CHAPTER 15

CHANGES IN THE ZOOPLANKTON OF THE EASTERN SEA OF MARMARA

Melek ISINIBILIR[1], Leonid SVETLICHNY[2], Ezgi E. TÜRKERİ[1], N. Eda TOPÇU[1], Ahmet E. KIDEYS[3]

[1]İstanbul University, Faculty of Aquatic Sciences, Department of Marine and Freshwater Resources Management, İstanbul, Türkiye

E-mail: melekis@istanbul.edu.tr; ezgi.turkeri@istanbul.edu.tr; edatopcu@istanbul.edu.tr

[2]I.I. Schmalhausen Institute of Zoology NAS of Ukraine, vul. B. Khmelnytskogo, 15, Kyiv, Ukraine

E-mail: leonid.svetlichny@gmail.com

[3]Middle East Technical University, Institute of Marine Sciences, Mersin, Türkiye

E-mail: kideys@gmail.com

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Abstract

The study conducted in the eastern Sea of Marmara from 2016 to 2022 aimed to investigate the spatio-temporal distributions of mesozooplankton in relation to changing environmental conditions. A total of 43 zooplankton taxa were identified, with the number of species varying between 4 and 19 in the brackish upper layer (resembling the Black Sea) and between 1 and 17 in the saline lower layer (resembling the Mediterranean Sea). The abundances of zooplankton ranged from 28 to 43,359 ind.m-3 in the upper layer and from 5 to 3,851 ind.m^{-3} in the lower layer. Significant differences were observed between the upper and lower layers in terms of the number of species, total zooplankton abundances, evenness, and Shannon diversity ($p<0.0001$). The most significant differences in zooplankton abundance and community structure were found to be seasonal rather than inter-year or regional variations. The highest total zooplankton abundance was recorded at station M14 during the summer season (June 2022), primarily due to the presence of *Paracalanus parvus* and *Penilia avirostris* (906 ind.m^{-3} and 722 ind.m^{-3}, respectively). The heterotrophic dinoflagellate *Noctiluca scintillans*, a major component of net samples in the Sea of Marmara, exhibited a clear seasonal distribution, with higher abundances consistently observed during winter months. The highest abundance of *Noctiluca scintillans* was recorded in February 2016 at station MD102 (42,514 ind.m^{-3}). *Paracalanus parvus, Acartia clausi,* and *Oithona nana* were identified as important year-round species in both the upper and lower layers of the Sea of Marmara. The presence of *N. scintillans* and *P. avirostris* distinguished the upper layer communities from the lower layer, with *N. scintillans* being more prevalent during winter and *P. avirostris* during summer. Notably, *P. avirostris* exhibited very low abundances during the summers of 2019, 2021, and 2022. The large-scale mucilage event that occurred in June 2021 had a significant impact on zooplankton, as evidenced by the low abundance and biomass observed during this period. The chlorophyll-*a* values, which reflect phytoplankton biomass, increased sharply during the dominating mucilage event, ranging from 12.2 to 14.2 µg.l^{-1}. Overall, this study emphasizes the vulnerability of the Sea of Marmara ecosystem, particularly zooplankton, to large-scale environmental disturbances such as mucilage events.

Keywords: Marmara, zooplankton, changes, mucilage, *Noctiluca scintillans, Penilia avirostris*

1. Introduction

The Sea of Marmara, located between the Black Sea and the Mediterranean, is an internal sea that holds significant importance as a spawning, nursery, foraging, and wintering habitat for numerous fish species (Kabasakal, 2009; Kahraman et al., 2021; Ulman et al., 2020; Yıldız et al., 2020). However, climate change and other detrimental human activities have caused structural and functional changes in the Sea of Marmara ecosystem over the past few decades. These changes include temperature increases (Kokal et al., 2023), pollution from plastics and microplastics (Çevik et al., 2022; Vardar et al., 2021), elevated eutrophication levels (Ediger et al. 2016), the ongoing introduction of invasive species (Inanmaz et al., 2003; Eker-Develi et al., 2022; 2023; Svetlichny et al., 2023), an upsurge in jellyfish and harmful algal blooms (Isinibilir, 2011; 2012; Isinibilir & Yılmaz, 2017; Taş et al., 2020; Türkoğlu, 2013), shifts in plankton and fish community structure (Svetlichny et al., 2006; Isinibilir et al., 2010a; 2015; Balkıs et al., 2014; Taş et al., 2020; Ulman et al., 2020), and overexploitation of fishery stocks (Saygu et al., 2023).

In both 2007-2008 and 2021, the Sea of Marmara encountered a basin-scale mucilage events, resulting in severe ecological consequences and being classified as an environmental disaster (Isinibilir Okyar et al., 2015; Balkıs-Özdelice, 2021; Isinibilir Okyar, 2023). This event received significant attention from the public due basin-scale surface aggregations that were visually unappealing and from scientists and decision-makers due to its negative impact on the entire ecosystem, including planktonic, benthic organisms as well as on fishery.

The mucilage, commonly known as Marmara mucilage or “sea snot,” is believed to be produced due to the excessive growth of certain phytoplankton species in the Sea of Marmara. A recent study by Eker-Develi et al. (2023) successfully identified one particular species, the coccolithophorid *Ochrosphaera neapolitana*, as a significant contributor to the production of mucilage in the Sea of Marmara. These organisms generate a slimy, gelatinous substance that forms a thick layer on the water surface, resembling floating mucus-like material. The presence of Marmara mucilage raises grave environmental concerns as it can smother marine life, disrupt ecosystems, and have detrimental effects on local fisheries and tourism.

Zooplankton play a crucial role as secondary producers and are key drivers of the biological pump in marine ecosystems (Turner, 2004; Robert et al., 2014; Steinberg & Landry, 2017). Zooplankton are poikilothermic and short-lived drifters, making them highly sensitive to environmental variables (Hays et al., 2005). Consequently, changes in zooplankton community dynamics serve as valuable indicators of adverse conditions such as mucilage events and climate change (Richardson, 2008; Batchelder et al., 2013; Isinibilir Okyar et al., 2015).

In stratified systems like the Sea of Marmara, the impact of climate change on the dynamics of upper layer zooplankton is particularly pronounced due to the reinforcement of stratification (Richardson, 2008; Coma et al., 2009). The alteration in zooplankton abundance patterns, species assemblages, and community structure can be utilized as an assessment tool to evaluate the overall health of an aquatic ecosystem. This highlights the importance of monitoring and understanding changes in zooplankton dynamics to gain insights into the impacts of environmental disturbances on marine ecosystems.

The main aim of this study is to evaluate the spatio-temporal variations in zooplankton in relation to anthropogenic influences and mass mucilage events, to gain insights into the complex interactions and potential disturbances occurring in the Sea of Marmara. This information can help inform management and conservation strategies to mitigate the adverse impacts on both zooplankton and the associated fish populations.

2. Material Methods

2.1. Sampling Design and Analysis of Samples

Sampling of this study covers the period of 2016-2022 in the Sea of Marmara. Upper layer samples, characterizing Black Sea originated waters were monthly collected at 21 stations in the Sea of Marmara (Figure 1) in February, May, July and December in 2016, in February, May, July and September in 2017, in May and October in 2018, in February and June 2019, in June and October 2020, in June 2021 and 2022 (Table 1). In June 2022, samples could not be taken from stations G2, MD10, MD3, MD4, MD6, MD7 and MY5 due to heavy mucilage aggregates. The 21 sampling sites were categorized into three groups (offshore, transitional and coastal zone). Stations İZ9, M11 and MD102 were located offshore the Sea of Marmara, where the influence of anthropogenic stress is minimized and represents the oceanic ecosystem of the Sea of Marmara, even though it is still affected by the Izmit Bay and the Strait's upper layer flow. Stations MD3, MD4 and MD8 were less affected by pollution and considered to be a transitional zone from neritic to oceanic environment. G2, KÇ, M12, M13, M14, MD1, MD2, MD3, MD4, MD5, MD6, MD7, MD9, MD10, MD75, MY5 and YK1 were located in coastal waters of the Sea of Marmara, where the influence of anthropogenic stress is maximum. Samples were collected from the Mediterranean-originated lower layer at 12 stations (İZ9, M11, MD102, MD1, MD2, MD3, MD4, MD5, MD6, MD7, MD8, MD75) during periods characterised by both thermal stratification and haline stratification.

All samples were collected vertically during daytime, by a WP2 closing net (157 mm mesh size, 0.5 m mouth diameter) from the interface, to the surface and from the bottom to the

interface for samples from the lower layers. After collection, the net was rinsed gently, and the samples were transferred into plastic containers. To preserve the specimens, a borax-buffered formaldehyde solution was added to achieve a final concentration of 4%. Identification of the specimens was conducted using a stereomicroscope and a Bogorov-Rass counting chamber. For common species, quantitative analysis was performed on sub-samples taken using a 1 ml Stempel pipette (at least twice). Rare species were identified from the entire sample. Cladocerans and copepods were identified to the species or genus level, while other taxa were identified to the lowest possible taxonomic level.

