Regional Studies in Marine Science 54 (2022) 102450



Contents lists available at ScienceDirect

Regional Studies in Marine Science

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Reproductive strategies and population characteristics of key Cladocera species in the Sea of Marmara



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ARTICLE INFO

Article history:
Received 23 February 2022
Received in revised form 16 May 2022
Accepted 17 May 2022
Available online 24 May 2022

Keywords:
Reproductive cycle
Birth rate
Penilia avirostris
Mucilage event
Sea of Marmara

ABSTRACT

Zooplankton is an essential component of marine ecosystems, with Copepoda and Cladocera being the most important zooplankton groups in all the world's seas. In the Sea of Marmara, Cladocera has the highest participation in zooplankton abundance. Here we investigated reproductive strategies and population characteristics of four Cladocera species; *Penilia avirostris*, *Pleopis polyphemoides*, *Evadne nordmanni*, and *Pseudoevadne tergestina* in the Sea of Marmara, northeastern part of Mediterranean Sea. Reproduction strategy, fecundity, and embryonic development of four Cladocera species were achieved. During our study period from 2004 to 2008, there was an extreme jellyfish bloom caused by *Liriope tetraphylla* and following mucilage event occurred between the years 2006 and 2008. Thus, we also compared the change in phenology and reproductive strategy of cladocerans amongst periods characterized by extreme events and against a suite of environmental parameters. The most dominant Cladocera species in the Sea of Marmara were *Penilia avirostris* and *Pleopis polyphemoides*. The population structures of Cladocera species according to their reproductive strategies, parthenogenetic female individuals provided rapid exponential reproduction, and were dominant at 60%–100%. Parthenogenetic fecundity success was found significantly different among Cladocera species. The most remarkable result during the study period was observation of increase in embryo production while populations were in decrease.

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1. Introduction

In marine ecosystems, zooplankton is a critical component that affects all living groups in the pelagic food web, starting from the primary producers with its high abundance, wide distribution and predator–prey relationships (Cushing, 1990; Clark, 1992). Cladocera, a prominent group of mesozooplankton like Copepoda, has more than 700 identified species on the earth (Smirnov, 2014). Contrasting its diversity, only eight Cladocera species are marine forms (Onbe, 1977), having a wide distribution in the world's seas. Although seasonal abundance peaks of marine cladocerans are well known, studies investigating that their reproductive strategies and fecundity are limited (Marazzo and Valentin, 2003a, 2004a; Atienza et al., 2008; Dvoretsky and ve Dvoretsky, 2020). Their life cycle is characterized by the alternation between gamogenesis and parthenogenesis. During parthenogenesis, the genetic characters of parthenogenetic embryos are the same as those of the parent individuals as genetic recombination does not occur (Hebert and Ward, 1972). This strategy is an effective biological mechanism of choice for achieving and maintaining rapid population growth under favourable environmental conditions (Hebert and Ward, 1972; Frey, 1982; Egloff et al., 1997). Immediately after the peak of their populations, parthenogenetic females in the water column change their reproductive strategy to become gamogenetic females. The gamogenesis stage is the only way for the species to produce resistant individuals (Rispe and Pierre, 1998). Furthermore, it is the preferred reproductive strategy when adverse environmental conditions develop (Egloff et al., 1997). Finally, gamogenetic females produce resting eggs to sink to the seafloor during the seasonal disappearance of Cladocera populations (Onbe, 1985; Egloff et al., 1997).

Here we investigated reproductive strategies and population characteristics of four Cladocera species; *Penilia avirostris*, *Pleopis polyphemoides*, *Evadne nordmanni*, and *Pseudoevadne tergestina* in the Sea of Marmara, northeastern part of Mediterranean Sea. The lack of knowledge on the phenology of Cladocera species in the SoM and the reason for their exceptionally high contribution to overall zooplankton abundance led us to carry out detailed studies on their life cycles in the SoM. Thus, we have studied reproduction strategy, fecundity, and embryonic development of four Cladocera species in the highly urbanized and eutrophic

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https://doi.org/10.1016/j.rsma.2022.102450
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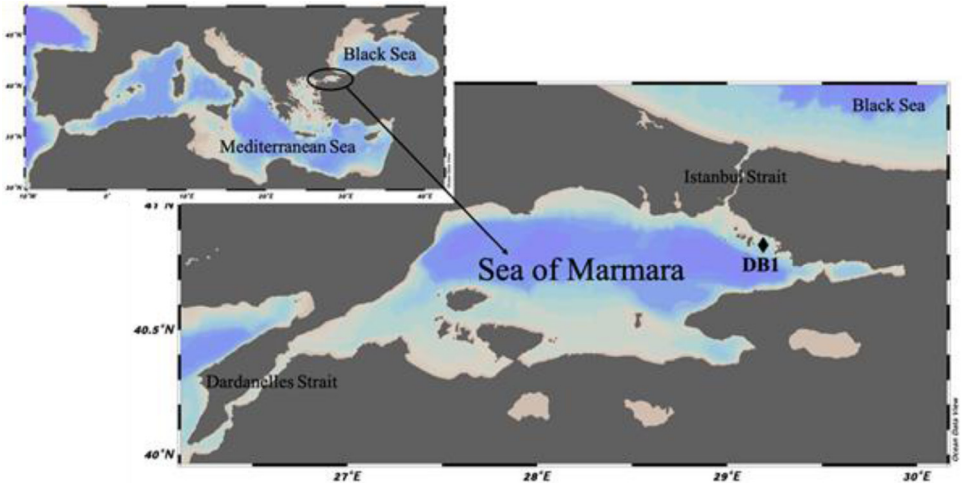


