			
Average species number	41±8			
Average similarity	48.21			
Clausocalanus pergens		4.10	16.78	
Oithona similis		2.70	11.13	27.91
Pleuromamma gracilis		1.47	6.85	34.76

Continued

Table 5 continued

		Av. Abundance	Contrib %	Cum.%
Clausocalanus paululus		1.52	6.52	41.27
Clausocalanus parapergens		1.46	5.39	46.66
Pleuromamma abdominalis		1.09	4.86	51.52
Mecynocera clausi		1.23	4.30	55.82
Pleuromamma juv.		1.14	4.20	60.02
Lucicutia flavicornis		1.13	3.98	64.00
Heterorhabdus juv.		1.13	3.98	67.98
Euchaeta acuta		0.71	3.48	71.46
CLUSTER 2b				
Average abundance	35.22±21.86			
Average diversity (H’)	2.59±0.19			
Average species number	35±6			
Average similarity	52.54			
Clausocalanus pergens		2.33	13.58	
Oithona similis		1.79	12.04	25.62
Haloptilus longicornis		1.28	8.25	33.86
Oithona setigera-group		1.29	8.19	42.05
Neomormonilla minor		1.21	7.68	49.73
Heterorhabdus juv.		1.19	7.03	56.76
Clausocalanus parapergens		1.10	6.33	63.09
Clausocalanus paululus		1.11	6.24	69.34
Lucicutia flavicornis		0.91	5.74	75.07
CLUSTER 2c				
Average abundance	20.53±12.68			
Average diversity (H’)	2.48±0.22			
Average species number	30±5			
Average similarity	52.54			
Oithona setigera-group		1.54	15.37	
Neomormonilla minor		1.55	13.70	29.06
Haloptilus longicornis		1.26	12.55	41.61
Clausocalanus pergens		1.04	8.48	50.09
Clausocalanus paululus		0.72	5.53	55.62
Pleuromamma gracilis		0.65	5.19	60.81
Spinocalanus longicornis		0.64	4.57	65.98
Clausocalanus parapergens		0.46	4.29	70.27
CLUSTER 3a				
Average abundance	8.51±3.76			
Average diversity (H’)	2.16±0.23			
Average species number	22±3			
Average similarity	59.11			
Oithona setigera-group		0.98	16.96	
Temoropia mayumbaensis		0.92	15.94	32.91
Neomormonilla minor		0.95	12.32	45.23
Spinocalanus oligospinosus		0.51	8.63	53.86
Subeucalanus monachus		0.72	7.37	61.23
Calanus helgolandicus		0.58	7.28	68.51
Spinocalanus longicornis		0.55	6.88	75.39
CLUSTER 3b				
Average abundance	9.66±6.02			
Average diversity (H’)	1.73±0.4			
Average species number	18±3			
Average similarity	62.97			
Temoropia mayumbaensis		1.16	22.83	
Neomormonilla minor		0.97	18.87	41.71
Monacilla typica		0.91	17.68	59.39
Calanus helgolandicus		1.01	8.08	67.47
Spinocalanus oligospinosus		0.43	7.96	75.42