Water temperature and salinity was measured vertically by SBE 9/11 CTD in station İZ9. Chlorophyll-*a* analyses were performed following the methodology of APHA (2000) in all stations in the upper water layer.

2.2. Data Analysis

Species richness, total zooplankton abundance, Pielou's evenness J' and diversity (as measured by Shannon H'($\log_e$)) between seasons and zones (coastal, offshore and transitional sites) for the upper and lower layers assemblages were compared by non-parametric Kruskal-Wallis tests. Multiple comparisons were conducted when overall test results gave significant differences. All these tests were performed with GraphPad Prism v9 for Windows.

For multivariate analyses of community structure, a similarity matrix was constructed from square root transformed zooplankton abundance data, using the Bray–Curtis coefficient of similarity and sample interrelations were mapped by non-metric multidimensional scaling (MDS). Group similarities > 65% were shown on nMDS based on group average cluster analysis. The upper layer samples in 2021 (mucilage year) located very distant from the rest of the samples causing them overlapping, therefore we re-organized the matrix without including 2021 samples and repeated the same steps to visualize the differences between the overlapping samples on nMDS. Principal coordinate analysis ordination (PCO) was used to visualize the natural groupings of the samples and 2D bubble plots were used to visualize variation of abundances (of the most common taxa) between groupings.

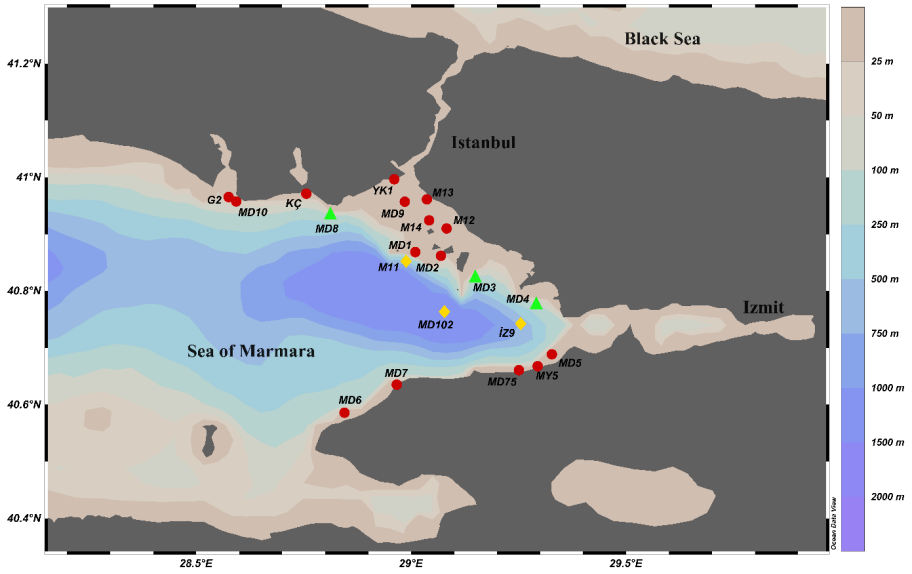


Figure 1. Zooplankton stations sampled in the eastern Sea of Marmara. Stations marked with "red circle" are in coastal zone, those marked with "green triangle" are in transitional zone and those marked with "diamond in yellow" are in offshore zone.

Table 1. Sampled seasons along years.

2016	2017	2018	2019	2020	2021	2022
Winter	Winter		Winter			
Spring	Spring	Spring				
Summer	Summer		Summer	Summer	Summer	Summer
Autmn	Autmn	Autmn		Autmn		

Differences in the zooplankton assemblages according to the tested factors were identified using permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001); while a similarity percentage analysis (SIMPER) was performed to determine the contribution of each taxon to the observed similarities and dissimilarities between groups. The first experimental design included two factors: factor "layer" (fixed, 2 levels: upper and lower) and factor "seasons" (fixed, 4 levels: winter, spring, summer, autumn). In order to reveal differences in the upper layer communities, the second experimental design included three factors: factor "years" (fixed, 7 levels: 2016; 2017; 2018; 2019, 2020, 2021 and 2022); factor "seasons" (fixed, 4 levels: winter, spring, summer, autumn) and factor "zones" (fixed, 3 levels: coastal, offshore and transitional zone). A canonical analysis of principal coordinates (CAP) was performed to model changes in assemblages' composition. Pearson correlations were estimated to identify the species that most effectively described the groups identified

by the CAP procedure. Only the variables with a Pearson correlation coefficient r > 0.50 were considered. The matching of the resemblance matrix of biotic data and normalized environmental parameters (temperature, salinity, chlorophyll a) was checked with BEST (BioENV method, Spearman rank correlation) and DistLM (Distance based Linear Models with Akaike information corrected criterion (AICc) and stepwise options for model). A test of significance of the multidimensional model was conducted with a permutation method with 999 permutations. The relative importance of environmental variables was visualized with a distance-based redundancy analysis (dbRDA).

All the above analyses and diversity index computations were carried out with the software Primer V6.1.16 & PERMANOVA + V1.0.6, according to Clarke & Gorley (2006).

3. Results

3.1. Hydrography

The two-layered structure is evident from the temperature and salinity profiles (Figure 2). The highest value for temperature was observed in July 2016 (25.3 °C, 1 m) and the lowest in February 2017 (6.1 °C, 1.3 m). The upper-layer waters with 22–29 ppt salinity were separated by a permanent pycnocline from the lower layer, which possessed a salinity of about 38 ppt. During the usual phytoplankton blooming period at the end of the winter, the highest value of chlorophyll-*a* concentration (6.15 µg l^{-1}), which is an indicator of primary production, was recorded at station M14 in February 2016, while the lowest value of 0.01 µg l^{-1} was recorded at station YK1 in February 2016 (Figure 3). However, it increased sharply during the dominating mucilage event in June 2021 and ranged between 12.2 -14.2 µg l^{-1}.

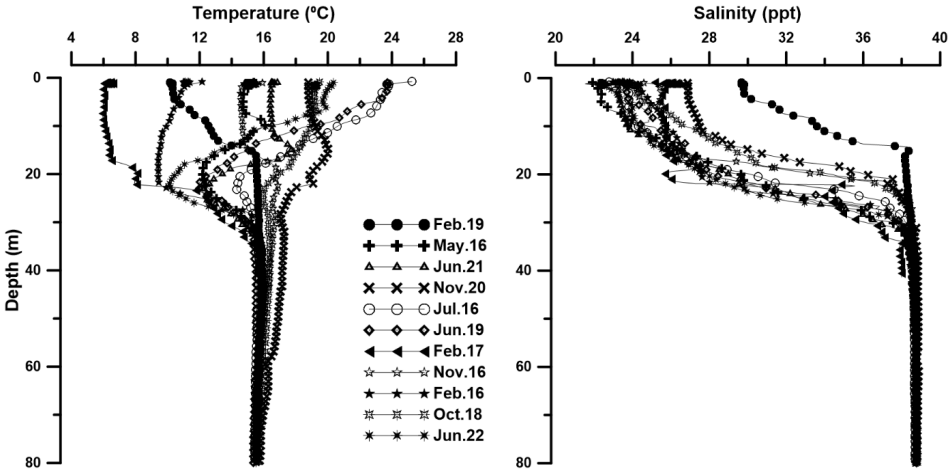


Figure 2. Temperature and salinity profiles in station İZ9.

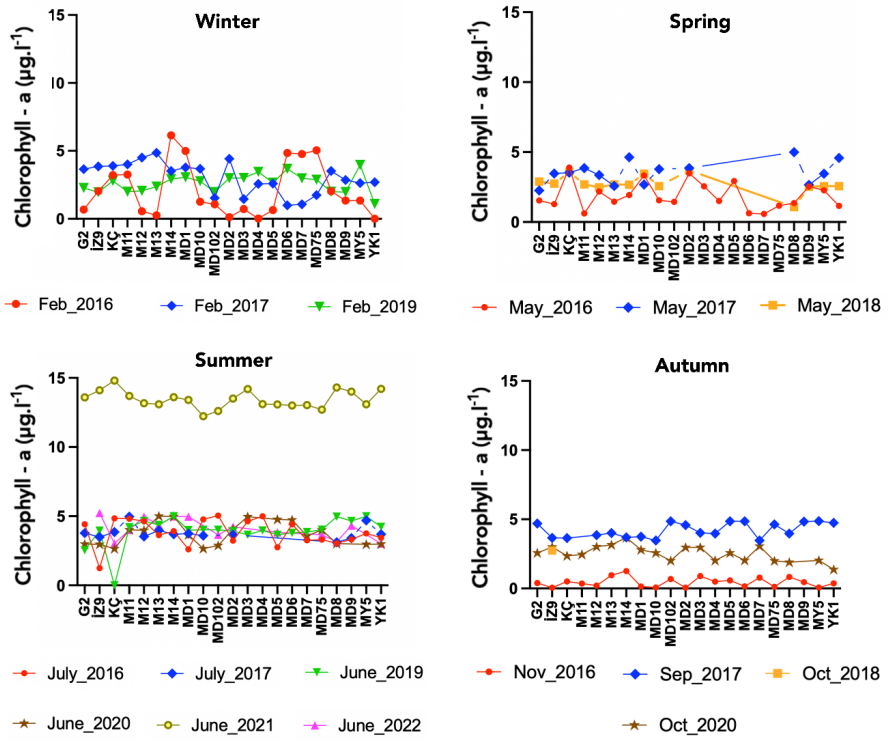


Figure 3. Fluctuation of chlorophyll-*a* at the sampling stations in the Sea of Marmara.