Fig. 1. Sampling station (indicated by the diamond symbol) and the location of the Sea of Marmara.

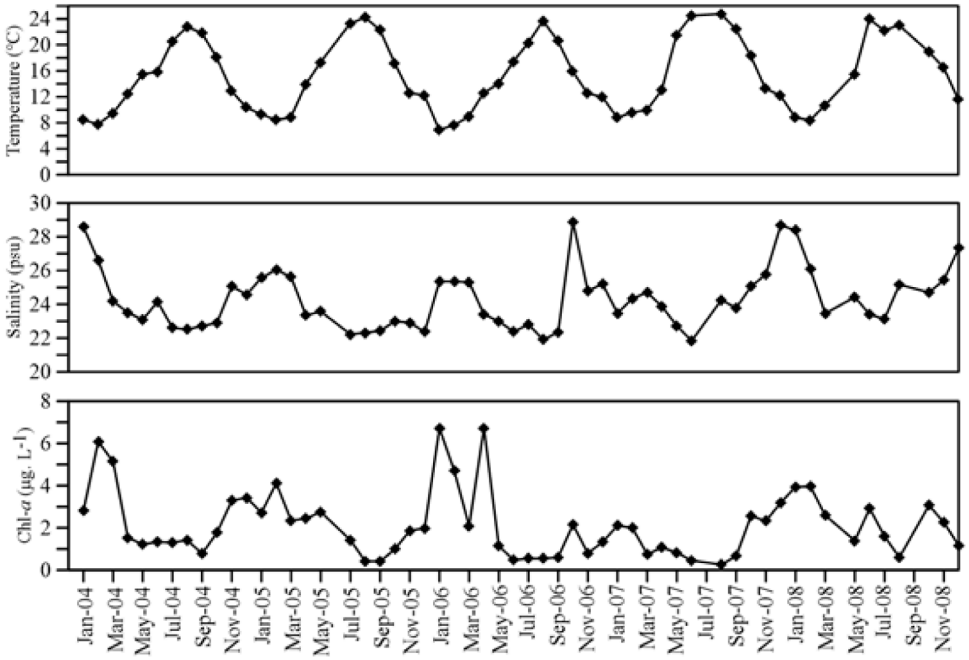


Fig. 2. Monthly variations in SST, SSS and Chl-a in sampling station (DB1).

northeastern part of the SoM. During our study period from 2004 to 2008, there was an extreme jellyfish bloom caused by *Liriope tetraphylla* (Yilmaz, 2015) and following mucilage event occurred between the years 2006 and 2008 in the SoM. Thus, we also compared the change in phenology and reproductive strategy of cladocerans amongst periods characterized by extreme events and against a suite of environmental parameters.

2. Material and methods

2.1. Study area

SoM is a nearly enclosed sea with a surface area of 11,500 km^2 (70 km × 250 km), bearing two different water bodies separated by distinct density gradients. It is connected to the Black Sea by the Istanbul Strait and the Mediterranean by the Dardanelles Strait (Fig. 1.). While the denser Mediterranean waters (∼38 psu) entering the SoM via Dardanelles Strait forms the lower layer, the low-density Black Sea waters (∼18 psu) that enters via the Istanbul Strait upper currents create the upper layer (∼25 m). Halocline, the intermediate layer where partial mixing occurs, separates these two different water bodies. While the strong halocline prevents mixing between the two layers, significant vertical mixing happens in the winter months due to the wind forcing (Beşiktepe et al., 1994). Surface discharges at the SoM and broad agricultural drainage basins of rivers discharging to the northwestern Black Sea increase nutrient budgets at its surface waters (Tugrul and Polat, 1995; Yalçın et al., 2017).

Samplings were performed monthly for five years in one station, DB1 (40°50.60N-29°10.00E), with 89 m depth (Fig. 1). Temperature and salinity profiles were measured by an SBE 9–11 CTD system. Acetone extraction method (Parsons et al., 1984) were used to determine Chl-*a*. Sea surface temperature (SST, °C) and sea surface salinity (SSS, psu) ranged from 6.9 °C (Jan. 2006) to 24.8 °C (Aug. 2008) and from ‰21.8 (Jun. 2007) to ‰28.9 (Oct. 2006). Chlorophyll *a* (Chl-a, µg L^{-1}) concentrations varied between 0.3 µg L^{-1} (Aug. 2007) and 6.7 µg L^{-1} (Jan.2006) and highest values were in winter months until mid-spring (Fig. 2).