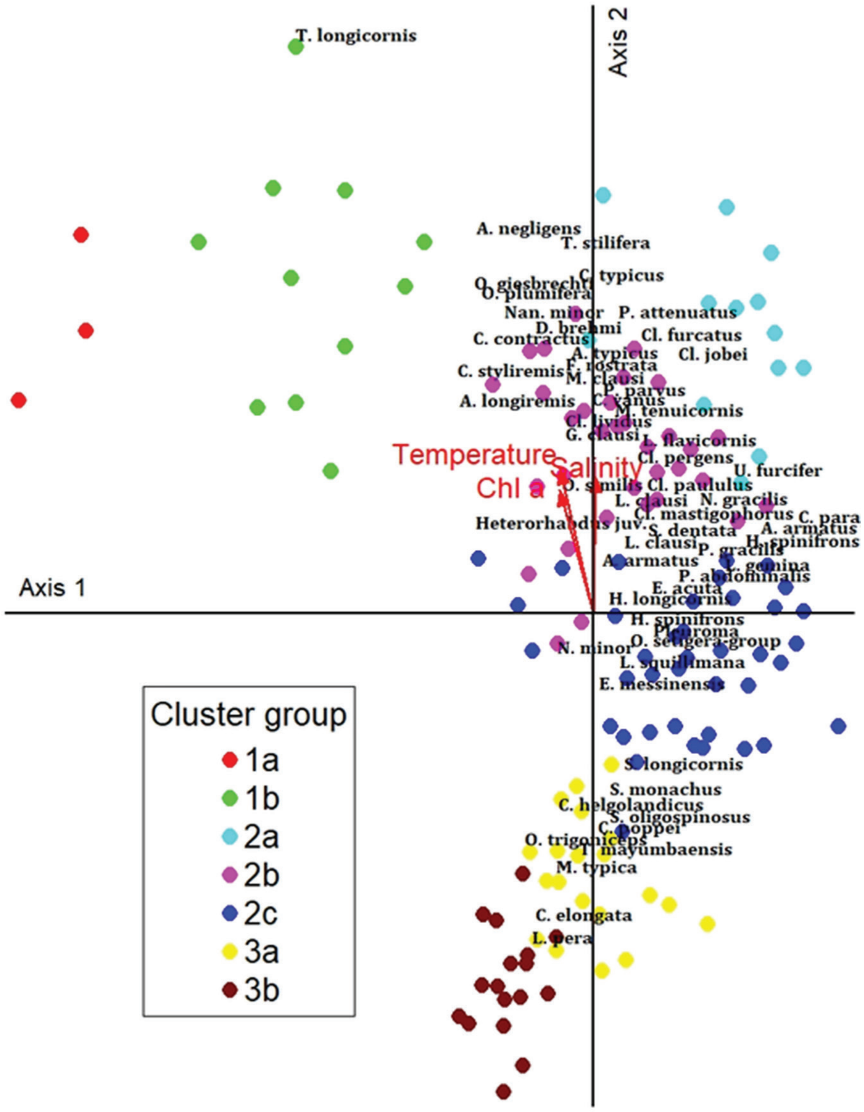


Fig. 7: Ordination joint plot from the non-metric multidimensional scaling (NMDS) with sample units labelled by cluster group and position of the representative taxa of each group with the environmental variables overlaid as vectors. Vector length and direction indicates relative strength of the correlation with axes.

Table 6. Results of non-metric multidimensional scaling (MNDS) analysis of the environmental conditions recorded for each cluster group. Randomization Monte Carlo test gave probability (p=0.00001) that the final stress level 12.84 could have been obtained by chance.

Environmental variables	**Axis 1**	**Axis 2**
Temperature	-0.252	0.528
Salinity	0.066	0.511
Chl *a*	-0.252	0.487

duction and thus a strong separation of samples by sampling depth along the same axes. Finally, MRPP analysis revealed that differences in community structure were significant between cluster groups and between sampling depth layers and seasons (Table 7). Additional MRPP analyses were conducted for each depth zone (photic epipelagic 0-100 m; upper mesopelagic 100-400 m, lower mesopelagic 400-600 m and deep zone (> 600 m)) to examine differences in copepod community structure as a function of sampling time (day versus night), season, and sampling depth. The results showed significant differences in species composition only in the epipelagic layer between day and night (T = -10.71, A = 0.09, $p < 0.000001$), but not between seasons (T = -2.72, A = 0.04, p = 0.01) and between upper (0-50 m) and lower (50-100 m) sampled layers (T = -1.38, A = 0.01, p = 0.09). Other habitat

Table 7. Multi-Response Permutation Procedure (MRPP) analysis for comparison of the copepod community structure per identified cluster group, sampling depth layer, and day-night sampling.

Group of sampling stations tested for the following hypotheses	T	A	P-value
Cluster group	-43.5395	0.2910	0.0000
Depth strata	-32.4428	0.2239	0.0000
Season	-7.2342	0.0342	0.0000
Day versus night	-0.9025	0.0024	0.1539

zones did not differ significantly in community structure when the above variables were taken into account.

Discussion

Most studies on the vertical migration of zooplankton focus on either the DVM or the SVM, while the understanding of the interactions between these two migrations and the influence of seasonal environmental conditions on them is still limited (Bandara *et al*., 2018, 2021). Our research on the vertical positioning of copepod communities over a period of several years showed clear temporal variability throughout the water column. This is particularly evident in the epipelagic layers, where certain hydrographic features shape the composition and distribution of the copepod communities.