3.2. Zooplankton Species Assemblages and Diversity

In total, 46 zooplankton taxa were identified in this study (Table 2). The number of species varied between 4 and 19 in the upper layer (mean±sd: 11.65±3.09 in the winter, 10.15±2.217 in spring, 11.05±2.416 in summer and 13.52±2.370 in autumn), and between 1 and 17 in the lower layer (mean±sd: 10.88±3.15 in the winter, 9.44±2.20 in spring, 10.09±2.009 in summer and 10.56±2.27 in autumn) (Figure 4).

Zooplankton abundances varied between 28 and 43359 ind.m^{-3} in the upper layer (mean±sd: 10085±8267 ind.m^{-3} in the winter, 2831±1695 ind.m^{-3} in spring, 1896±1068 ind.m^{-3} in summer and 2299±1700 ind.m^{-3} in autumn) and between 5 and 3851 ind.m^{-3} in the lower layer (mean±sd: 230.3±277.8 ind.m^{-3} in the winter, 236.9±243.9 ind.m^{-3} in spring, 453.5±792.4 ind.m^{-3} in summer and 232.7±205.5 ind.m^{-3} in autumn). Shannon diversity varied between 0.009 and 2.36 in the upper layer (mean±sd: 0.72±0.57 in the winter, 1.15±0.39 in spring,

1.54±0.30 in summer and 1.82±0.29 in autumn) and between 0 and 2.39 in the lower layer (mean±sd: 1.79±0.35 in the winter, 1.46±0.31 in spring, 1.69±0.28 in summer and 1.91±0.38 in autumn). The number of species, total zooplankton abundances, evenness and Shannon diversity significantly differed between upper and lower layers ($p<0.0001$; H=94.96, H=309.2, H=206.6, H=214.7 respectively) (Table 3). In multiple comparisons however, the number of species between the two layers was significantly different only in Autumn. Abundances and evenness on the other hand, were significantly different between the two layers in all seasons ($p<0.05$). Shannon diversity in multiple comparisons was significantly different between the upper and lower layers only in winter ($p<0.05$), despite the overall Shannon diversity in the lower layer (mean±sd: 1.72±0.36) is higher than in the upper layer (mean±sd: 1.37±0.56).

The number of species and abundances were not significantly different between the lower layer samples in different seasons ($p>0.05$). Evenness in the lower layer samples significantly differed only between Spring and Autumn ($p<0.05$ ****) while Shannon diversity was significantly different between Spring and Autumn ($p<0.05$ ****) but also between Summer and Autumn to a less degree ($p<0.05$ *).

The number of species in zooplankton assemblages, total abundance, evenness and Shannon indices in the upper layer communities did not differ significantly among zones ($p>0.05$) but were significantly different between seasons (H=62.10, $p<0.0001$; H=66.61, $p<0.0001$; H=120, $p<0.0001$; H=152.5, $p<0.0001$respectively). Multiple comparisons showed significant differences between abundances of upper layer winter samples with the other seasons and between spring and summer abundances ($p<0.05$) while there were no significant differences between 'spring versus autumn' and 'summer versus autumn' samples ($p>0.05$). In the upper layer, evenness and Shannon indices were not significantly different between winter and spring samples ($p>0.05$) while all other pairwise comparisons were significantly different between season pairs ($p<0.05$).

Tablo 2. List of zooplanktonic taxa in the northeastern Marmara Sea (U: upper water, and L: lower water)

	2016		2017		2018		2019		2020		2021		2022	
	U	**L**	**U**	**L**	**U**	**L**	**U**	**L**	**U**	**L**	**U**	**L**	**U**	**L**
COPEPODA														
Acartia clausi	X	X	X	X	X	X	X	X	X	X	X		X	X
Acartia tonsa			X		X		X	X	X				X	X
Aetideus armatus		X						X						
Calanus euxinus	X	X	X	X	X	X	X	X	X	X			X	

Centropages ponticus	X		X				X							
Centropages typicus	X		X		X		X		X				X	
Clausocalanus spp.					X		X		X				X	
Ctenocalanus vanus				X		X		X		X				X
Euchaeta marina		X		X										
Mesocalanus tenuicornis				X		X		X		X			X	
Metridia lucens	X		X	X	X	X	X	X	X	X			X	X
Microcalanus pygmaeus	X		X	X	X	X	X	X	X	X			X	X
Paracalanus parvus	X	X	X	X	X	X	X	X	X	X			X	X
Pseudocalanus elongatus	X		X	X	X	X	X	X	X	X			X	
Temora stylifera	X		X		X		X		X	X			X	
Oithona davisae	X		X		X		X		X				X	
Oithona nana	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
Oncaea minuta	X	X	X	X	X	X	X	X	X	X			X	X
Euterpina acutifrons	X	X	X	X	X	X	X	X	X	X			X	X
Microsetella rosea				X				X		X				
Copepoda (nauplii and copepodit)	X	X	X	X	X	X	X	X	X	X			X	X
CLADOCERA														
Evadne nordmanni	X	X	X	X		X	X	X	X	X			X	
Evadne tergestina									X					
Penilia avirostris	X	X	X	X	X	X	X		X	X			X	X
Pleopis polyphemoides	X	X	X	X	X	X	X	X	X	X			X	X
Appendicularia														
Oikopleura dioica	X	X	X	X	X	X	X	X	X	X			X	X
Chaetognatha														
Parasagitta setosa	X	X	X	X	X	X	X	X	X	X			X	X
OTHER SPECIES AND GROUPS														
Foraminifera	X		X						X				X	
Bivalvia larvae	X	X	X	X	X	X	X	X	X	X			X	X
Gastropoda larvae	X	X	X	X		X	X	X		X				X
Cirripedia larvae	X		X	X	X	X		X						
Bryozoa larvae		X		X			X			X				
Decapoda larvae	X	X	X	X	X	X	X	X	X	X			X	X
Isopoda larvae	X	X			X	X			X	X				

Polychaeta larvae	X	X	X	X	X	X	X	X	X	X			X	X
Ostracoda larvae	X	X	X	X	X	X	X	X	X	X			X	X
Ichtyoplankton	X	X	X	X	X	X	X	X	X	X			X	X
Aurelia aurita	X	X	X	X	X	X	X	X	X	X			X	X
Aglaura hemistoma	X	X		X	X	X		X	X	X				X
Siphonophora		X		X		X		X	X	X			X	X
Beroe ovata	X	X	X	X	X	X	X	X	X	X			X	
Mnemiopsis leidyi	X		X		X		X		X				X	
Pleurobrachia pileus	X	X	X	X	X	X	X	X	X				X	X
Ctenophora larvae	X													
Noctiluca scintillans	X	X	X	X	X	X	X		X	X			X	X

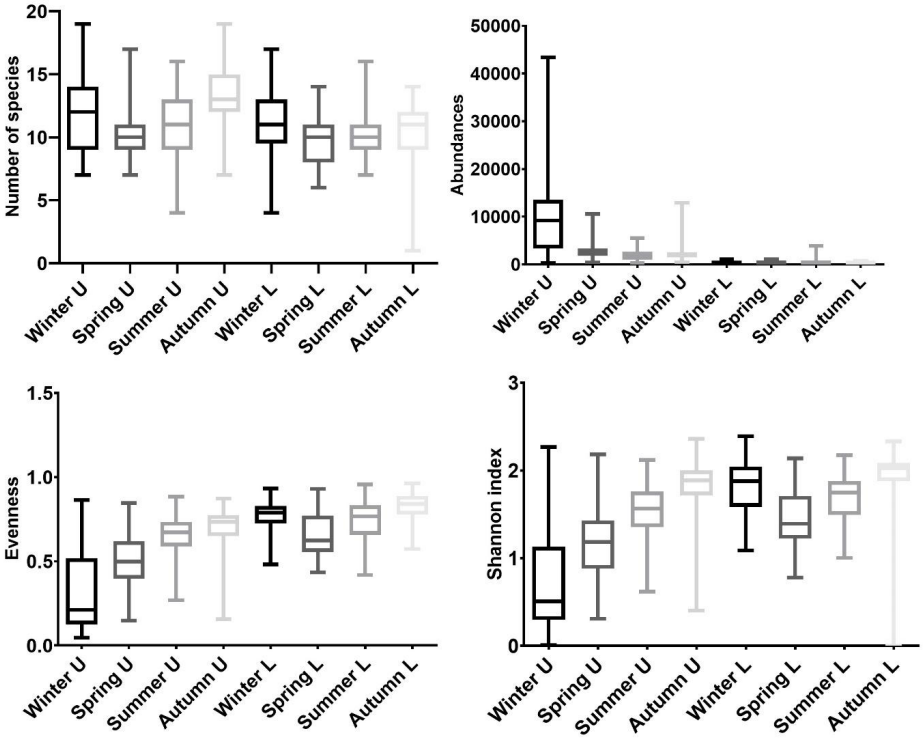


Figure 4. Box and whisker plots of the number of species, abundances (ind m^{-3}), Pielou's evenness and Shannon index of the upper (U) and lower (L) layer samples in different seasons. All years combined.