Table 1
Individual classifications and embryo developmental stages for Cladocera (Della Croce and Bettanin, 1965; Wong et al., 2004).

Individual categories	Description
Juvenile (J)	Non-reproducing females, <500 μm only for *Penilia avirostris*
Female (F)	Non-reproducing females
Parthenogenetic Female (PF)	Embryos in the brood pouch
Gamogenetic Female (GF)	Resting eggs in the brood pouch
Male (M)	With copulation organ
Embryo development	**Description**
Resting egg	Flattened, with a thick chitinous membrane and are opaque, occupying the entire brood pouch.
Stage A	Ellipsoidal, surrounded by an elastic membrane and almost completely filled with yolk granules.
Stage B	The cover membrane disappears, the second antenna starts to develop, and the thorax region is differentiated
Stage C	The second antenna is fully formed, and the first antenna starts to elongate. All the thoracic segments are visible, and sometimes rudiments of thoracic appendages are evident. The compound eye becomes apparent in *P. tergestina* and *P. polyphemoides* species; the pigment structure has not yet developed
Stage D	Embryos are similar to adults, with all the thoracic appendages wholly formed and the carapace and the eye fully developed.

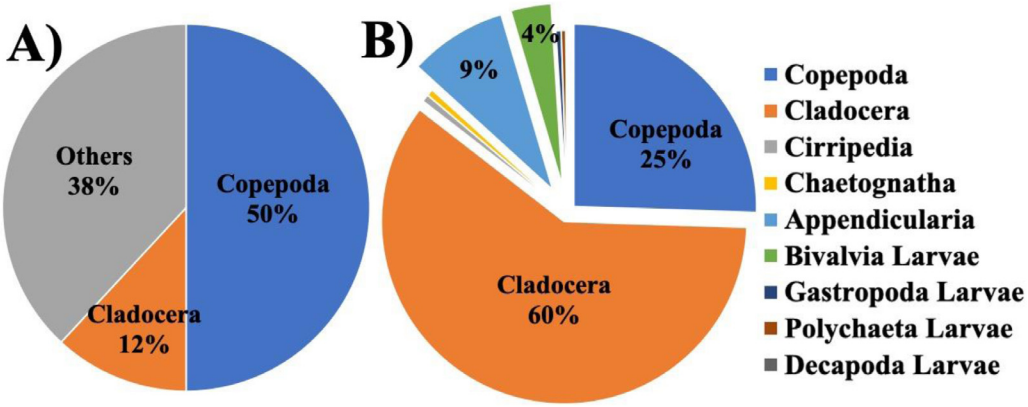


Fig. 3. Percentage of mesozooplankton species (A) and relative abundance of major mesozooplankton groups (B) in the SoM between 2004 to 2008.

2.2. Zooplankton samplings and laboratory analyses

Zooplankton samples were collected monthly using a Nansen net (0.57 m diameter, 200 μm mesh size) from January 2004 to December 2008. Samplings were confined to the depths shallower than the thermocline (6–24 m), which was detected by a CTD profiler. Zooplankton samples were fixed by adding borax buffered formaldehyde solution to a final concentration of 4%. No samples were collected in June 2005, July 2007, April 2008 and September 2008.

Following Alden et al. (1982), mesozooplankton samples were defined at the lowest possible taxonomic level and their abundances were calculated (ind. m^{-3}). Replicate subsamplings were carried out using 1–10 ml Stempel pipettes. Subsample volume size depended on the sample concentration and composition (Alden et al., 1982) and varied from 1/5 to 1/250 of the sample. Cladocera abundance were standardized to individual numbers per unit sea water volume (ind. m^{-3}). Species numbers and abundances were defined as percentages to describe the contribution of Cladocera to mesozooplankton in the 5-year dataset.

Fifty individuals from each target species (*P. avirostris*, *P. polyphemoides*, *E. nordmanni*, and *P. tergestina)* were randomly selected, and their sex, size, and brood compositions were determined. When a species abundance was low in the sample (<100 ind. m^{-3}), it was excluded from the measurements. All individuals were counted in the following categories: juveniles (J), females (F), parthenogenetic females (PF), gamogenetic females (GM) and males (M) (Table 1). Embryonic development was divided into four stages (A–D) following the classification by Della Croce and Bettanin (1965) and the simplified approach by Wong et al. (2004) (Table 1). The fecundity of parthenogenetic (the number of embryos) and gamogenetic females (the number of resting eggs) were also determined.