Day-night variation in the copepod abundance, composition and diversity

Typical vertical profiles of abundance in the Adriatic Sea and the entire Mediterranean offshore waters show that copepod density is concentrated in the epipelagic zone and decreases with depth (Scotto di Carlo *et al*., 1984; Mazzocchi *et al*., 1997; Siokou-Frangou *et al*., 1997; Siokou *et al*., 2013). During our sampling period, when patterns of total copepod abundance were generally shaped by calanoid density, this was only confirmed during the night. In contrast, the highest copepod concentrations were found during the day in the layers between 100 m and 400 m depth, which was accompanied by the greater diversity observed. This is consistent with previous records of a depth-dependent increase in copepod diversity with peaks in mesopelagic waters during the day (Bode *et al*., 2018; Gaard *et al*., 2008; Hure *et al*., 2018; Zagami *et al*., 2020). The highest densities were recorded in the 200-300 m layer, where the species-specific depth appearance showed a concentration of mesopelagic fauna with eleven indicative taxa (Table 4). The influence of DVM on the increase of copepod diversity in the surface layers during the night by upward migrating mesopelagic species has been widely reported in the open Mediterranean (Scotto di Carlo *et al*., 1984; Weikert & Trinkaus, 1990; Andersen, 2001; Brugnano *et al*., 2012; Hure *et al*., 2022). Low densities and diversity values below 600 m depth were also observed in the oligotrophic eastern Mediterranean (Siokou *et al*., 2013, 2019) and in the Adriatic Sea (Hure *et al*., 2020). The episodic increase in copepod abundance in the lower layers (600-1200 m) (September 2021; February and September 2023) was due to a higher density of *C. helgolandicus* (mainly concentrated at 800-1200 m depth) and *S. monachus* (600-800 m). A high abundance of these two species has already been observed in the Levantine Sea (Weikert *et al*., 2001), the Ligurian Sea (Zagami *et al*., 2020) and the Aegean Sea (Siokou *et al*., 2013). As these two species are among the largest copepods in the Adriatic Sea, this increase has a huge impact on the total biomass of mesozooplankton in the deep pelagic and further studies are being conducted to investigate the biology of these species and understand their role in the SA pelagic food web.

The order Mormonilloida was quite evenly distributed throughout the water column, although its contribution to the total copepod abundance increased with depth. Our result contrasts with previous records for the Adriatic Sea (Hure & Kršinić, 1998; Hure & Scotto di Carlo, 1969) and the Mediterranean Sea (Scotto di Carlo *et al*., 1984; Siokou *et al*., 2013), where the distribution of the only member of the Mormonilloida, *N. minor*, was deeper, with a core population at 400 m depth. Detailed seasonal DVM differences of this species were described by Hure *et al*. (2022), where *N. minor* was shown to contribute significantly during winter convection in the upper 100 m from midnight to early morning.

Temporal and vertical distribution of copepod communities and their relationship to environmental conditions

In the present study, cluster analysis identified three main depth zones of copepod distribution, which is consistent with a classical model of vertical zonation in the Mediterranean Sea (Hure *et al*., 1980; Scotto di Carlo *et al*., 1984; Weikert & Trinkaus, 1990; Brugnano *et al*., 2012). Nevertheless, our results show that the timing of sampling can have a remarkable influence on the vertical positioning of copepods in the water column on a diel and seasonal basis.

The majority of copepod populations in the Mediterranean remain permanently in the epipelagic layer (Scotto di Carlo *et al*., 1984; Weikert & Trinkaus, 1990). In our study, the surface copepod community was present during the day and was formed of the typical surface species. These included species that were significant in SIMPER, which is highly sensitive to abundance patterns (e.g. *O.*

similis), as well as species more strongly associated with this layer identified by ISA (*M. clausi, T. stylifera, C. typicus, C. styliremis*) (Tables 4 and 5). During stratification, a special community (subgroup 1a) characterized by low abundance and diversity occurred in the upper layers. This was probably due to certain copepod species (e.g. *Mesocalanus tenuicornis, C. paululus, C. vanus, M. clausi*), which are common in the epipelagic but tend to avoid the warm surface water by staying mainly below the thermocline (Hure, 1961; Fragopoulu & Lykakis, 1990; Ramfos *et al*., 2006). This subgroup was also characterized by the presence of *A. negligens*. This copepod occurs sporadically in small numbers throughout the Adriatic Sea (Hure & Kršinić, 1998) and in the surface layers of the Mediterranean Sea (e.g. Siokou-Frangou *et al*., 1997; Brugnano *et al*., 2010; Nowaczyk *et al*., 2011; Zakaria *et al*., 2016; Belmonte, 2018).

