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Long-term changes in size and community structure of Zooplankton in a semi-enclosed ecosystem

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ABSTRACT

Zooplankton community structure and body size are recognized as sensitive indicators of marine ecosystem responses to environmental variability and human-induced pressures. In this study, we used a two-decade dataset (2002–2022) collected from a coastal station in the Sea of Marmara to investigate long-term changes in zooplankton community components, dominance patterns, and body size dynamics. Copepoda and Cladocera remained the dominant components throughout the study period; however, a notable seasonal expansion of Cladocera dominance and a replacement of key copepod species were observed over time. Two distinct periods (P1: 2002–2009; P2: 2017–2022) were compared to identify structural and functional shifts. Body size declines were recorded in major taxa, particularly in *Acartia clausi* and *Paracalanus parvus*, coinciding with seasonal temperature anomalies and major ecological events. Generalized Additive Models were applied to assess the influence of temperature and chlorophyll-a concentration on species-specific dominance and body size variability. Results indicated significant relationships between environmental variables and zooplankton traits, with species showing distinct responses to thermal and productivity shifts. Our findings emphasize the importance of implementing such as body size and trophic role into future assessments of ecosystem resilience under changing environmental conditions.

1. Introduction

Zooplankton, through their roles as both prey and predator, facilitate the transfer of trophic energy between primary producers and planktivorous organisms. During this process, their vertical migrations within the water column contribute to the transport of particulate matter and support biogeochemical cycles (Beaugrand et al., 2003; Steinberg and Landry, 2017; Cavan et al., 2017). The short life spans and sensitivity of zooplankton organisms to environmental changes make them effective indicators of ecosystem responses to climate change and anthropogenic pressures (Richardson, 2008; Mitra et al., 2014).

Long-term shifts in zooplankton community structure and body size can alter, predator-prey interactions, and the efficiency of energy transfer in marine food webs (Corona et al., 2021; Feuilloley et al., 2022). Changes in body size and species composition influence the availability and nutritional quality of prey for higher consumers, with potential impacts on fisheries and ecosystem functioning (Brosset et al., 2016; Saraux et al., 2019). In many marine regions, zooplankton phenology and community composition have been linked to large-scale climate fluctuations such as the North Atlantic Oscillation (Molinero et al., 2005; García-Comas et al., 2011), underlining the need for long-term observational datasets to detect and interpret ecological changes.

Body size is a fundamental trait affecting physiological rates, vulnerability to predation, and energy transfer efficiency (Horne et al., 2016). One commonly observed response to environmental warming is a reduction in body size, known as the Temperature-Size Rule (Atkinson, 1994). This pattern is widely observed in aquatic ectotherms across seasons, latitudes, and experimental settings (Forster et al., 2012; Horne et al., 2016), and is considered one of the three "universal responses" of marine life to climate change, alongside shifts in phenology and geographic distributions (Gardner et al., 2011). However, food availability, competition, and predation can also modulate temperature-size responses, leading to species-specific and context-dependent outcomes (Corona et al., 2021).

Semi-enclosed basins such as the Sea of Marmara (SoM) offer valuable natural laboratories for studying ecosystem responses to environmental variability. The SoM is characterized by strong vertical

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stratification resulting from the inflow of low-salinity Black Sea water and high-salinity Mediterranean water through the Bosphorus and Dardanelles Straits (Beşiktepe et al., 1994). Primary production is largely confined to the upper ~30 m of the water column, making pelagic communities particularly sensitive to changes in physical and biological conditions (Ediger and Yılmaz, 1996; Öztürk et al., 2024). In recent decades, the SoM has been subjected to increasing anthropogenic pressures, including eutrophication, pollution, and warming (Demirel et al., 2023a), culminating in extreme events such as large-scale mucilage outbreaks that drastically impacted plankton communities.

In this study, we investigate whether zooplankton community structure and body size in the SoM have undergone significant changes over the past two decades. Using a long-term dataset collected at a coastal station, we focus on four key species: *Acartia (Acartiura) clausi* Giesbrecht, 1892, *Paracalanus parvus parvus* (Claus, 1863), *Penilia avirostris* Dana, 1849, and *Pleopis polyphemoides* (Leuckart, 1859). We test the following hypotheses: (I) Seasonal patterns and dominant species composition of zooplankton components have changed over time, including a shift toward smaller-size taxa; (II) Body size of dominant zooplankton species has declined over time and is associated with variations in temperature and chlorophyll-a concentration. By analyzing long-term biological and environmental data, this study aims to improve understanding of how zooplankton assemblages respond to environmental variability in a semi-enclosed marine ecosystem.

2. Materials and methods

2.1. Samplings and laboratory analysis

In this study, zooplankton samples and environmental variables were obtained from two different monitoring programs. The first monitoring program (entitled as P1), spanning from 2002 to 2009 was carried out under the General Directorate of Istanbul Water and Sewerage Administration (ISKI) and involved seasonal sampling in winter, spring, summer, and autumn. Sampling was conducted regularly throughout this period, except for winter 2009. The second monitoring program (entitled as P2), spanning between 2017 and 2022, was conducted under the Turkish Ministry of Environment, Urbanization and Climate Change (DEN-IZ), included sampling in winter, spring, and summer. This phase began in spring 2017, and the only interruption occurred in spring 2020 due to COVID-19 lockdown restrictions. No sampling or monitoring efforts were conducted between 2010 and 2016 (Supp. Table 1).