3. Results

During study period, general mesozooplankton structure were defined as (1) The highest species number was belonging to Copepoda group by 50% percentage (Fig. 3A) and (2) Cladocera group was reached the highest abundance which its relative abundance was 60% (Fig. 3B). Other prominent groups were Appendicularia and Bivalvia larvae, respectively (Fig. 3B).

3.1. Temporal variability

Abundance of Cladocera species showed a clear seasonality in the northeastern part of the SoM. Following their first appearance in the water column, they immediately reached a peak in abundance and then gradually decreased before their population disappearance (Fig. 4). This temporal pattern was observed for all species annually except for *P. polyphemoides* during 2004–2005. *E. nordmanni* mainly occurred during the winter season until mid-spring (6.9–17.3 °C) with an abundance peak in late winter (2966 ind. m^{-3} in February 2004), except in 2008 when the species was observed in the summer period with the highest SST (23 °C). This temperature was significantly higher than the previous years' conditions for this species (Fig. 4). The warm-water species *P. avirostris* was significantly dominant during the summer and reached peak values (29245 ind. m^{-3} in June 2007) over a wide SST range (11.6–24.8 °C). Another warm-water species, *P. tergestina,* had lower abundance during late-summer mid-autumn over three consequent years, then disappeared in 2007, and unexpectedly occurred in December 2008.

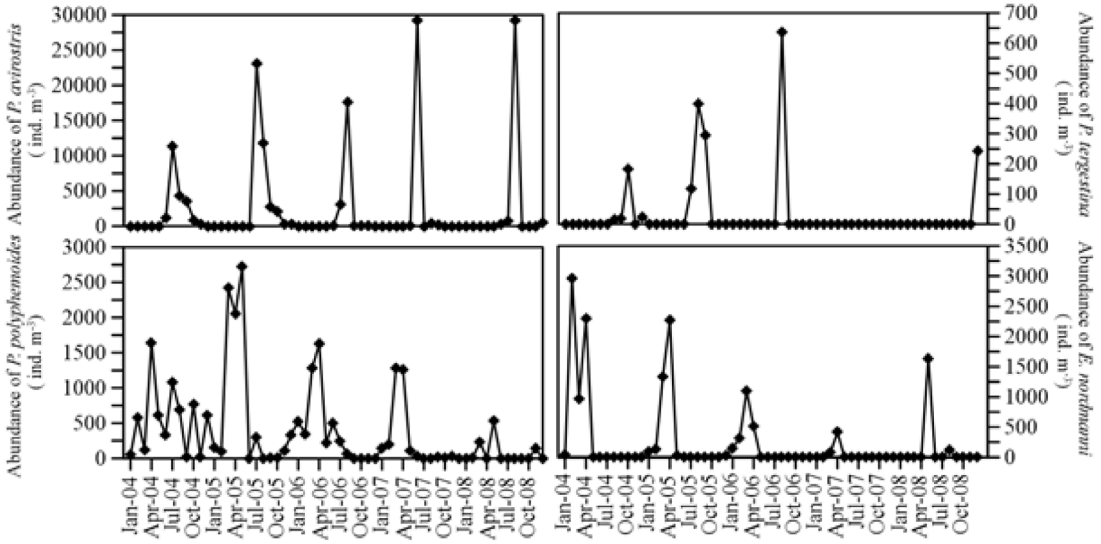


Fig. 4. Monthly variations in the abundance of four Cladocera species.