The DVM was found to have no significant influence on the distribution of total zooplankton abundance in the eastern Mediterranean (Mazzocchi *et al*., 1997). In addition, no significant differences in species composition between daytime and nighttime epipelagic samples were found in the Mediterranean Sea, which can be attributed to the low abundance of copepod species that perform vertical migrations (Weikert & Koppelmann, 1993; Kouwenberg, 1994; Raybaud *et al*., 2008; Brugnano *et al*., 2012; Zagami *et al*., 2020). In contrast, our results showed a statistically significant separation of copepod communities in the epipelagic layer between day and night, as detected by MRPP analysis. Cluster analysis also separated these two sample groups, indicating clear differences in the copepod communities in the epipelagic layer in terms of copepod species composition and abundance. Accordingly, the upper layers during the night consisted of typical epipelagic copepod species as well as the species that ascend at night (genus *Pleuromamma*, *E. acuta*). Although the most abundant copepod of subgroup 2a, *C. pergens*, is not a diel migrant, its vertical distribution showed a remarkable descent during the strongest solar radiation in June, while it remained in the subsurface chlorophyll maximum layer during the rest of the 24-hour cycle (Hure *et al*., 2022). A similar vertical positioning was found for *Lucicutia flavicornis* and *C. parapergens* (Hure *et al*., 2022), which were also more abundant in the night epipelagic subgroup 2a than in the daily epipelagic sample group. Thus, it seems that the formation of the different copepod communities in the epipelagic during the night is not only influenced by strong migrants, but also by smaller, sub-surface oceanic copepod species whose vertical positioning was more subtle and dependent on various environmental characteristics of the upper layers. On the night of March 2022 (for which unfortunately no daily data are available) and May 2023, a subgroup 2a was found down to a depth of 200 m, probably due to the higher Chl *a* value in the surface layers in spring, which probably caused the mesopelagic organisms to move upward and feed at the surface.

The typical mesopelagic zone was further subdivided into an upper, shallower zone and a deeper zone, composed of the mainly non-migratory animals that remain in these layers and utilize the energy transported from the epipelagic zone via physical or biological conveyor processes. These species and groups generally occurred at depths between 100 m (or 200 m) and 600 m and represent the typical mesopelagic fauna of the Mediterranean Sea (Hure *et al*., 1980; Scotto di Carlo *et al*., 1984; Siokou-Frangou *et al*., 1997; Siokou *et al*., 2013). The community of the upper part was characterized by higher abundances of subsurface and mesopelagic species/taxa (*C. pergens*, *O. similis*, *Heterorhabdus* copepodites), while the lower mesopelagic community was also dominated by the *Oithona setigera* - group, *P. gracilis* and the genus *Spinocalanus*. The upper and lower boundary of the mesopelagic zone is difficult to determine due to the gradual transition from one boundary layer to another and the constant diel shifting of mesopelagic species. Differently from the epipelagic zone, no significant day/night differences were recorded in the mesopelagic layer, indicating relatively low contribution of migratory species whose abundances are not high enough for the formation of a specific copepod community.

The deep-sea copepod fauna of the Mediterranean is characterized by the absence of bathypelagic species and is replaced by mid-water species that live at great depths (Scotto di Carlo *et al*., 1984). In the Tyrrhenian Sea, they live at depths below 600 m (Scotto di Carlo *et al*., 1984), while in the Adriatic Sea they live below 500 m (Hure & Scotto di Carlo, 1969; Hure *et al*., 1980). Our results suggest that it may occasionally extend even to the 400-600 m layer, although it should be noted that we did not consider the layers between 400 m and 500 m and between 500 and 600 m separately. Recently, very few data have been collected on copepods below 1000 m in the SA (Batistić *et al*., 2012; Hure *et al*., 2020; Kršinić *et al*., 2020). We found a weak separation between copepod subgroups at greater depths, mainly characterized by higher abundances of the genus *Spinocalanus* in the upper group, while *M. typica* and *C. helgolandicus* were more abundant in the deeper-layer community. Most studies reported similar deep copepod communities with the same genera and species in the eastern and western Mediterranean (Scotto di Carlo *et al*., 1984; Weikert & Trinkaus, 1990; Andersen *et al*., 2001; Brugnano *et al*., 2012; Zagami *et al*., 2020), although seasonal fluctuations in community composition may be common in the low mesopelagic and bathypelagic zones in areas dominated by ontogenetically migrating calanoids (Vinogradov, 1997; Siokou *et al*., 2013). There was no visible seasonality evident in our cluster groupings. However, for a more detailed analysis of this deep community, samples should be taken in finer vertical layers, especially after the observations that *C. helgolandicus* was at times much more abundant in the 1000-1200 m depth layer (personal observation).