Zooplankton abundance and biomass (without *N. scintillans*) showed a seasonal distribution in the Sea of Marmara (Figures 5 and 6). The highest total zooplankton abundance occurred at station M14 (3666 ind.m^{-3}) in summer season (June 2022), particularly due to *Paracalanus parvus* and *Penilia avirostris* (906 ind.m^{-3} and 722 ind.m^{-3} respectively) (Figure 5). The zooplankton biomass, on the other hand, was the highest at station KÇ in May 2018, due to *Aurelia aurita* (Figure 6). *Calanus euxinus*, a psychrophile species, had a high abundance in winter and low abundance in spring and autumn.

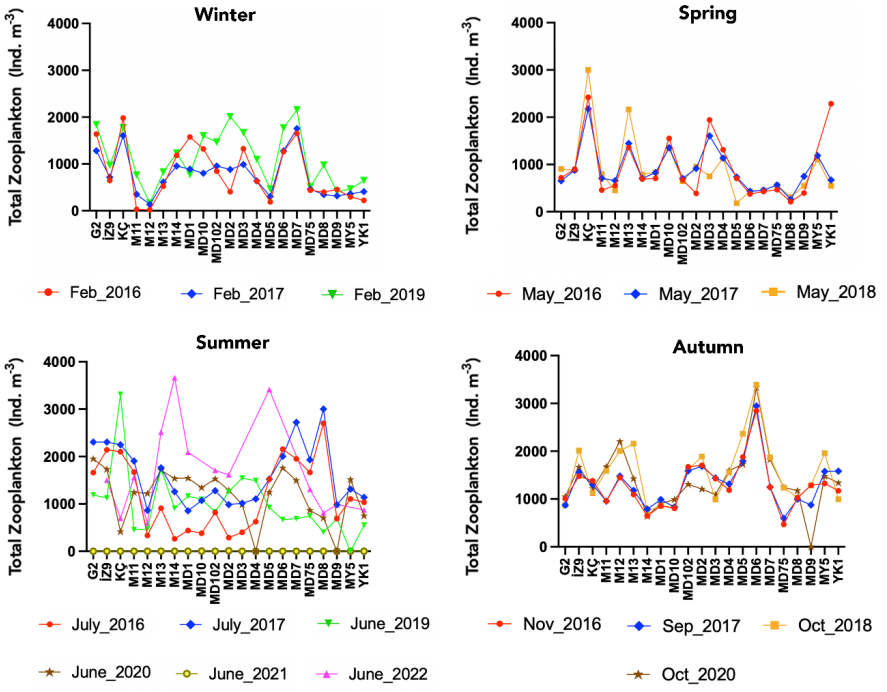


Figure 5. Fluctuations in abundance of total zooplankton (without *N. scintillans*) in the upper layer.

The heterotrophic dinoflagellate *Noctiluca scintillans*, as a major component of net samples in the Sea of Marmara, also has a very clear seasonal distribution in the Marmara Sea and was always high during winter months (Figure 7), with the highest value in February 2016 in station MD102 (42514 ind. m^{-3}). *N. scintillans* density dropped sharply to minimum levels following winter peaks, and abundances were very low from summer to autumn months.

The above-mentioned patterns were also detected in the multivariate analysis. We found significant differences between the zooplankton communities of the upper and lower layer

Table 3. Seasonal Variation in Upper and Lower Layers Zooplankton Assemblages: range and mean (± standard deviation) of Species Richness, Total Abundance, Shannon Diversity, and Evenness.

	Range		Mean ± sd							
			Winter		Spring		Summer		Autumn	
	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower
Number of species	4 -19	1 -17	11.65±3.09	10.88±3.15	10.15±2.22	9.44±2.20	11.05±2.42	10.09±2.01	13.52±2.37	10.56±2.27
Abundances (ind.m^{-3})	28 - 43359	5 - 3851	10085±8267	230.3±277.8	2831±1695	236.9±243.9	1896±1068	453.5±792.4	2299±1700	232.7±205.5
Shannon Diversity	0.009 - 2.36	0 - 2.39	0.72±0.57	1.79±0.35	1.15±0.39	1.46±0.31	1.54±0.30	1.69±0.28	1.82±0.29	1.91±0.38
Evenness	0.046 - 0.884	0.419-0.963	0.318±0.242	0.767±0.105	0.498±0.159	0.657±0.136	0.650±0.117	0.740±0.119	0.705±0.113	0.824±0.092

samples, between seasons, and their interaction (layer x season) seem to cause significant differences in zooplankton communities (Table 4; Figure 8). Pairwise tests showed significant differences between the two layers at each season. Similarly, zooplankton communities in each layer were significantly different between seasons. However, zooplankton communities in the upper layer at different zones of the Sea of Marmara were not significantly different and "zone" as a factor does not seem to contribute significantly to the differences observed between samples (Table 5; Figure 9). Post-hoc tests of upper layer communities showed significant differences between seasons in all years. In both layers, *Paracalanus parvus, Acartia clausi* and *Oithona nana* are year-round present important species in the Sea of Marmara (Table 6; Figure 10 and 11). In the upper layer the increase of *Noctiluca scintillans* marks the winter season while *Penilia avirostris* marks the summer and distinguishes the upper layer communities from the lowers (Figure 9). The number of species contributing to the Autumn community in the upper layer is higher than in other seasons in accordance with diversity results. However, zooplankton community in station M12 in winter 2016 differs from other samples in that the diversity is very low and *Aurelia aurita* has high biomass (2336 mg.m^{-3}) (Figure 9).

Zooplankton communities of the upper layer in 2016, 2017, 2018 and 2020 did not seem to be different between each other in any season. However, the years 2019 and 2022, while not significantly different from each other, exhibited notable distinctions from the other years durin the summer season (Table 5, Figure 12). The abundance

of *P. avirostris* which is either absent or at low levels in winter/spring undergoes a significant increase during the summer season. However, this species showed a very low abundance during the summers of 2019, 2021 and 2022, setting them apart from the other years (Figure 12). During the summer of 2021, when mucilage continued to cover the Sea of Marmara, only a limited number of zooplankton species, such as *A. clausi* and *O. nana*, were present.

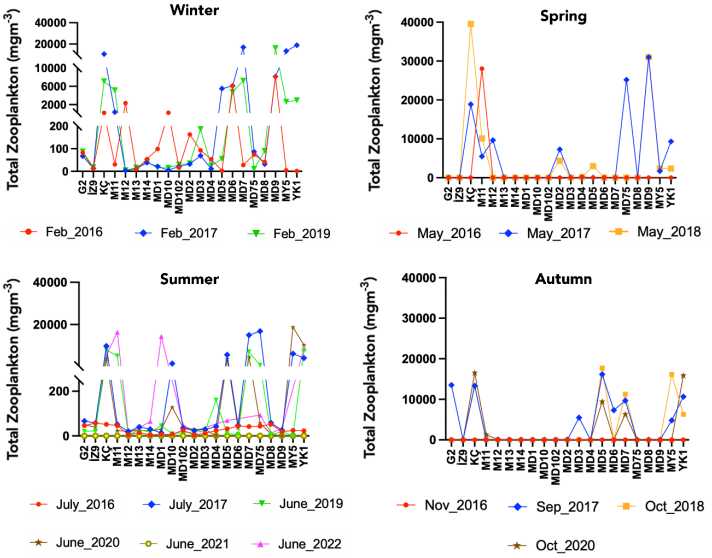


Figure 6. Fluctuations in biomass of total zooplankton (without *N. scintillans*) in the upper laye