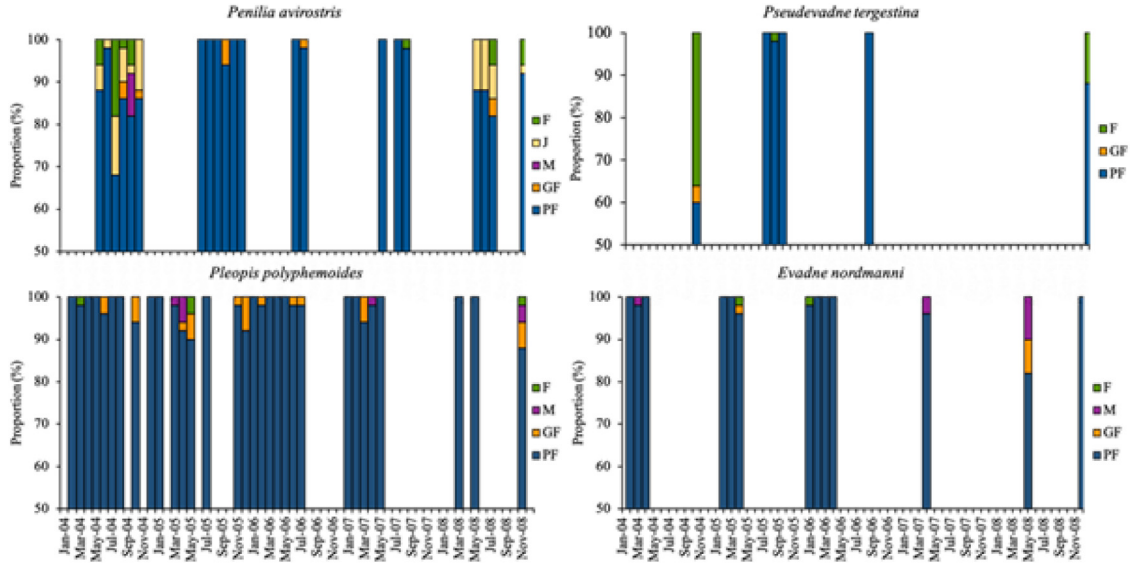


Fig. 5. Frequency of individual categories of four Cladocera species.

3.2. Population structure

PF individuals were predominant (60%–100%), and other individual classes (GF, F, J, and M) frequencies have differed between 2%–36%. The lowest individual classes were GF and M (2% and 10% respectively) and were observed in the period of population peak through decrease for all species except *P. polyphemoides*. Although GF individuals were recorded more frequently than M individuals, their percentage was lower (Fig. 5).

Stage C was the most common embryo in the brood pouches of PF of *P. avirostris*, and stage D was the lowest. The most encountered embryos were stage A in all other species, and the lowest was stage D (Fig. 6). Two PFs, one *E. nordmanni* and one *P. tergestina,* had a morphological abnormality in 2006. We observed that both individuals kept the D stage embryos in their carapace and could not release them but continued to develop stage A embryos (Fig. 7). GFs generally had only one resting egg in all species, except *P. avirostris* in which we found two GFs, each carrying two resting eggs in October 2005.

3.3. Reproductive strategies

PFs dominated the Cladocera population in the SoM. We evaluated their reproductive strategies by comparing embryo numbers. Except for *E. nordmanni*, embryo numbers were higher when the species first appeared annually (Fig. 8). However, in December 2008, almost half of the PF individuals of *P. tergestina* carried only one embryo. This parthenogenetic reproduction was the lowest during the study period (Fig. 8).

4. Discussion

In our study, we found that occurrence and abundance four Cladocera species show strong seasonality related to SST in the SoM except for *Pleopis polyphemoides*. During 2004–2006 study period, all species showed peak abundance period and then disappearance pattern. However, starting in late 2006 and following years, Cladocera community showed unexpected annual and seasonal patterns. The SoM faced two major ecological problems between 2006 and 2008; *Liriope tetraphylla* blooms and dense

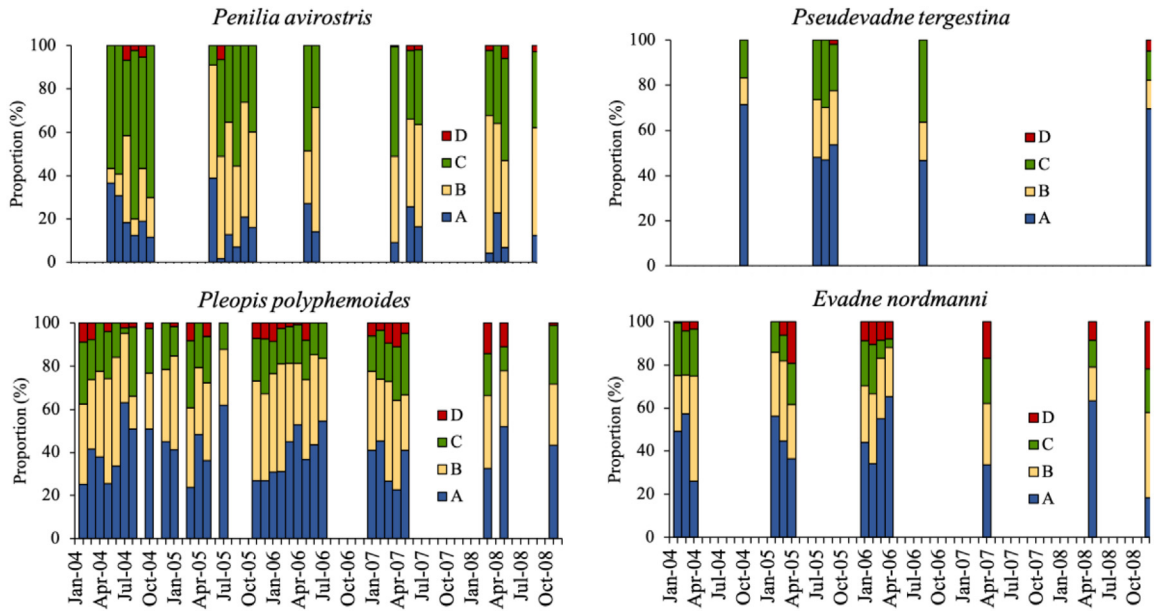


Fig. 6. Frequency of embryo stages PFs of dominant Cladocera species.