Winter mixing and summer stratification at our sampling site in a SA revealed clear seasonal differences in environmental conditions in the upper 100 m layer. The NMDS showed that the vertical distribution and abundance of copepods in the upper sampling layers was positively related to temperature, salinity and Chl *a* concentration. Despite relatively homogeneous physical and chemical conditions in the layers below 100 m depth, the distribution of the copepod community in the water column exhibited different dynamics and cluster grouping on a daily, seasonal and annual basis. For example, in winter 2021, the surface community was absent and was replaced by a mesopelagic community reaching down to 800 m depth. In February 2021 the cruise took place immediately after strong Bora wind episodes, and deep mixing occurred down to 600 m depth, which was visible in the vertical profiles of the environmental data. Our results show that the copepod community structure reflected the homogenization of the water column both during the day and at night. The disappearance of the DVM signal within a few days after the mixing in February 2008, which was also associated with Bora episodes, was already recorded by Ursella *et al*. (2018) using the Acoustic Doppler Current Profiler, which could indicate that the zooplankton had sufficient food in the deeper layers and did not need to perform a vertical migration. In contrast, the 2023 cruise took place 10 days after vertical mixing, a period apparently sufficient for a short-lasting increase in the subsurface phytoplankton and for the formation of the typical surface and subsurface communities during the day and night. This study confirms the short duration of winter connective events and the early establishment of a typical day/night profile of the copepod community. Furthermore, our work emphasizes the complexity of the system with a strong coupling of meteorological, environmental and biological conditions. The typical ship-based programs may overlook the importance of the sampling timing in relation to the Bora events (Batistić *et al*., 2012), which can strongly influence the results of studies conducted in the Adriatic Sea.

Although depth was the primary factor in structuring copepod communities, overall environmental changes and the complexity of processes throughout the water column may influence different positioning of copepod groups on the diel, seasonal and interannual time scales. Clear day-night differences were observed in the epipelagic layer, which can be attributed to the nocturnal enrichment of migratory species. In addition, the phenomenon of winter connective mixing leads to a homogenization of the water column and the distribution of copepods, so that the typical surface community disappears both during the day and at night. However, these events are short-lived, and the typical vertical formation reestablishes after a few days. Further detailed studies (e.g. species-specific distribution and life strategies, trophic relationships, targeted sampling of specific zones, biomass measurements) are required to identify the processes and mechanisms that shape the copepod communities occupying discrete layers of the water column.

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References

Andersen, V., 2001. Zooplankton Community During the Transition from Spring Bloom to Oligotrophy in the Open NW Mediterranean and Effects of Wind Events. 2. Vertical Distributions and Migrations. *Journal of Plankton Research*, 23 (3), 243-261.

Bachiller, E., Irigoien, X., 2015. Trophodynamics and diet overlap of small pelagic fish species in the Bay of Biscay. *Marine Ecology Progress Series*, 534, 179-198.

Bandara, K., Varpe, Ø., Ji, R., Eiane, K., 2018. A high-resolution modeling study on diel and seasonal vertical migrations of high-latitude copepods. *Ecological Modelling*, 368, 357-376.

Bandara, K., Varpe, Ø., Wijewardene, L., Tverberg, V., Eiane, K., 2021. Two hundred years of zooplankton vertical migration research. *Biological Reviews*, 96 (4), 1547-1589.

Batistić, M., Jasprica, N., Carić, M., Čalić, M., Kovačević, V. *et al.,* 2012. Biological evidence of a winter convection event in the South Adriatic: A phytoplankton maximum in the aphotic zone. *Continental Shelf Research*, 44, 57-71.

Batistić, M., Garić, R., Molinero, J.C., 2014. Interannual variations in Adriatic Sea zooplankton mirror shifts in circulation regimes in the Ionian Sea. *Climate research*, 61, 3, 231-240.

Batistić, M., Viličić, D., Kovačević, V., Jasprica, N., Garić, R. *et al.,* 2019. Occurrence of winter phytoplankton bloom in the open southern Adriatic: Relationship with hydroclimatic events in the Eastern Mediterranean. *Continental Shelf Research*, 174, 12-25.

Belmonte, G., 2018. Calanoida (Crustacea: Copepoda) of the Italian fauna: a review. *The European Zoological Journal*, 85 (1), 273-289.

Bode, M., Koppelmann, R., Teuber, L., Hagen, W., Auel, H., 2018. Carbon Budgets of Mesozooplankton Copepod Communities in the Eastern Atlantic Ocean –Regional and Vertical Patterns Between 24°N and 21°S. *Global Biogeochemical Cycles*, 32 (5), 840-857.

Böttger-Schnack, R., Schnack, D., 2009. Taxonomic diversity and identification problems of oncaeid

microcopepods in the Mediterranean Sea. *Marine Biodiversity*, 39, 131-145.

Bray, J.R., Curtis, J.T., 1957. An Ordination of the Upland Forest Communities of Southern Wisconsin. *Ecological Monographs*, 27 (4), 325-349.

Brugnano, C., Bergamasco, A., Granata, A., Guglielmo, L., Zagami, G., 2010. Spatial distribution and community structure of copepods in a central Mediterranean key region (Egadi Islands—Sicily Channel). *Journal of Marine Systems*, 81 (4), 312-322.