Within the scope of this study, station MY2 (40°50.60′N-29°10.00′E), which exhibited approximately 75 % representativeness among the zooplankton sampling stations in the monitoring programs, was selected for analysis (Fig. 1, Supp. Fig. 1). Water column profiles were obtained using CTD rosette systems (SBE 9–11 in P1 and SBE 25Plus in P2).

The SoM is characterized by a permanent halocline, and the upper layer is defined as the portion of the water column extending from the surface to the depth where the first abrupt increase in salinity occurs. Zooplankton samples were collected from this upper layer through vertical hauls. Throughout the study period, sampling depths for this layer ranged between 7 and 20 m (Supp. Table 1). In both periods, zooplankton sampling was conducted using nets with a 57 cm mouth diameter and 200 μm mesh size. A Nansen-type net without a flowmeter was used in P1, while a WP2-type net with a flowmeter was used in P2. All samples were preserved in 4 % formaldehyde buffered with borax. In both periods, chlorophyll-a (Chl-a) concentrations were determined using the acetone extraction method (Parsons et al. 1984). Temperature and Chl-a values were averaged across the upper water column corresponding to the zooplankton sampling depths and used in subsequent analyses.

Mesozooplankton samples were analyzed following the removal of macrozooplankton. Subsamples were taken using 1 mL Stempel pipettes and identified to the lowest possible taxonomic level through repeated subsampling. The volume of subsamples varied depending on the concentration and composition of the original sample, ranging from 1/25 to 1/500 of the total. The counting method ensured that at least 30 individuals from each of the three most dominant species were included in the analysis, providing a 95 % confidence level with a ±30 % error margin around the mean. Abundances, calculated as individuals per cubic meter (ind. m^{-3}), were standardized across duplicate counts and among samples collected using different net types of the same specifications.

Key species were identified based on their dominance, and thirty individuals were randomly selected from each for meristic measurements. Adult females were used for *Acartia (Acartiura) clausi* and *Paracalanus parvus parvus* (Copepoda), while parthenogenetic females were selected for *Penilia avirostris* and *Pleopis polyphemoides* (Cladocera = Diplostraca). To maintain random selection and avoid size-biased

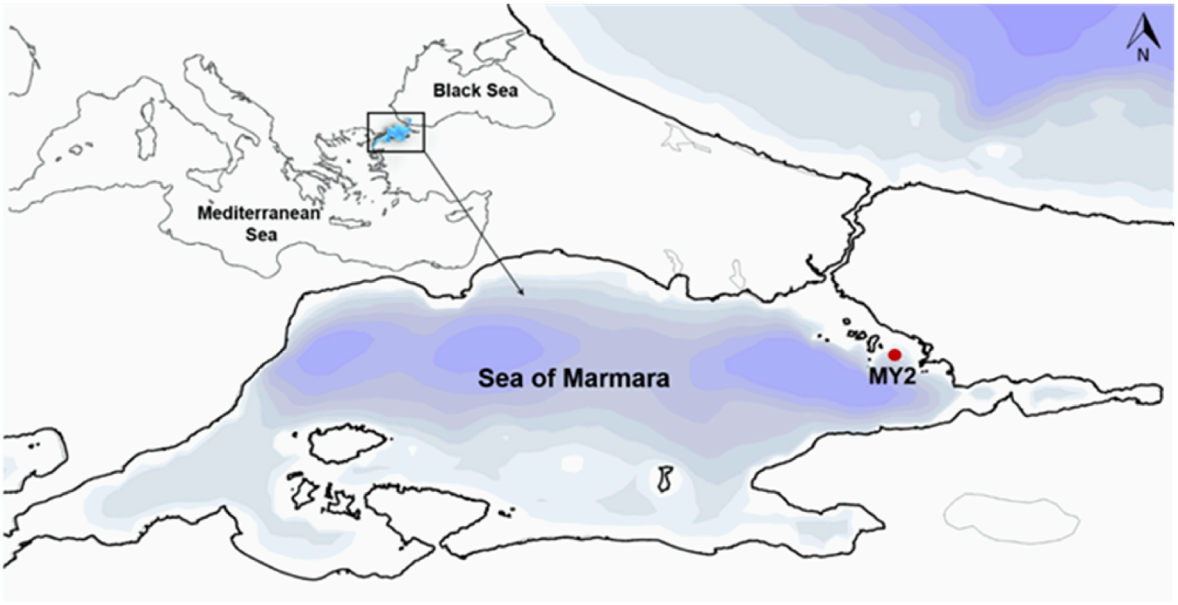


Fig. 1. Sampling station (indicated by red dot) and the location of the Sea of Marmara. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

sampling in Cladocera, individuals from all species were measured only when their abundance exceeded 100 ind.m^{-3}. Copepoda individuals were photographed dorsally, whereas Cladocera individuals were photographed laterally. Body size measurements were conducted using ImageJ (Schneider et al., 2012) software following magnification calibration. For Copepoda, prosome length was measured from the top of the head to the end of the prosome. For Cladocera, body length was measured from the top of the head to the tip of the caudal process.

2.2. Data processing and GAMs construction

Zooplankton abundance was assessed based on the relative contributions of three major components. Copepoda and Cladocera species were treated as distinct components, while all remaining holoplanktonic and meroplanktonic species were grouped under the "Others" component. Seasonal anomalies of Copepoda, Cladocera, temperature, and Chl-a were calculated using standardized anomaly scores. For each parameter, the overall mean and standard deviation of all seasonal values were computed across P1 and P2. Each seasonal value was then standardized by subtracting the overall mean and dividing by the standard deviation. Thresholds were applied to identify strong anomalies, reflecting notable departures from typical seasonal conditions: a ±1.5 standard deviation threshold was used for temperature and Chl-a, while a more conservative threshold of ±1 standard deviation was applied for Copepoda and Cladocera. The Berger-Parker Dominance Index (Berger and Parker, 1970) was applied to four key species in order to evaluate their temporal dominance both at the overall zooplankton community level and within the Copepoda and Cladocera components.