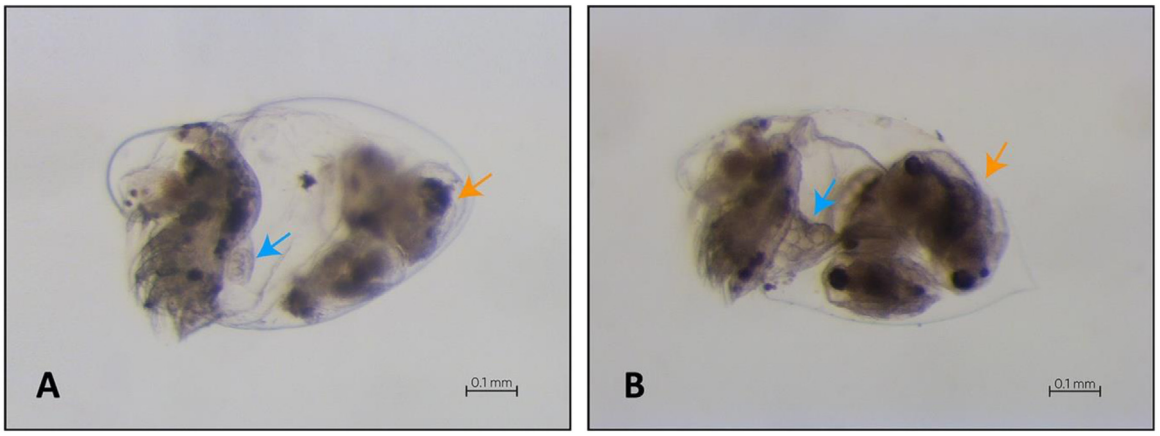


Fig. 7. Photos of (A) Parthenogenetic female of the *Pseudevadne tergestina* with four A-stage embryos (blue arrow) in brood pouch, and also three D-stage embryos (orange arrow) below carapace (in August 2006). (B) Parthenogenetic female of the *Evadne nordmanni* with six A-stage embryos (blue arrow) in brood pouch, and also four D-stage embryos (orange arrow) below carapace (February 2006 in). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

mucilaginous aggregates. These two events led to a drastic reduction in Cladocera abundance, and the Cladocera population collapsed in December 2006, December 2007, and January 2008. Prior to mucilage formation, a population increase of a hydrozoa species *Liriope tetraphylla* in 2006–2007 were detected. Frequent distribution of *L. tetraphylla* was first detected particularly at the northern parts of SoM in 2005 and following year, the dominance of the species over other macrogelatinous species was reached up 63% (Yilmaz, 2015). The abundance of the species reached 2978 ind. m^{-3} in 2007 (Yilmaz, 2015), while the abundance of the species in the Mediterranean was recorded a maximum of 65 ind. m^{-3} (Buecher et al., 1997; Molinero et al., 2008), reaching such a high abundance in the SoM in such a short time has caused significant changes in the pelagic system (Yilmaz, 2015). In 2007, while the abundance of *L. tetraphylla* reached its highest, we found remarkable differences in zooplankton abundance and Cladocera almost vanished from our samples. It has been reported that a picoplanktonic cyanobacterium Synechococcus abundance was highest in November 2007, coinciding with mucilage formation (Toklu-Alicli et al., 2020), however, no notable change in phytoplankton abundance during the periods when mesozooplankton abundance decreased (Tas et al., 2020). This shows that the predator effect of *L. tetraphylla* was mainly effective on the main two groups of mesozooplankton as it was not included in the SoM pelagic food web before 2005. These fluctuations in mesozooplankton were similar with mucilage events in the Adriatic (Umani et al., 2005). Unlike mucilage events in the Adriatic, *P. avirostris* reached the expected abundance peak after mucilage in the SoM. We also observed that, none of the Cladocera species showed decrease in fecundity and their population recovered quickly following these two extreme events.

The temperature is associated with the percentage of Cladocera in zooplankton communities and the cyclicity in their reproductive strategy (Marazzo and Valentin, 2003a,b, 2004a,b; Atienza et al., 2008). *Penilia avirostris* as the most dominant Cladocera species in the SoM, were found between 11.6–24.8 °C SST and reached its highest abundance at 20.3–24.8 °C during summer season. Another warm water species *Pseudevadne tergestina* had the lowest frequency of occurrence and abundance which was found between 10.4–24.2 °C SST. Our results