Brugnano, C., Granata, A., Guglielmo, L., Zagami, G., 2012. Spring diel vertical distribution of copepod abundances and diversity in the open Central Tyrrhenian Sea (Western Mediterranean). *Journal of Marine Systems*, 105-108, 207-220.

Cardin, V., Gačić, M., 2003. Long-term heat flux variability and winter convection in the Adriatic Sea. *Journal of Geophysical Research: Oceans*, 108 (C9), 2002JC001645.

Civitarese, G., Gačić, M., Batistić, M., Bensi, M., Cardin, V. *et al.,* 2023. The BiOS mechanism: History, theory, implications. *Progress in Oceanography*, 216, 103056.

Clarke, K.R., Gorley, R.N., 2015. *PRIMER v7: UserManual/ Tutorial*. https://learninghub.primer-e.com/books/primer-v7-user-manual-tutorial (Accessed 4 March 2025).

Clarke, K.R., Warwick, R.M., 1994. Similarity-based testing for community pattern: The two-way layout with no replication. *Marine Biology*, 118 (1), 167-176.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species:the need for a flexible asymmetrical approach. *Ecological Monographs*, 67 (3), 345-366.

Faganeli, J., Gačić, M., Malej, A., Smodlaka, N., 1989. Pelagic organic matter in the Adriatic Sea in relation to winter hydrographic conditions. *Journal of Plankton Research*, 11 (6), 1129-1141.

Fragopoulu, N., Lykakis, J.J., 1990. Vertical distribution and nocturnal migration of zooplankton in relation to the development of the seasonal thermocline in Patraikos Gulf. *Marine Biology*, 104 (3), 381-387.

Gaard, E., Gislason, A., Falkenhaug, T., Søiland, H., Musaeva, E. *et al.,* 2008. Horizontal and vertical copepod distribution and abundance on the Mid-Atlantic Ridge in June 2004. *Deep Sea Research Part II: Topical Studies in Oceanography*, 55 (1-2), 59-71.

Gačić, M., Marullo, S., Santoleri, R., Bergamasco, A., 1997. Analysis of the seasonal and interannual variability of the sea surface temperature field in the Adriatic Sea from AVHRR data (1984-1992). *Journal of Geophysical Research: Oceans*, 102 (C10), 22937-22946.

Gačić, M., Civitarese, G., Miserocchi, S., Cardin, V., Crise, A. *et al.,* 2002. The open-ocean convection in the Southern Adriatic: A controlling mechanism of the spring phytoplankton bloom. *Continental Shelf Research*, 22 (14), 1897-1908.

Gačić, M., Borzelli, G.L.E., Civitarese, G., Cardin, V., Yari, S., 2010. Can internal processes sustain reversals of the ocean upper circulation? The Ionian Sea example. *Geophysical Research Letters*, 37 (9), 2010GL043216.

Gačić, M., Ursella, L., Kovačević, V., Menna, M., Malačič, V. *et al.,* 2021. Impact of dense-water flow over a sloping bottom on open-sea circulation: Laboratory experiments and an Ionian Sea (Mediterranean) example. *Ocean Science*, 17 (4), 975-996.

Hure, J., 1955. Distribution annuelle verticale du zooplancton sur une station de l'Adriatique meridionale. *Acta Adriatica*, 7 (7), 1-72.

Hure, J., 1961. Dnevna migracija i sezonska vertikalna raspodjela zooplanktona dubljeg mora. *Acta Adriatica*, 9 (6), 1-59.

Hure, J., 1964. Rythme saisonnier de la distribution verticale du zooplancton dans les eaux plus profondes se l'Adriatique meridionale. *Acta Adriatica*, 11 (22), 167-172.

Hure, J., Scotto di Carlo, B., 1969. Diurnal vertical migration of some deep water Copepods in the Southern Adriatic (East Mediterranean). *Pubblicazioni Della Stazione Zoologica Di Napoli*, 37, 581-598.

Hure, J., Kršinić, F., 1998. Planktonic copepods of the Adriatic sea. Spatial and temporal distribution. *Natura Croatica*, 7 (2), 1-135.

Hure, M., Mustać, B., 2020. Feeding ecology of *Sardina pilchardus* considering co-occurring small pelagic fish in the eastern Adriatic Sea. *Marine Biodiversity*, 50 (3), 40.

Hure, J., Ianora, A., Scotto di Carlo, B.S., 1980. Spatial and temporal distribution of copepod communities in the Adriatic Sea. *Journal of Plankton Research*, 2 (4), 295-316.