The construction of Generalized Additive Models (GAMs) was based on two distinct datasets and was performed using the "mgcv" package in R (R Development Core Team, 2020). The first dataset was designed to examine temporal changes in the zooplankton community and their relationships with environmental variables across periods P1 and P2. It included dominance index values of selected species, along with seasonal anomaly scores for temperature and Chl-a. Prior to modeling, the normality of the data distribution was visually assessed using Quantile-Quantile (Q-Q) plots and histograms. Deviations from the reference line in the Q-Q plots were used to identify departures from normality, indicating that the data were not normally distributed. The index dataset was rescaled using a modified min-max normalization function to ensure numerical stability and avoid extreme values (i.e., exactly 0 or 1). This transformation rescaled all continuous predictor variables to the (0.001, 0.999) interval, thereby improving model convergence and preventing saturation effects during modeling. Due to the non-normal distribution, a beta regression family was chosen for this dataset. The second dataset included only the sampling periods in which body size measurements were conducted for the key species, along with the corresponding temperature and Chl-a values. This subset was used to explore potential changes in species' body sizes across P1 and P2 and to investigate their relationships with environmental drivers. The distribution of these data was tested using the Shapiro-Wilk test, and based on the results, the Gaussian family was selected.

Before model construction, multicollinearity among predictor variables was evaluated using the Variance Inflation Factor (VIF) for both datasets. Since all VIF values were below five, no multicollinearity was detected which allowed the combined effects of the variables to be assessed in the GAMs (Supp. Table 2). The best-fitting models were selected based on the Akaike Information Criterion (AIC) (Supp. Table 2).

3. Results

3.1. Long-term variations in zooplankton community structure, temperature and Chl-a

Copepoda and Cladocera generally represented the dominant zooplankton components across the study period, although the "Others" component occasionally became dominant during winter 2003 (70 %), winter 2007 (57 %), and autumn 2007 (59 %) (Fig. 2). In P1 (2002–2009), Copepoda were predominantly dominant in winter and spring, whereas Cladocera dominated in summer. In P2 (2017–2022), Cladocera dominance expanded into spring and remained consistent in summer.

During winter, Copepoda dominance reached a maximum contribution of 79 % in 2018 and a minimum of 23 % in 2003. An exception was observed in 2022, when Cladocera surpassed Copepoda with a contribution of 57 %. In spring, Copepoda dominated during P1, but Cladocera consistently dominated during P2, reaching contributions up to 93 %. In summer, Cladocera maintained dominance in most years, except in 2018 when Copepoda contributed 59 %. In autumn, Copepoda dominance varied, peaking at 83 % in 2008 and dropping below 50 % in 2002, 2003, and 2022 (Fig. 2).

Strong negative anomalies in Copepoda and Cladocera abundance were recorded during mucilage events, specifically in winter 2008 for Copepoda and in spring 2021 for Cladocera. In P1, negative anomalies were observed both before and after the mucilage event, while in P2 they were primarily associated with pre-mucilage conditions (Fig. 3). Positive anomalies in zooplankton components were generally absent during the study period.

Upper seawater temperatures ranged between 7 °C and 24 °C during the study period (2002–2022). In P1, strong positive temperature anomalies were observed in autumn 2002 and spring 2007. In P2, strong negative anomalies occurred in summer 2019 and spring 2021, while an extreme positive anomaly was recorded in winter 2022 (Fig. 3).

Chl-a concentrations ranged from 0.5 to 6.8 mgL^{-1}. Positive Chl-a anomalies were detected during winter 2006 and autumn 2007 in P1, and during spring 2018, summer 2019, and summer 2022 in P2 (Fig. 3).

3.2. Co-occurrence patterns among key species

Key species selected from the dominant components were *A. clausi*, *P. parvus*, *P. avirostris*, and *P. polyphemoides*. The dominance index of these species remained below 0.5 during periods when the "Others" component prevailed or when alternative species such as *Calanus euxinus* Hulsemann, 1991, *Centropages typicus* Krøyer, 1849, or *Oithona similis Claus, 1866* became temporarily dominant. Community collapses were recorded during mucilage events in winter 2008 and spring 2021, characterized by marked decreases in the dominance of key species (Fig. 2).

Within the Copepoda component, *A. clausi* was dominant during winter and spring, in P1. *P. parvus* was dominant only in autumn during the same period; however, its frequency of occurrence and dominance increased between spring 2005 and summer 2007. In P2, *P. parvus* either co-dominated with *A. clausi* or became the sole dominant species across most seasons. Notably, following winter 2021, the contribution of *A. clausi* declined to as low as 0.02. During P1, *A. clausi* dominated the winter community from 2002 to 2005, but *P. parvus* replaced it between 2006 and 2008. In spring, *A. clausi* remained dominant except in 2007. In summer, dominance alternated between the two species, while in autumn *P. parvus* maintained dominance except in 2007 and 2008. In P2, *P. parvus* dominated the winter assemblages, although it co-dominated with *A. clausi* in 2019 (0.44 and 0.41, respectively). In spring, *A. clausi* dominated in 2017 and 2018, whereas *P. parvus* prevailed in 2019 and 2022. In summer, *P. parvus* dominated every year except 2020; however, in 2022 the dominance index of both species fell below 0.1. In P2, autumn was represented only in 2022, when *P. parvus* again dominated (Fig. 4).