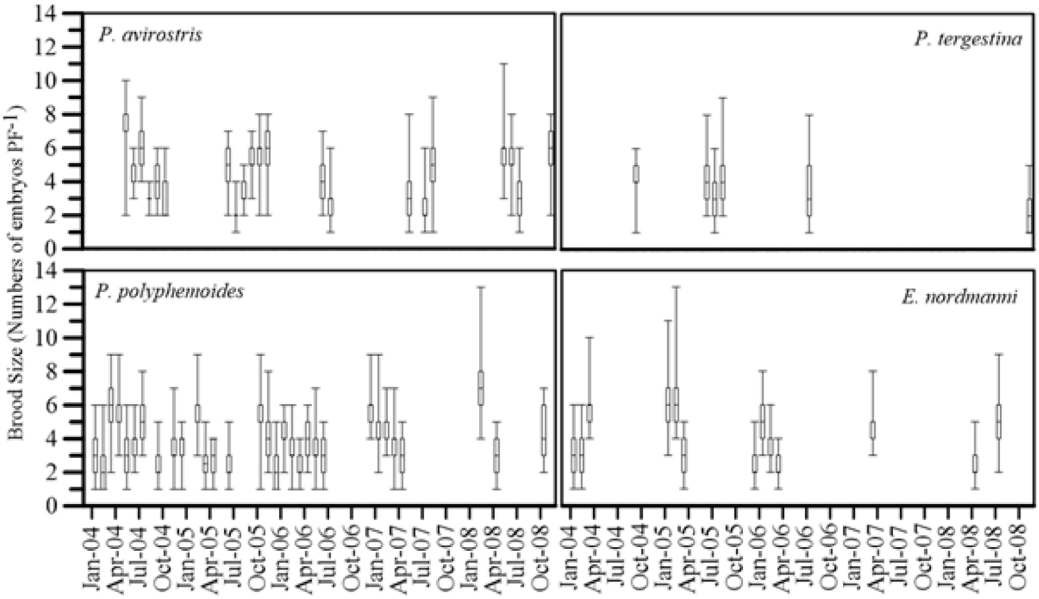


Fig. 8. Monthly brood size change in parthenogenetic females of four Cladocera species.

for the occurrence with peak abundance of those species and preferred temperature range are similar with previous studies (Table 2). On the other hand, *P. polyphemoides* as the second most abundant species, is recognized its high abundance during spring and summer in other regions (Eriksson, 1974; Miyashita et al., 2011), while it was found throughout the year in this study. In addition, *E. nordmanni* is known as cold water species and its occurrence was limited to the winter and spring (Dvoretsky and ve Dvoretsky, 2020), during our sampling in 2008, it was recorded in August, at a temperature this high (23 °C) was the first record for the last 20 years compared to previous studies (Table 2).

In freshwater cladocerans, the transformation of reproductive strategies from parthenogenesis to gametogenesis is hormonal (Minelli and Fusco, 2006). Fluctuations in temperature, photoperiod and food availability cause this hormonal change (Egloff et al., 1997). The cyclicity in reproductive strategy is triggered when at least two of these three environmental factors deviate from the optimum (Stross and Hill, 1965). Cladocerans are present at a broader temperature range in the SoM compared to other seas. In case of *P. avirostris*, its high fecundity has explained with its high abundance (Table 2), because the appearance of *P. avirostris* overlaps with the population decline of other cladocerans. This succession pattern may be a combined outcome of higher fecunidty of *P. avirostris* and their more efficient feeding strategy (Broglio et al., 2004). During the peak abundance period, only PF individuals were recorded, but GF and M individuals were observed lowest in the periods of decline that followed. Dominant PF individuals was reported in previous studies for other regions, but also with higher GF and M ratios than our results (Marazzo and Valentin, 2001, 2003a, 2004b; Atienza et al., 2008). This kind of expected temporality in the cyclical reproductive strategy of Cladocera was only evident for *P. avirostris* in the SoM. We concluded that the high abundance levels and success in fecundity of *P. avirostris* may be due to the eutrophic characteristics of the SoM and its permanently stratified system that resulting in higher food availability in relatively narrow upper layer (annual average 15 m by Beşiktepe et al., 1994).

Different form other regions (Table 2), *P. polyphemoides* was present throughout the year in the SoM. For this species, the transformation is effective under predation pressure on neonates and deviation from the optimum temperature (Marazzo and Valentin, 2003b). We found high frequency of PF, but very low frequency of Gametogenetic (GF and M) individuals even the period of their population growth. Compared to previous studies, the highest embryo numbers of *P. polyphemoides* (13 embryos, 10.7 °C) was recorded in this study (Table 2). *P. tergestina* was present in adequate numbers only in one month of the year, except 2005. We found GF individuals only in 2004, and they constitute 4% of the population. *P. tergestina* embryo numbers were lower in the SoM than other regions (Table 2). Although PF individuals were dominant in the *E. nordmanni* population, GF and M individuals had lower frequency during the peak or collapse period of the population.