Hure, M., Mihanović, H., Lučić, D., Ljubešić, Z., Kružić, P., 2018. Mesozooplankton spatial distribution and community structure in the South Adriatic Sea during two winters (2015, 2016). *Marine Ecology*, 39 (1), e12488.

Hure, M., Batistić, M., Kovačević, V., Bensi, M., Garić, R., 2020. Copepod Community Structure in Pre- and Post-Winter Conditions in the Southern Adriatic Sea (NE Mediterranean). *Journal of Marine Science and Engineering*, 8 (8), 567.

Hure, M., Batistić, M., Garić, R., 2022. Copepod Diel Vertical Distribution in the Open Southern Adriatic Sea (NE Mediterranean) under Two Different Environmental Conditions. *Water*, 14 (12), 1901.

Isla, A., Scharek, R., Latasa, M., 2015. Zooplankton diel vertical migration and contribution to deep active carbon flux in the NW Mediterranean. *Journal of Marine Systems*, 143, 86-97.

Ivančan-Picek, B., 2021. *Meteorološki i hidrološki bilten. Državni hidrometeorološki zavod*. https://radar2.dhz.hr/~stars2/bilten/2021/bilten0321.pdf (Accessed 4 April 2025).

Ivančan-Picek, B., 2023. *Meteorološki u hidrološki bilten. Državni hidrometeorološki zavod*. chrome-extension://efaidnbmnnnibpcajpcglclefindmkaj/https://radar2.dhz.hr/~stars2/bilten/2023/bilten0623.pdf (Accessed 4 April 2025).

Jónasdóttir, S. H., Visser, A. W., Richardson, K., Heath, M. R., 2015. Seasonal copepod lipid pump promotes carbon sequestration in the deep North Atlantic. *Proceedings of the National Academy of Sciences*, 112 *(*39), 12122-12126.

Kiørboe, T., 2011. What makes pelagic copepods so successful? *Journal of Plankton Research*, 33 (5), 677-685.

Kouwenberg, J.H.M., 1994. Copepod Distribution in Relation to Seasonal Hydrographics and Spatial Structure in the North-western Mediterranean (Golfe du Lion). *Estuarine, Coastal and Shelf Science*, 38 (1), 69-90.

Kršinić, F., Bottger-Schnack, R., Vidjak, O., 2020. Small copepods of the deep South Adriatic Pit: Diversity, seasonal and multi-annual dynamics, and implications from the regional hydrography. *Environmental Monitoring and Assessment*, 192 (545), 1-30.

Ljubimir, S., Jasprica, N., Čalić, M., Hrustić, E., Dupčić Radić, I. *et al.,* 2017. Interannual (2009-2013) variability of winter-spring phytoplankton in the open South Adriatic Sea: Effects of deep convection and lateral advection. *Continental Shelf Research*, 143, 311-321.

Lučić, D., Ljubešić, Z., Babić, I., Bosak, S., Cetinić, I. *et al.,* 2017. Unusual winter zooplankton bloom in the open southern Adriatic Sea. *Turkish Journal of Zoology*, 41, 1024-1035.

Malanotte-Rizzoli, P., Robinson, A.R., Roether, W., Manca, B., Bergamasco, A. *et al.,*1996. Experiment in eastern Mediterranean probes origin of deep water masses. *Eos, Transactions American Geophysical Union*, 77 (32), 305-311.

Mazzocchi, M.G., Christou, E.D., Fragopolou, N., Siokou-Frangou, I., 1997. Mesozooplankton distribution from Sicily to Cyprus (Eastern Mediterranean): I. General aspects. *Oceanologica Acta*, 20, 521-535.

Mazzocchi, M.G., Nervegna, D., D'Elia, G., Di Capua, I., Aguzzi, L. *et al.,* 2003. Spring mesozooplankton communities in the epipelagic Ionian Sea in relation to the Eastern Mediterranean Transient. *Journal of Geophysical Research: Oceans*, 108 (C9), 2002JC001640.

McCune, B., Grace, J.B., 2002. *Analysis of ecological communities.* MjM Software Design, Gleneden Beach, Oregon, U.S.A..

McCune, B., Mefford, M.J., 2006. *PC-ORD. Multivariate analysis of Ecological Data, Version 5.0 for Windows.* MjM Software, Gleneden Beach, Oregon, U.S.A.

Nowaczyk, A., Carlotti, F., Thibault-Botha, D., Pagano, M., 2011. Distribution of epipelagic metazooplankton across the Mediterranean Sea during the summer BOUM cruise. *Biogeosciences*, 8 (8), 2159-2177.