Within the Cladocera component, *P. polyphemoides* dominated in winter and spring, while *P. avirostris* prevailed in summer and autumn. During P1, *P. polyphemoides* replaced *P. avirostris* in autumn 2007 and summer 2009. In P2, the seasonal pattern among Cladocera species persisted; however, the dominance of *P. polyphemoides* increased in

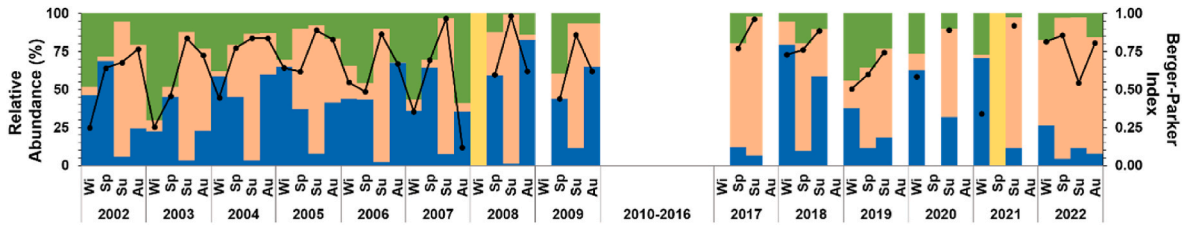


Fig. 2. Relative abundance of zooplankton components (blue bars: Copepoda, orange bars: Cladocera, green bars: Others, yellow bars: Mucilage event). The dotted line represents the dominance index of four key species (*A. clausi*, *P. parvus*, *P. avirostris*, and *P. polyphemoides*) within the zooplankton community between 2002 and 2022. Sampling was not conducted between 2010 and 2016 due to a break in long-term monitoring efforts. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

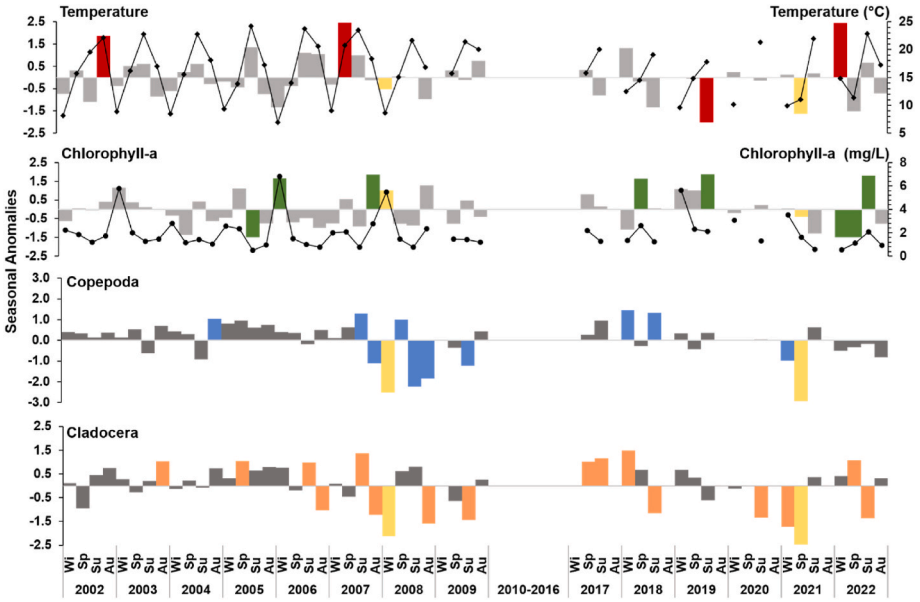


Fig. 3. Seasonal anomalies in temperature, chlorophyll-a, Copepoda, and Cladocera between 2002 and 2022. Colored bars indicate strong anomalies more than 1.5 for temperature (red) and Chl-a (green) and more then 1 for Copepoda (blue) and Cladocera (orange). Yellow bars represent mucilage events. Dotted lines indicate temporal variation in temperature and Chl-a. Sampling was not conducted between 2010 and 2016 due to a break in long-term monitoring efforts. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

winter and spring and extended throughout 2022 (Fig. 4). While the frequency of occurrence and dominance of *P. parvus* increased in the Copepoda component during P2, the dominance of *P. avirostris* declined in the Cladocera component, and *P. polyphemoides* exhibited an increasing trend (Fig. 4).

Changes in the Copepoda and Cladocera components were analyzed using the dominance indices of key species and the seasonal anomalies of environmental variables (temperature and Chl-a). GAMs based on dominance indices revealed significant interannual and seasonal variation for *A. clausi* and *P. polyphemoides*, whereas only seasonal variation was significant for *P. parvus* and *P. avirostris* ($p < 0.05$). The interannual and seasonal shifts observed in *P. polyphemoides* were driven by temperature, while no significant influence of environmental variables was detected for *A. clausi*. In contrast, the seasonal variability detected in *P. avirostris* and *P. parvus* was associated with Chl-a (Fig. 5, Supp. Table 2).

3.3. Size changes of Copepoda and Cladocera species

The key species exhibited distinct body size ranges; *A. clausi* was the largest, while *P. polyphemoides* was the smallest. A size difference of approximately 0.3 mm was observed between the key species pairs in each component (Fig. 6a).