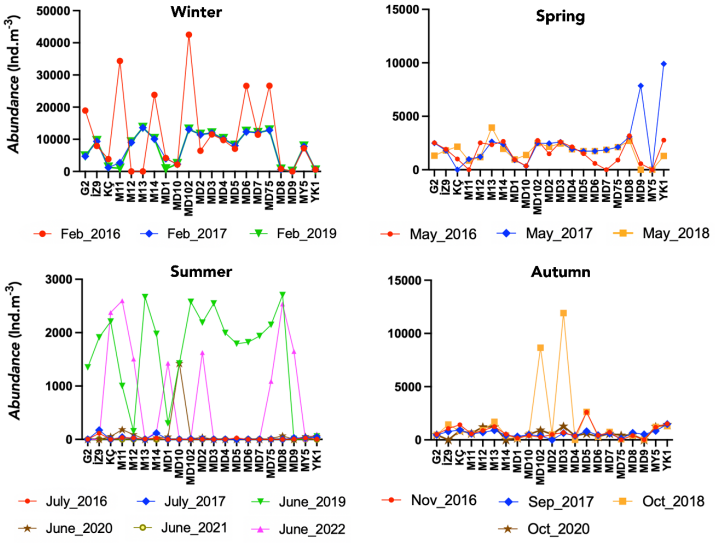


Figure 7. Fluctuations in abundance of *Noctiluca scintillans* in the upper layer.

Table 4. PERMANOVA results of the main test between layers, seasons and their interactions; Pairwise tests of layers compared within each season, and seasons compared within each layer. Significant results are bold.

Maın Test	**Source**	**df**	**SS**	**MS**	**Pseudo-F**	**P(perm)**	**Unique perms**	
	Layer: La	1	2,27E+05	2,27E+05	217,34	**0,0001**	9929	
	Season: Se	3	78686	26229	25,145	**0,0001**	9884	
	La x Se	3	32677	10892	10,442	**0,0001**	9888	
	Res	447	4,66E+05	1043,1				
	Total	454	8,24E+05					
Pairwise Tests:	**Within level 'Winter' of factor 'Seasons'**				**Within level 'Spring' of factor 'Season'**			
	Groups	t	P(perm)	perms	Groups	t	P(perm)	perms
Term 'LaxSe' for pairs of levels of factor 'Layer'	**L, U**	7,9854	**0,0001**	9939	**L, U**	8,6948	**0,0001**	9945
	Within level 'Summer' of factor 'Season'				**Within level 'Autumn' of factor 'Season'**			
	Groups	t	P(perm)	perms	Groups	t	P(perm)	perms
	L, U	6,1681	**0,0001**	9943	**L, U**	9,151	**0,0001**	9930
Pairwise Tests:	**Within level 'Upper' of factor 'Layer'**				**Within level 'Lower' of factor 'Layer'**			
	Groups	t	P(perm)	perms	Groups	t	P(perm)	perms
Term 'Year x season' for pairs of levels of factor 'season'	**Winter, Spring**	5,4668	**0,0001**	9949	**Winter, Spring**	2,4254	**0,0001**	9941
	Winter, Summer	8,2681	**0,0001**	9946	**Winter, Summer**	2,1414	**0,0002**	9944
	Winter, Autumn	8,9169	**0,0001**	9953	**Winter, Autumn**	2,4928	**0,0001**	9944
	Spring, Summer	6,7376	**0,0001**	9933	**Spring, Summer**	2,3099	**0,0002**	9952
	Spring, Autumn	7,9099	**0,0001**	9941	**Spring, Autumn**	3,4658	**0,0001**	9935
	Summer, Autumn	4,0341	**0,0001**	9946	**Summer, Autumn**	1,857	**0,003**	9937

Table 5. PERMANOVA results of the main test between years, seasons, zones and their interactions in the upper layer; Pairwise tests of years compared within each season, and seasons compared within each year. Significant results are bold.

Main Test	**Source**	**df**	**SS**	**MS**	**Pseudo-F**	**P(perm)**	**Unique perms**	
	Zone: Zo	2	2379,7	1189,8	1,7999	0,0489	9921	
	Season: Sea	3	59202	19734	29,852	0,0001	9898	
	Year: Ye	6	24705	4117,4	6,2284	**0,0001**	9897	
	SeaxZo	6	5172,4	862,07	1,3041	0,1013	9876	
	YexZo	10	4285,8	428,58	0,64831	0,9823	9853	
	YexSea	6	13050	2174,9	3,29	**0,0001**	9856	
	YeaxSeaxZo	12	3474,1	289,51	0,43794	1	9855	
	Res	259	1,71E+05	661,07				
	Total	304	3,41E+05					
Pairwise Tests:	**Within level 'Summer' of factor 'Season'**				**Within level 'Spring' of factor 'Season'**			
	Groups	t	P(perm)	perms	Groups	t	P(perm)	perms
Term 'Ye x sea' for pairs of levels of factor 'Year'	2016, 2017	1,1082	0,2703	9952	2016, 2017	0,6382	0,8883	9944
	2016, 2019	4,4518	**0,0001**	9937	2016, 2018	0,65858	0,8507	9938
	2016, 2020	1,3939	0,0572	9943	2017, 2018	0,33613	0,9904	9947
	2016, 2021	3,2841	**0,0009**	9918	**Within level 'Autumn' of factor 'Season'**			
	2016, 2022	2,5101	**0,0001**	9920	Groups	t	P(perm)	perms
	2017, 2019	5,0293	**0,0001**	9946	2016, 2017	0,40638	0,9871	9931
	2017, 2020	1,2562	0,127	9952	2016, 2018	1,4415	0,06	9940
	2017, 2021	3,8764	**0,0007**	9891	**2016, 2020**	1,6728	**0,013**	9945
	2017, 2022	2,7291	**0,0001**	9944	2017, 2018	1,4193	0,0644	9928
	2019, 2020	3,7853	**0,0001**	9948	**2017, 2020**	1,5396	**0,0249**	9934
	2019, 2021	3,4489	**0,0012**	9907	2018, 2020	0,9506	0,5016	9941
	2019, 2022	1,2264	0,1826	9959	**Within level 'Winter' of factor 'Season'**			
	2020, 2021	3,0956	**0,0017**	9918	Groups	t	P(perm)	perms
	2020, 2022	1,961	**0,0025**	9931	2016, 2017	0,83551	0,6185	9944
	2021, 2022	2,7611	**0,0035**	9820	2016, 2019	1,2938	0,1557	9947
					2017, 2019	0,94692	0,4246	9953
Pairwise Tests:	**Within level '2016' of factor 'Year'**				**Within level '2017' of factor 'Year'**			
	Groups	t	P(perm)	perms	Groups	t	P(perm)	perms
Term 'Yex sea' for pairs of levels of factor 'season'	**Winter, Spring**	2,6081	**0,0001**	9945	**Winter, Spring**	2,1296	**0,0026**	9951
	Winter, Summer	4,5423	**0,0001**	9946	**Winter, Summer**	5,4777	**0,0001**	9936
	Winter, Autumn	3,7496	**0,0001**	9938	**Winter, Autumn**	4,0242	**0,0001**	9951
	Spring, Summer	5,1745	**0,0001**	9942	**Spring, Summer**	5,152	**0,0001**	9940
	Spring, Autumn	4,2669	**0,0001**	9927	**Spring, Autumn**	3,7508	**0,0001**	9938
	Summer, Autmn	3,0031	**0,0001**	9937	**Summer, Autmn**	3,4848	**0,0001**	9942
	Within level '2018' of factor 'Year'				**Within level '2019' of factor 'Year'**			
	Groups	t	P(perm)	perms	Groups	t	P(perm)	perms
	Spring, Autumn	2,6414	**0,0002**	9941	**Winter, Summer**	2,0895	0,003	9951
	Within level '2020' of factor 'Year'							
	Groups	t	P(perm)	perms				
	Summer, Autumn	2,5547	**0,0001**	9940				

Table 6. Species contributions to similarity percentages (SIMPER results) among upper layer communities in each season across all "Year-Season" groups. Only species contributions > 5% are shown.