Ramfos, A., Isari, S., Somarakis, S., Georgopoulos, D., Koutsikopoulos, C. *et al.,* 2006. Mesozooplankton community structure in offshore and coastal waters of the Ionian Sea (eastern Mediterranean) during mixed and stratified conditions. *Marine Biology*, 150 (1), 29-44.

Raybaud, V., Nival, P., Mousseau, L., Gubanova, A., Altukhov, D. *et al.,* 2008. Short term changes in zooplankton community during the summer-autumn transition in the open NW Mediterranean Sea: Species composition, abundance and diversity. *Biogeosciences*, 5 (6), 1765-1782.

Schnetzer, A., Steinberg, D., 2002. Natural diets of vertically migrating zooplankton in the Sargasso Sea. *Marine Biology*, 141 (1), 89-99.

Scotto di Carlo, B.S., Ianora, A., Fresi, E., Hure, J., 1984. Vertical zonation patterns for Mediterranean copepods from the surface to 3000 m at a fixed station in the Tyrrhenian Sea. *Journal of Plankton Research*, 6 (6), 1031-1056.

Shannon, C.E., Weaver, W., 1963. *The mathematical theory of communication*. University of Illinois Press, Urbana, 117 pp.

Siokou, I., Zervoudaki, S., Christou, E.D., 2013. Mesozooplankton community distribution down to 1000 m along a gradient of oligotrophy in the Eastern Mediterranean Sea (Aegean Sea). *Journal of Plankton Research*, 35 (6), 1313-1330.

Siokou, I., Zervoudaki, S., Velaoras, D., Theocharis, A., Christou, E.D. *et al.,* 2019. Mesozooplankton vertical patterns along an east-west transect in the oligotrophic Mediterranean sea during early summer. *Deep Sea Research Part II: Topical Studies in Oceanography*, 164, 170-189.

Siokou-Frangou, I., Christaki, U., Mazzocchi, M.G., Montresor, M., Ribera d'Alcalá, M. *et al.,* 2010. Plankton in the open Mediterranean Sea: A review. *Biogeosciences*, 7 (5), 1543-1586.

Siokou-Frangou, I., Christou, E.D., Fragopoulu, Mazzocchi, M.G., 1997. Mesozooplankton distribution from Sicily to Cyprus (Eastern Mediterranean) .2. Copepod assemblages. *Oceanolica Acta*, 20 (3), 537-548.

Takahashi, K., Kuwata, A., Sugisaki, H., Uchikawa, K., Saito, H., 2009. Downward carbon transport by diel vertical migration of the copepods *Metridia pacifica* and *Metridia okhotensis* in the Oyashio region of the western subarctic Pacific Ocean. *Deep Sea Research Part I: Oceanographic Research Papers*, 56 (10), 1777-1791.

Ursella, L., Cardin, V., Batistić, M., Garić, R., Gačić, M., 2018. Evidence of zooplankton vertical migration from continuous Southern Adriatic buoy current-meter records. *Progress in Oceanography*, 167, 78-96.

Vinogradov, M.E., 1997. Some Problems of Vertical Distribution of Meso- and Macroplankton in the Ocean. *Advances in Marine Biology,* 32, 1-92.

Weikert, H., Trinkaus, S., 1990. Vertical mesozooplankton abundance and distribution in the deep Eastern Mediterranean Sea SE of Crete. *Journal of Plankton Research*, 12 (3), 601-628.

Weikert, H., Koppelmann, R., 1993. Vertical structural patterns of deep-living zooplankton in the ne atlantic, the levantine sea and the red-sea –A comparison. *Oceanolica Acta*, 16 (2), 163-177.

Weikert, H., Koppelmann, R., Wiegratz, S., 2001. Evidence of episodic changes in deep-sea mesozooplankton abundance and composition in the Levantine Sea (Eastern Mediterranean). *Journal of Marine Systems*, 30 (3-4), 221-239.

Zagami, G., Granata, A., Brugnano, C., Minutoli, R., Bonanzinga, V. *et al.,* 2020. Spring copepod vertical zonation pattern and diel migration in the open Ligurian Sea (north-western Mediterranean). *Progress in Oceanography*, 183, 102297.

Zakaria, H.Y., Hassan, A.-K.M., Abo-Senna, F.M., El-Naggar, H.A., 2016. Abundance, distribution, diversity and zoogeography of epipelagic copepods off the Egyptian Coast (Mediterranean Sea). *Egyptian Journal of Aquatic Research*, 42 (4), 459-473.

Zimmerman, G.M., Goetz, H., Mielke, P.W., 1985. Use of an improved statistical method for group comparisons to study the effects of prairie fire. *Ecology*, 66, 606-611.