The prosome length of *A. clausi*, the larger Copepoda species, ranged from 0.71 to 1.07 mm, with the smallest individuals recorded in summer and the largest in winter. The smaller Copepoda species, *P. parvus*, exhibited a size range of 0.41–0.73 mm, with minimum sizes in summer and maximum sizes in autumn (Fig. 6b).

In the Cladocera component, the body size of *P. avirostris* varied between 0.41 and 0.73 mm. This species was observed only during summer and autumn, with both small and large individuals present in summer samples. *P. polyphemoides* ranged from 0.14 to 0.44 mm in body length, with the smallest individuals found in autumn and the largest in winter (Fig. 6b).

Overall, a clear seasonal pattern in body size was evident for the Copepoda species, while such seasonal variation was not observed in the Cladocera species (Fig. 6b).

Significant interannual differences ($p < 0.05$) were detected in the annual mean body size, temperature, and Chl-a values derived from seasons in which species abundances exceeded 100 ind. m^{-3} (~>0.15 dominance index) (Fig. 7a, c, 7e, 7g). Because these significant differences reflected the fact that species reached sufficient abundance for analysis in different seasons, temporal changes in body size were examined seasonally (Supp. Table 2). GAMs revealed that body size variations in Copepoda species were influenced by environmental drivers, whereas no significant relationships with environmental variables were detected for Cladocera species. The seasonal body size variations of *A. clausi* were driven by both temperature and Chl-a, while

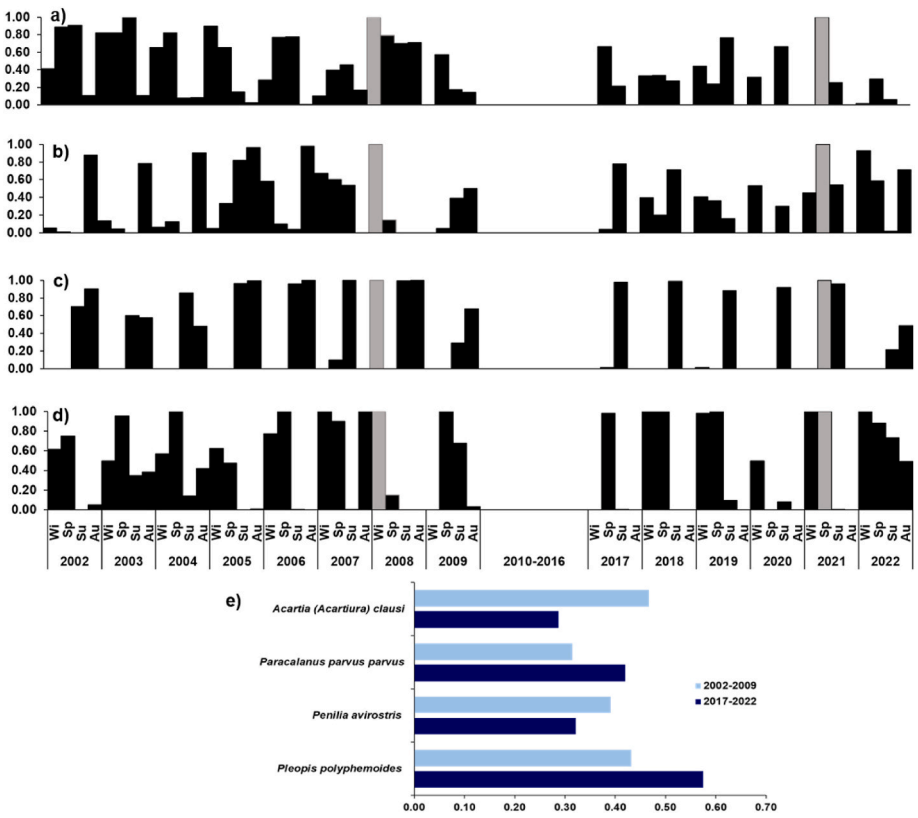


Fig. 4. Seasonal changes in the Berger-Parker dominance index of a) *A. clausi*, b) *P. parvus*, c) *P. avirostris*, and d) *P. polyphemoides* within their respective components between 2002 and 2022. The grey bars indicates mucilage events. e) the mean dominance index of each species for P1 (2002–2009) and P2 (2017–2022). Sampling was interrupted between 2010 and 2016 due to a break in the long-term monitoring program.