Group 'Winter' Average similarity: 62,76							**Group 'Spring' Average similarity: 68,95**					
Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**		**Species**	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Noctiluca scintillans	83,76	33,72	1,75	53,73	53,73		*Noctiluca scintillans*	40,58	27,1	1,98	39,31	39,31
Paracalanus parvus	16,23	7,63	2,47	12,16	65,88		*Oithona nana*	14,47	9,73	2,97	14,11	53,42
Acartia clausi	12,38	6,24	2,35	9,94	75,82		*Acartia clausi*	11,41	8,48	3,9	12,3	65,72
Oithona nana	9	4,54	1,95	7,23	83,05		*Paracalanus parvus*	10,78	8,03	3,51	11,65	77,36
							Pleopis polyphemoides	10,58	5,79	1,97	8,4	85,76
Group 'Autumn' Average similarity: 72,35												
Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**		**Group 'Summer' Average similarity: 65,15**					
Noctiluca scintillans	25,87	13,75	2,1	19,01	19,01		Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Paracalanus parvus	18,44	11,58	3,67	16,01	35,02		*Acartia clausi*	16,4	12,48	3,36	19,16	19,16
Acartia clausi	15,56	10,58	4,97	14,63	49,65		*Penilia avirostris*	14,92	11,56	1,14	17,75	36,91
Penilia avirostris	14,34	8,23	1,76	11,37	61,02		*Paracalanus parvus*	14,51	11,4	2,94	17,5	54,42
Oithona nana	9,75	6,24	2,83	8,62	69,63		*Noctiluca scintillans*	14,22	7,41	0,63	11,38	65,8
Oithona similis	10,17	6,12	2,34	8,46	78,1		*Oithona nana*	10,18	7,1	2,09	10,89	76,69
Oikopleura dioica	7,21	3,99	1,81	5,51	83,61		Bivalvia	5,41	3,73	1,69	5,73	82,42
Bivalvia	7,88	3,87	1,73	5,34	88,95							

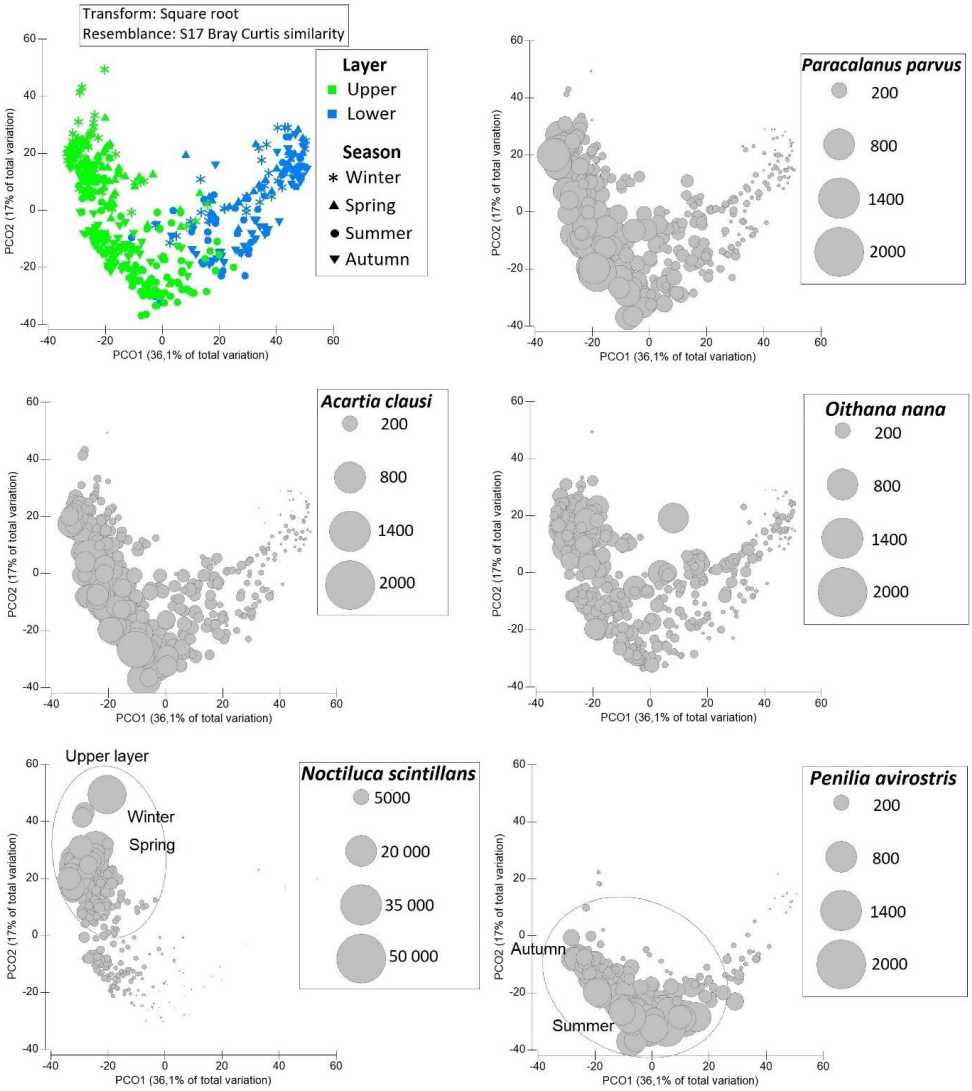


Figure 8. Principal coordinate analysis ordination (PCO) plot of the samples color coded with the factor layer and shape coded for the factor season. 2D bubble plots visualize variation of the abundances of the most common taxa among samples.

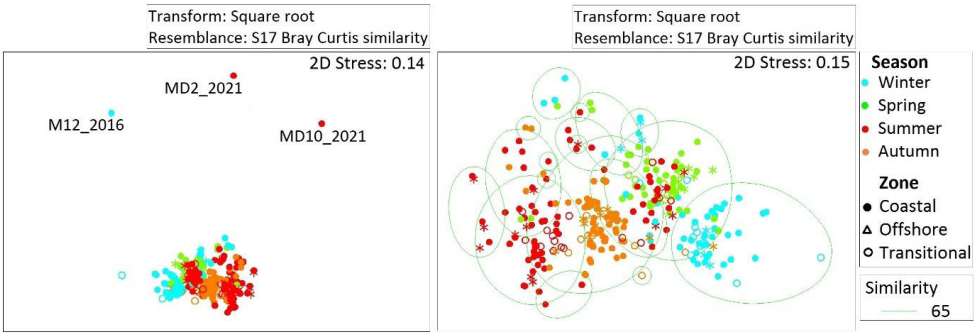


Figure 9. nMDS plots of upper layer samples color coded with the factor season (Left). nMDS plot of samples when samples from 2021 and station M12 in 2016 are excluded from the analysis, color coded with the factor season; zones are shape coded (Right). Similarities of 65 % are grouped with a green line.

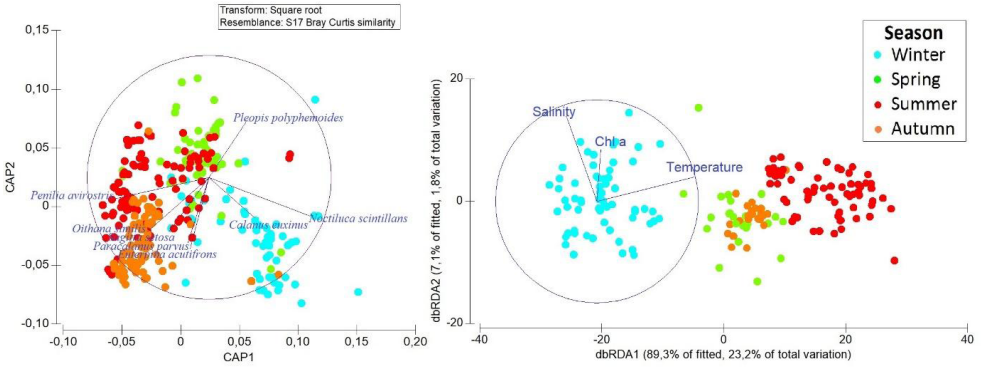


Figure 10. Canonical analysis of principal coordinates plot of upper layer samples grouped according to the factor "season"; vector overlay are Pearson correlations of species with r > 0.5 (Left). Distance based redundancy analysis plot of samples for combined environmental variables (temperature, salinity and Chl a) and combined fractions by season (Right).

In terms of the effects of environmental variables, although marginal tests showed significant contributions from each variable to explain the variation in the structure of the zooplankton community (pseudo F=50.45, p=0.001 for temperature, pseudo F=13.06, p=0.001 for salinity and pseudo F=3.63, p=0.01 for chl a), temperature accounted for the most important proportion. Sequential tests showed similar results, with pseudo F=50.45, p=0.001, cumulative proportion=0.23 for temperature, pseudo F=3.85, p=0.004, cumulative proportion=0.24 for salinity and pseudo F=3.34, p=0.003, cumulative proportion=0.26 for chl a. Best solution presented an r^2=0.26 for all 3 variables. The BEST test showed that temperature was the variable explaining most of the variation in zooplankton community, with $\rho = 0.39$ ($p < 0.01$). Salinity

and Chl a showed relatively low values of ρ = 0.084 and ρ = 0.022 respectively. The first axis of the dbRDA plot, correlated mainly with temperature, captured 89.3% of the fitted variability and 23.2% of the total variation. The second axis captured 7.1% of the fitted variability and 1.8% of the total variation, correlated mainly with salinity (Figure 10).