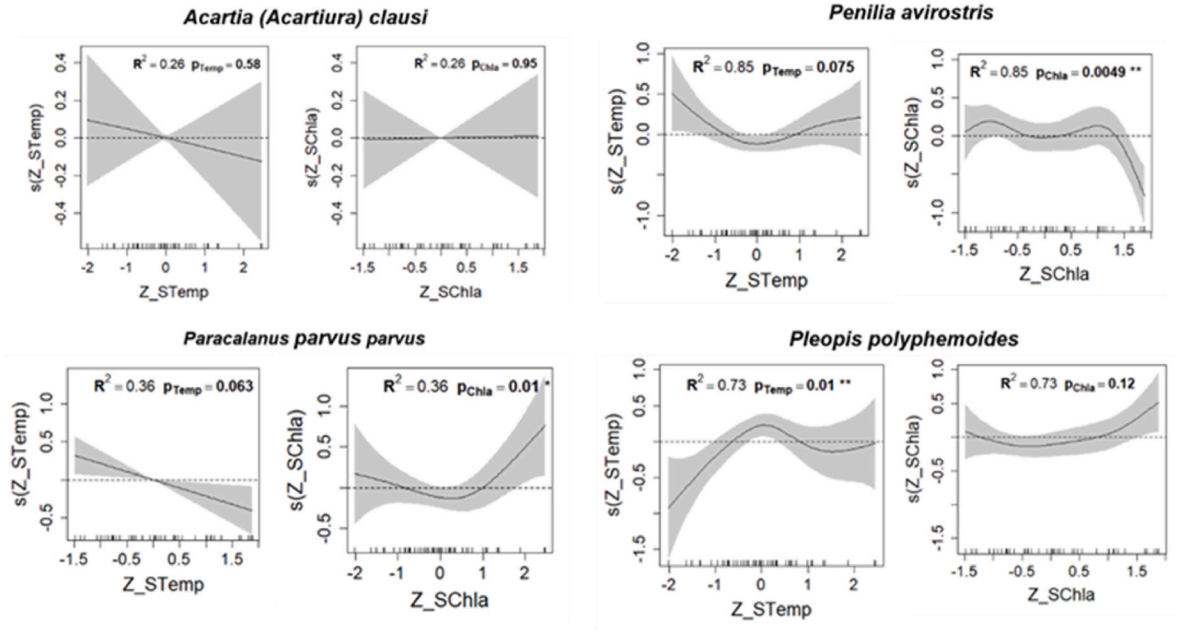


Fig. 5. GAM plots for the partial effects of environmental variables on key species dominance index between 2002 and 2022 in SoM. Shaded areas represent 95 % confidence intervals, with R^2 values and significance levels (p-values) displayed for each model.

those of *P. parvus* were associated only with temperature ($p < 0.05$) (Fig. 7b, d, 7f, 7h).

4. Discussion

Our study indicates clear changes in the zooplankton community structure and body size dynamics in the coastal waters of the Sea of Marmara (SoM) over two decades. Notable shifts included a seasonal

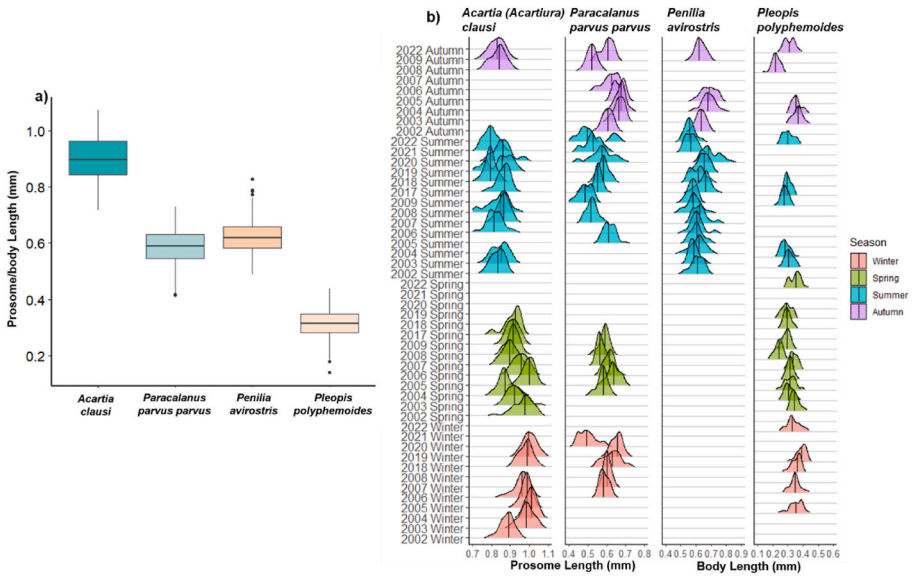


Fig. 6. Body and prosome size changes of four dominant zooplankton species. (a) Boxplot showing overall body size distributions of four key species. (b) Ridge plot illustrating seasonal distributions of body and prosome lengths between 2002 and 2022 in the SoM. Solid lines median prosome/body length for each seasonal distribution.