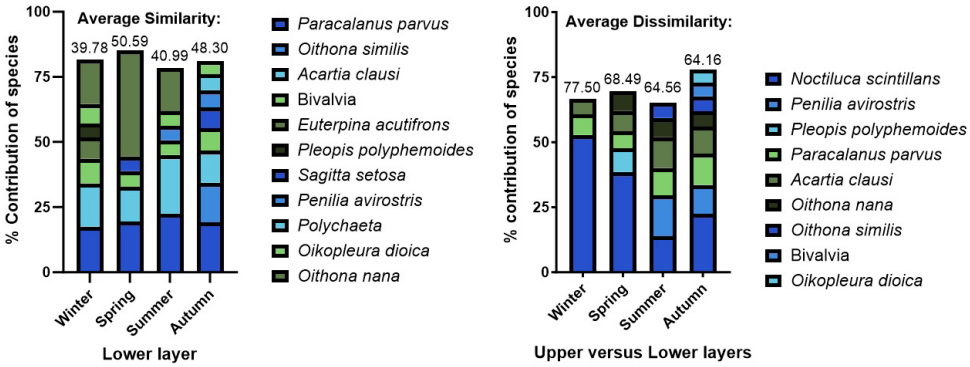


Figure 11. Graphical presentation of species contributions to similarity percentages (SIMPER results) among lower layer communities in each season and dissimilarity percentages between layer pairs. Only species contributions > 5% are shown.

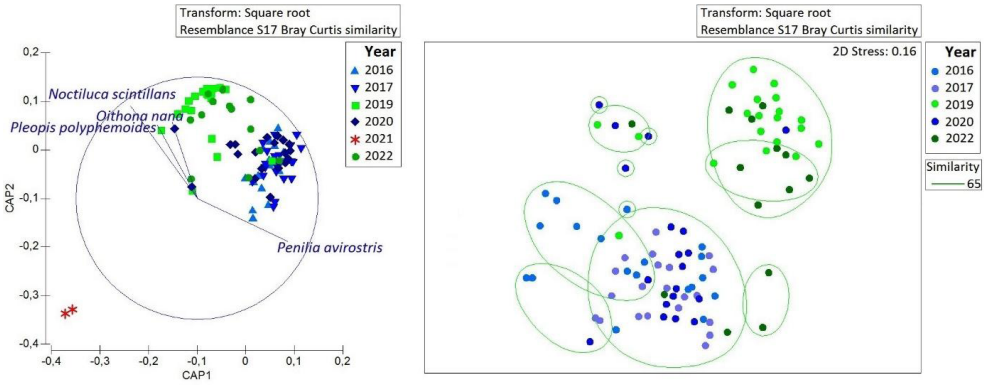


Figure 12. Canonical analysis of principal coordinates plot of Summer samples grouped according to the factor "year"; 2016, 2017 and 2020 are blue shaded while 2019 and 2022 are green shaded and 2021 is red shaded. Vector overlay are Pearson correlations of species with r > 0.5 (Left). nMDS plot of Summer samples color coded with the factor year when 2021 samples are excluded from the analysis; similarities of 65 % are grouped with a green line (Right).

4. Discussion

The present study focuses on the neritic area of the Sea of Marmara and aims to provide insights into the main zooplankton species and their seasonality. The study reveals that the most abundant zooplankton species in the region are also the most widely distributed. These

species include *Paracalanus parvus, Acartia clausi, Oithona nana, Penilia avirostris, Pleopis polyphemoides, Oikopleura dioica*, bivalve larvae, and *Noctiluca scintillans*. These findings align with previous studies conducted in the Marmara Sea, which have reported similar species compositions and abundances (Tarkan & Erguven, 1988; Unal et al., 2000; Isinibilir, 2009, 2010a; Isinibilir et al., 2008; 2011).

According to the findings of Turan et al. (2016), there is an increasing trend in water temperature within the Marmara Sea. In the current study, it was observed that, with the exception of February 2017, the water temperatures during the winter months consistently exceeded 10°C (Figure 2). These temperatures were notably higher than the average winter temperatures typically observed in the Marmara Sea.

In our study, which covered the period from 2016 to 2022, the most significant spatio-temporal difference in zooplankton abundance and community structure in the Marmara Sea was seasonal, compared to inter-year or regional differences. As predicted, temperature was the most crucial parameter in regulating the zooplankton community in the Sea of Marmara.

In our study, the highest mesozooplankton abundance (excluding *Noctiluca scintillans*) occurred at station M14 (3666 ind.m^{-3}) during the summer season in June 2022, primarily attributed to the presence of *Paracalanus parvus* and *Penilia avirostris* (906 ind.m^{-3} and 722 ind.m^{-3}, respectively) (see Figure 5). Notably, these values are considerably lower than historical records. For instance, the highest zooplankton abundance recorded was 79,332 ind.m^{-3} in İzmit Bay (located in the shallow eastern Sea of Marmara) in October 2001, driven mainly by elevated abundances of *Penilia avirostris* and *Oithona nana* (18,650 ind. m^{-3} and 19,261 ind.m^{-3}, respectively) (Isinibilir et al., 2008). Similarly, in October 2005, mesozooplankton abundance (excluding *Noctiluca scintillans* and Ctenophora) decreased from 127,837 ind.m^{-2} in the Black Sea near the Bosphorus to 88,920 ind.m^{-2} in the Marmara Sea outlet of the Bosphorus Strait, before slightly increasing to 103,104 ind.m^{-2} near the Prince Islands (Svetlichny et al., 2006).

During winter periods, we observed a higher abundance of the dinoflagellate *Noctiluca scintillans* and the copepod *Calanus euxinus*, while the cladoceran *Pleopis polyphemoides* was more abundant during spring periods similar to the findings of Isinibilir et al. (2009). *N. scintillans* is known to thrive in semi-closed and eutrophic bays within the basin (Isinibilir et al., 2008). Previous research by Isinibilir et al. (2014) has indicated that the Marmara Sea, being heavily impacted by anthropogenic stresses including eutrophication, provides a favorable environment for the mass development of opportunistic species like *N. scintillans.*

The high concentration of phytoplankton in the upper layers of the Marmara Sea is attributed to the transportation of nutrients from surrounding areas enriched with organic matter carried from the Black Sea (Kocatas et al., 1993; Yuksek et al., 2002). This nutrient-rich environment contributes to the proliferation of Cladocera and *N. scintillans* populations in the upper layer of the Marmara Sea.

The Marmara Sea exhibits distinct vertical stratification, with brackish waters from the Black Sea entering the upper layer through the Bosporus Strait, while hypersaline waters from the Aegean Sea form the lower layers. This stratification creates different ecological conditions in the Marmara Sea. The Black Sea ecosystem, which is eutrophic, supports a more abundant zooplankton community compared to the oligotrophic Aegean Sea (Kovalev et al., 2001). As a result, the upper layers of the open areas in the Marmara Sea have been found to have significantly higher zooplankton abundance compared to the lower layers (Unal et al., 2000). This pattern of higher abundance in the upper layers has also been observed in the Istanbul Strait (Tarkan et al., 2005) and the Izmit Bay (Isinibilir et al., 2008). The strong stratification present in the Marmara Sea restricts the diurnal vertical migration pattern of zooplankton, leading to the concentration of its main biomass in the upper layer (Isinibilir et al., 2011; Mutlu, 2005).

The zooplankton community in the Sea of Marmara is currently characterized by a relatively small number of species, with 46 taxa identified. The composition of this community can change over time. Certain mesoplanktonic copepods, such *as Copilia quadrata, Corycaeus furcifer, Corycella rostrata, and Eucalanus attenuatus*, which are typical of the Mediterranean Sea, as well as hyponeustonic species like *Labidocera brunescens, Parapontella brevicornis, Pontella lobiancoi, Pontella villosa*, which are commonly found in the Mediterranean Sea, and *Anomalocera petersoni* and *Pontella mediterranea*, typical of the Black Sea, have disappeared from the Sea of Marmara over the past 50 years (Kovalev et al., 2001). The disappearance of these species can be attributed to various factors, including increased pollution, jellyfish blooms, and mucilage events (Isinibilir, 2010b). The ecological disturbances mentioned have had detrimental impacts on the populations of these species, resulting in their decline or local extinction within the Sea of Marmara. Nevertheless, copepods belonging to the family Pontellidae and certain others have the ability to lay diapausing eggs, which can accumulate in bottom sediments for extended periods. Viable diapause eggs from marine copepods have been estimated to be as old as 70 years and can rejuvenate populations of temporarily extinct copepod species following the redistribution of deposited sediment particles in the water column due to hydrodynamic forces (Holm et al., 2018). However, it remains unclear which other copepod species produce resting stages in the Sea of Marmara.

The seasonal patterns observed for these abundant taxa in the eastern Marmara Sea are consistent with previous records from other areas within the Marmara Sea (Isinibilir, 2009; 2010a).

Acartia clausi, a copepod species known for its wide temperature and salinity tolerance, has a broad distribution in temperate and warm waters, including the Atlantic and Pacific oceans and the Mediterranean basin (including the Aegean Sea, the Sea of Marmara, and the Black Sea). Recent studies have demonstrated that this species exhibits greater resistance to microplastic pollution when compared to certain other Marmara copepods, such as *Centropages typicus* (Svetlichny et al., 2021). Additionally, it has been shown to lower its respiration rates in response to starvation, distinguishing it from *Calanus helgolandicus* (Svetlichny et al., 2022). In regions experiencing strong anthropogenic stress such as eutrophication, pollution, and invasive species, *A. clausi* is often the dominant copepod species observed during the summer months (Lakkis, 1974; Gubanova et al., 2001). However, it is also known to reproduce throughout the year (Siokou-Frangou et al., 2004; Hubareva et al., 2008; Isinibilir et al., 2008; 2011; 2014; Gubanova et al., 2001). These findings are consistent with the results of the present study, which also indicate the dominance and year-round occurrence of *A. clausi* in the region, reflecting the eutrophic characteristics of the area. *Paracalanus parvus, Oithona similis*, and *Oithona nana* are additional copepod species identified in the study with high tolerance to environmental variability (Lampitt & Gamble, 1982, Siokou-Frangou et al., 2004) and efficient food utilization (Villate et al., 1997; Fernández de Puelles et al., 2003). These species exhibit adaptabilities to changes in their surroundings, allowing them to thrive in diverse environmental conditions.

It is worth mentioning that two live specimens of the northern Atlantic copepod species *Calanus finmarchinus* were observed for the first time in the Sea of Marmara, in both April 2018 and 2019 (Svetlichny et al., 2023). However, it is important to note that this cold-water species is not anticipated to establish itself in this environment. *Acartia tonsa* and *Oithona davisae* are, on the other hand, non-native species that have recently established themselves in the zooplankton community of the Marmara Sea (Hubareva et al., 2008; Isinibilir et al., 2011; Doğan & Isinibilir, 2016). These species have the potential to compete with native species, as observed in the Black Sea (Gubanova et al., 2014) and noted in the Golden Horn Estuary (Isinibilir et al., 2016). However, in the Marmara Sea, both *A. tonsa* and *O. davisae* were consistently present in small quantities throughout the years of sampling.

The significant decline in the abundance of *Penilia avirostris* during the summers of 2019, 2021, and 2022 is an intriguing observation. This species is known for its efficient filtering

capabilities, as it feeds on small prey, including bacterioplankton (Turner et al., 1988). The population of *P. avirostris* can undergo rapid growth and explosions due to parthenogenetic reproduction and continuous somatic growth (Egloff et al., 1997). The upper layer of the Marmara Sea, with its high productivity, provides favorable conditions for the thermophilic filter feeder *P. avirostris* (Yılmaz & Isinibilir, 2016). The stratification of the Sea of Marmara's top layer can enhance *Penilia*'s feeding rates by concentrating prey in a relatively thin layer and keeping the newborns within the prey-rich upper layer.

However, the near complete absence of *Penilia avirostris*, one of the most important filter feeders, from the system in 2019 and subsequent years, and its failure to reach previous abundance levels, combined with the decrease in total zooplankton abundance due to the presence of high levels of the jellyfish *Aurelia aurita* and the gelatinous dinoflagellate *Noctiluca*, has led to a shift in phytoplankton size structure and abundance. Ultimately, this shift has contributed to a widespread mucilage event impacting benthic organisms and small pelagic fisheries throughout the basin. It has been reported that the feeding behaviour of the dominant summer species *P. avirostris* was particularly affected by the mucilage events in the Adriatic Sea and did not reach the normal seasonal maxima in the following year (Fonda Umani et al., 2005). However, none of these studies reported a collapse of zooplankton stocks, particularly cladocerans, as witnessed in the Sea of Marmara (Isinibilir Okyar et al., 2015). Although zooplankton species have a short life cycle, they have a high reproduction rate and due to these characteristics, they respond quickly to stress factors such as climate change, predator pressure and invasive species (Isinibilir, 2009; 2010a; b). Furthermore, *Acartia clausi* and *Oithona nana* are predatory species and they hunt their prey by ambush, probably this feeding behaviour is the reason why they are the species encountered during the mucilage period in June 2021.

In the Marmara Sea, the occurrence of intense marine mucilage formation was first documented in 2007-2008 (Aktan et al. 2008). This event had a profound impact on the marine ecosystem, leading to significant short-term losses in fisheries in the Sea of Marmara (Aktan et al., 2008; Isinibilir Okyar et al., 2015). In June 2021, a widespread mucilage formation was observed once again throughout the Sea of Marmara. The mucilage structure was found to be associated with the excessive growth of unicellular microscopic organisms (Aktan et al. 2008). Several dominant phytoplankton species were identified during the mucilage event, including *Cylindrotheca closterium, Skeletonema costatum, Thalassiosira spp., Gonyaulax fragilis*, and *Phaeocystis pouchetii* (Aktan et al., 2008; Balkıs-Ozdelice et al., 2021).

Similar species have also been reported as dominant in large mucilage aggregates in the Adriatic and Tyrrhenian Seas during the period of 1988-1991, although the responsible species

were not clearly identified at that time (Rinaldi et al., 1995). MacKenzie et al. (2002) identified the dinoflagellate *Gonyaulax hyalina* as the causative organism of mucilage accumulation in Tasman Bay through laboratory experiments. Similarly, Eker-Develi et al. (2023) suggested that the coccolithophorid *Ochrosphaera neapolitana*, a recently described species from the Sea of Marmara, might be the causative agent of the mucilage event in the Sea of Marmara. They observed that *Ochrosphaera neapolitana* produced significant levels of mucilage in laboratory experiments and showed high abundance in field samples during June 2021.

Phytoplankton exudates are known to affect particularly zooplankton production by increasing mortality in the naupliar stage of copepods, inhibiting grazing, or by altering the entire food web structure (Malej & Harris, 1993). It has been determined that marine mucilage directly or indirectly affects the abundance and distribution of zooplankton by reducing the abundance of copepoda nauplii (Krsinić, 1995), by changing the feeding capacity (Malej & Harris, 1993), food web structure and functioning (Cataletto et al., 1996; Fonda Umani et al., 2005). Compared to previous studies (Isinibilir, 2009; Isinibilir et al., 2008; 2011), it was determined that the total zooplankton abundance, which was reported to be quite low in the 2008 mucilage period (Isinibilir Okyar et al., 2015), completely collapsed in the 2021 mucilage period.

The distinctiveness of the 2021 samples compared to previous years underscores the ecological impact of the mucilage event on the zooplankton community. The scarcity of zooplankton during the mucilage event is striking and indicates a disruption in the normal population dynamics. Mucilage, with its gelatinous and dense nature, can directly affect zooplankton by physically impairing their movement and feeding capabilities. The presence of abundant mucilage may hinder the availability of suitable food sources for zooplankton, leading to a decline in their abundance and biomass. This finding highlights the vulnerability of zooplankton to large-scale environmental disturbances and emphasizes the need for further investigation into the long-term effects of mucilage events on the marine ecosystem of the Sea of Marmara.

It is more likely that the decrease in zooplankton abundance might be a combined effect of jellyfish predation and mucilage event, strengthening the decline in zooplankton even further. The effect of jellyfish could be best followed in the autumn of 2006 and although there was no mucilage, the zooplankton community structure was reported to show similarities to the mucilage period in the autumn of 2007 (Yılmaz, 2015).

It is indeed intriguing to observe the exceptionally high chlorophyll-*a* (chl-*a*) values during the 2021 summer, coinciding with the mucilage event, compared to previous measurements in the Marmara Sea. The chl-*a* values ranged from 12.2-14.2 $\mu g\ l^{-1}$ during the mucilage event surpassing

the maximum value of 6.15 μg l^{-1} recorded during the winter bloom in February 2016. This observation clearly shows the link between the high chl-*a* values and the absence of zooplankton grazing on phytoplankton. Similar patterns have been observed in other ecosystems. For instance, in the Caspian Sea, the invasive ctenophore *Mnemiopsis leidyi* significantly reduced zooplankton populations, leading to elevated chl-*a* levels due to the lack of top-down predation pressure on phytoplankton (Kideys et al., 2005; 2008). This indicates that the grazing activity of zooplankton plays a crucial role in regulating phytoplankton abundance and chl-a levels in marine ecosystems.

Our study highlights the intricate interactions between different components of the ecosystem and the cascading effects and calls for an integrated management of the Sea of Marmara ecosystem (Kideys, 2013). Further research is necessary to fully understand the underlying mechanisms and implications of these observed changes.

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