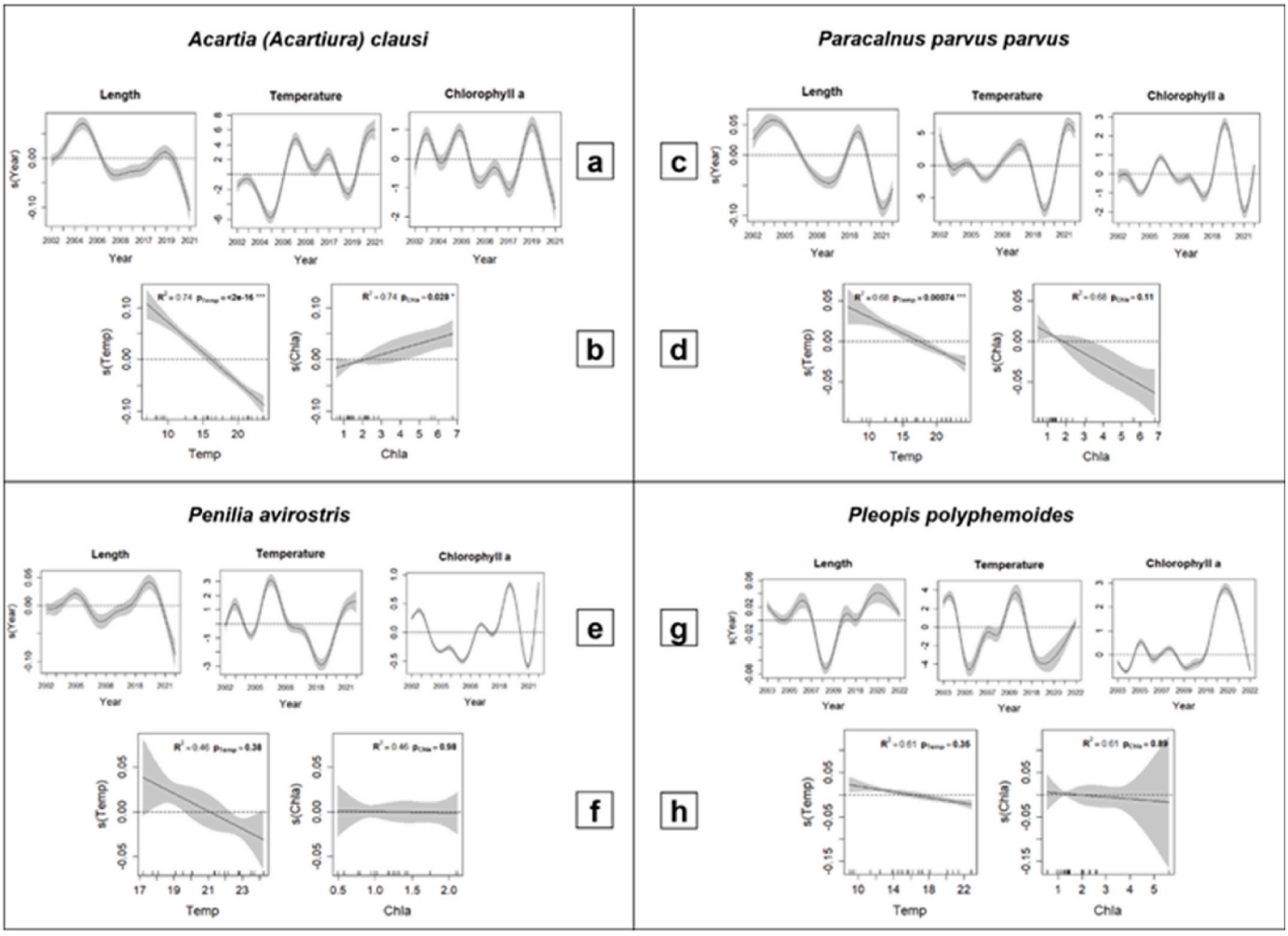


Fig. 7. GAM plots for (a,c,e,g) the effect of years on body size, temperature and Chl-a and (b,d,f,h) the partial effects of environmental variables on body size between 2002 and 2022 in SoM. The shaded areas indicate the 95 % confidence intervals.

expansion of Cladocera dominance, a replacement of dominant copepod species within the Copepoda component, and a general trend toward smaller body sizes in key species. These biological phenomena coincided with seasonal and interannual variability in upper-layer temperature and chlorophyll-a concentration, suggesting that both environmental drivers and biological processes influenced the observed patterns.

The replacement of large-sized copepod species by smaller ones had been recognized as a consequence of eutrophication, it was also reported that both Copepoda and Cladocera species expanded their distribution ranges or increased their abundances in response to rising temperatures (Uye, 1994; Beaugrand, 2009; Lee et al., 2022). The zooplankton community of the eutrophic Sea of Marmara, located as a transitional zone between the Mediterranean and the Black Sea, has been represented by smaller-sized copepod species since the early 2000s, when compared to neighboring seas (Ediger et al., 2016; Feuilloley et al., 2022; Kharytonova et al., 2021).

The seasonal dominance shifts from Copepoda to Cladocera components, particularly during spring in P2, align with the expectation that warming conditions favor smaller-size, fast-reproducing taxa (Sommer and Lewandowska, 2011; Daufresne et al., 2009). In P2, the expansion of *P. polyphemoides* dominance within Cladocera and the increased co-dominance of *P. parvus* within Copepoda further support this view. The dominance shifts observed in Copepoda appeared to be driven by the effect of seasonal Chl-a variability on *P. parvus*. However, while *A. clausi* declined within the component over time and *P. parvus* gained prominence, neither species showed a significant direct interaction with temperature, although the relationship was negative for both. In addition, *P. polyphemoides*, which increased its dominance within Cladocera, was found to be significantly influenced by temperature. Known to be more tolerant of colder waters compared to *P. avirostris*, *P. polyphemoides* is also reported to persist almost year-round in the Sea of Marmara (Gubanova et al., 2022; Bedikoğlu et al., 2022). The seasonal temperature anomalies detected in P2, warmer winters and cooler summers, support the idea that such conditions provided a more favorable environment for *P. polyphemoides* relative to *P. avirostris*. Thus, the interspecific shifts observed within Cladocera were attributed to the direct effect of temperature, whereas in Copepoda the influence of temperature was indirect and explained by the significant effect of Chl-a. As demonstrated in this study, smaller-size cyclopoid species within the Copepoda component were able to achieve dominance, and non-native species such as *Oithona davisae* have been reported to maintain viable populations in the Sea of Marmara (Doğan and İşinibilir, 2016; Türkeri and İşinibilir, 2024). Our findings therefore indicate a shift toward smaller-size taxa, consistent with the overall trend detected in the zooplankton community. Although the relationship between Copepoda and temperature was identified as indirect, it was negative in direction, concluded that in the coming decades the Copepoda component of the Sea of Marmara may increasingly shift toward smaller species such as *Oithona similis* or *O. davisae*. These results are consistent with studies showing that zooplankton communities can be restructured under the influence of warming and eutrophication, favoring smaller taxa with opportunistic life histories (Feuilloley et al., 2022; Corona et al., 2021).

Temperature anomalies were associated with variations in dominance patterns and body size dynamics, highlighting the importance of thermal forcing. The general decline in body size observed in *A. clausi* and *P. parvus* is consistent with the Temperature-Size Rule (Atkinson, 1994), which posits that ectothermic organisms mature at smaller sizes under warmer conditions. Seasonal reductions in size were more pronounced in Copepoda than in Cladocera, reflecting possible differences in physiological sensitivity to thermal stress (Horne et al., 2016). Notably, GAM analyses indicated that body size in *A. clausi* and *P. parvus* was significantly negatively associated with temperature anomalies, confirming temperature as a major driver of intra-specific size variability.

The relationships between body size and Chl-a concentration were species-specific. For *A. clausi*, larger body sizes were associated with higher Chl-a levels, consistent with the notion that improved food availability can affect thermal constraints (Gardner et al., 2011; García-Comas et al., 2014). However, no significant relationship between Chl-a and body size was detected for *P. parvus* or the Cladocera species, suggesting species-specific responses to bottom-up processes. This observation supports findings from other semi-enclosed or temperate systems, where food quantity and quality can differentially affect zooplankton size structures (Mousing et al., 2016; Corona et al., 2021).

4.1. Notable ecological shifts and zooplankton community in the SoM

The pelagic food web of the SoM underwent various changes since the 1990s; it was characterized as a system under bottom-up control, where anchovy and zooplankton were considered keystone components, and which was subjected to intense fishing pressure (Demirel et al., 2023a; Saygu et al., 2023). In P1, overfishing of both small (anchovy) and large (bluefish) pelagic fish species was reported between 2005 and 2007 (Demirel et al., 2023c), along with a significant increase in the abundance of the non-native hydromedusa *Liriope tetraphylla* (Yilmaz, 2015). In P2, continued overfishing (Demirel et al., 2023c) and increases in gelatinous species such as *Pleurobrachia pileus*, *L. tetraphylla*, and *Rhizostoma pulmo* were documented (Öztürk and Sümen, 2020; Demirel and Bedikoğlu, 2025). Two major mucilage events were recorded in the SoM between 2002 and 2022. The first occurred between October 2007 and February 2008 (P1), and the second between November 2020 and June 2021 (P2) (Yilmaz, 2015; Demirel et al., 2023b). In our study, these two events were marked as seasonal collapses of zooplankton in winter 2008 and spring 2021, respectively.

Prior to these collapses, the dominance of *A. clausi* declined sharply in winter 2007, 2020, and 2021, and replaced by the smaller-size *P. parvus*. Fluctuations in fish and jellyfish populations may have contributed to the sharp decline of *A. clausi* observed prior to the mucilage events. In the subsequent spring and summer seasons following both mucilage events, both copepod species were represented by smaller individuals. Similarly, within Cladocera, the smallest individuals of *P. polyphemoides* were observed after the P1 event, while the smallest *P. avirostris* occurred following both P1 and P2 mucilage events in summer. Mucilage events are recognized to disrupt food webs by altering oxygen dynamics and food pathways (Danovaro et al., 2009; Hosia et al., 2011), while small-sized zooplankton, capable of exploiting the dense organic matter produced during these events (KiØrboe, 2000; Möller et al., 2012), may have been advantageous in the post-event period.

In ecosystems where large predators were removed, new ecological niches were reported to have been created for small pelagic fish species (Arrhenius and Hansson, 1993) and jellyfish (Larson, 1987; Malej et al., 2007), which compete with zooplankton for food (Pauly et al., 1998). In systems governed primarily by bottom-up control, sudden shifts in zooplankton communities were suggested to result from changes in predation pressure (Feuilloley et al., 2022). While no consistent long-term decline in body size associated with temperature and Chl-a was detected in this study, the pronounced reductions observed in 2007 and 2020 may instead have resulted from fluctuations in pelagic fish populations combined with increases in native or non-native jellyfish, which likely altered predation dynamics (Beaugrand et al., 2003; Suthers et al., 2006; Boero, 2013). High Chl-a concentrations were consistently observed in winter during both P1 and P2, which was interpreted as an indication of winter diatom blooms in the SoM (Tas et al., 2020; Bayram-Partal, 2025). The effective predation ability of Copepoda on large phytoplankton Armengol et al. (2017) may have constituted an important control mechanism during winter phytoplankton blooms in the SoM, the sharp decline of the *A. clausi* (larger than *P. parvus*) in the winters of 2007, 2020, and 2021 may have played a role in the mechanisms leading to mucilage formation.

Overall, our results demonstrate that the zooplankton community structure and body size in the SoM have shifted under the combined

influence of seasonal thermal variability, productivity changes, altered predation dynamics, and episodic extreme events. These patterns are consistent with broader regional and global trends in marine ecosystems subjected to climate change and anthropogenic pressures (Richardson, 2008; Beaugrand et al., 2003; Feuilloley et al., 2022). The coupling of warming-induced body size declines with community composition shifts suggests that such as body size, trophic role, and response to episodic disturbances should be central to future assessments of ecosystem resilience. Given the complex interactions between bottom-up and top-down drivers, interpreting zooplankton changes in semi-enclosed seas such as the SoM requires an integrated perspective that accounts for physical, biological, and human-induced factors. Continued long-term and multidisciplinary monitoring efforts will be essential to detect future changes and support ecosystem management in the SoM.

CRediT authorship contribution statement

Dalida Bedikoğlu: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Data curation, Conceptualization. **Nazli Demirel:** Writing – review & editing, Supervision, Project administration, Methodology, Data curation, Conceptualization.

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Dalida Bedikoğlu reports financial support was provided by istanbul university. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107552.

Data availability

Data will be made available on request.

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