5. Conclusion

We found monthly dynamics of Cladocera species were primarily affected by changes in sea water temperature, thus displaying high seasonality. The population structures according to their reproductive strategies, parthenogenetic female individuals provided rapid exponential reproduction, and were dominant at 60%–100% in the SoM. Parthenogenetic reproductive fecundity was found significantly different among Cladocera species. The most remarkable result during the study period was observation of increase in embryo production while populations were in decrease. We also observed that the collapse of Cladocera population during bloom of *L. tetraphylla*, by possible predation pressure, did not affect their fecundity success, as well as Cladocera species was able to observed again in samples with fertility success immediately after the mucilage event. We concluded that the fast recovery of Cladocera population were strictly related with the advantage of their parthenogenetic reproductive strategy. Thus, the higher Cladocera abundance in the SoM compared to neighbouring seas, may be due to their success in high fecundity by gametogenetic reproduction where SoM serves the suitable environmental conditions. Finally, it is clear that monitoring of zooplankton dynamics can be successful indicators for understanding ecosystem changes.

Table 2
Review of the recorded temperature, salinity, embryo numbers and body measurements of four Cladocera species around the world seas.

Species	Temperature (°C)	Salinity (psu)	Embryo Numbers (n)	Mesh Size/ Abundance (ind. m^{-3})	Sampling years	Region	References
Penilia avirostris	29–31	31.8–33.9	1–12	125 μm/3700	1969–1971	Gulf of Bengal, Indian Ocean	Vijayalakshmi and Venugopalan (1972)
	14.2–21.8	35.1–35.5	1–13		1964–1967	Agulhas, South Atlantic Ocean	Angelino and Della Croce (1975)
	9.02.2028	25–35	–	100 μm/21 491	1982–1983	Gulf of Chinhae, North Pacific Ocean	Yoo and Kim (1987)
	16–32	7.3–37.2	1–14	125 μm/>2000	1980–1991	North Pacific Ocean	Tang et al. (1995)
	20.5–27.5	23–36	3–9	200 μm/1823	2000	Gulf of Guanabara, South Atlantic Ocean	Marazzo and Valentin (2003a)
	23.6–28.5	24.6–35	1–11	200 μm/1928	2001	Gulf of Guanabara, South Atlantic Ocean	Marazzo and Valentin (2004a)
	–	–	–	125 μm/∼100	1998–1999	Tolo Harbour, North Pacific Ocean	Wong et al. (2004)
	27–30	34–36	1–8	200 μm/2179	1992–1993	Kingston Harbour, Caribbean Sea	Rose et al. (2004)
	16–27	–	1–8	200 μm/3000	2003–2004	Catalan Sea, Western Mediterranean	Atienza et al. (2008)
	14.8–28.2	31.1–36	1–12	200 μm/2000	2005–2008	Gulf of Ubatuba, South Atlantic Ocean	Miyashita et al. (2010)
	11.5–24.7	**21.8–28.8**	**1–11**	200 μm/29 245	**2004–2008**	**Sea of Marmara, Turkey**	**This study**
Pleopis polyphemoides	8–26.5	25–35	–	100 μm/17 629	1982–1983	Gulf of Chinhae, North Pacific Ocean	Yoo and Kim (1987)
	21–28	23–35	5–8	200 μm/1468	2000	Gulf of Guanabara, South Atlantic Ocean	Marazzo and Valentin (2003b)
	–	–	–	125 μm/>2000	1998–1999	Tolo Harbour, North Pacific Ocean	Wong et al. (2004)
	5–25	1–6	1–10	100 μm/7350	2006	Gulf of Parnu, Baltic Sean	Pollupüü et al. (2010)
	15.3–25	33.7–35.7	1–6	200 μm/20	2007–2008	Gulf of Ubatuba, South Atlantic Ocean	Miyashita et al. (2011)
	6.9–24.5	**21.8–28.5**	**1–13**	200 μm/2719	**2004–2008**	**Sea of Marmara, Turkey**	**This study**
Evadne nordmanni	–	–	1–10		1941–1942	Kelt Sea, North Atlantic Ocean	Cheng (1947)
	9–20	32–34	1–20		1978–1979	Shinkai Maru, North Pasific Ocean	Ramirez and Perez Seijas (1985)
	–	–	1–21	153 μm/10 000	1968	Nova Scotia, North Atlantic Ocean	Platt and Yamamura (1986)
	9.5–19.8	30–35	–	100 μm/<1000	1982–1983	Gulf of Chinhae, North Pasific Ocean	Yoo and Kim (1987)
	6–13	17–34	–	168 μm/11 709	2007–2014	Barents Sea	Dvoretsky and ve Dvoretsky (2020)
	6.9–23	**23.3–26.6**	**1–13**	200 μm/2967	**2004–2008**	**Sea of Marmara, Turkey**	**This study**
Pseudevadne tergestina	25.2–29.6	14.4–31.16	3–12		1973 and 1975	Gulf of Chesapeake, North Atlantic Ocean	Bryan (1979)
	10–28	25–35	–	100 μm/3779	1982–1983	Gulf of Chinhae, North Pasific Ocean	Yoo and Kim (1987)
	23–28	–	1–7		–	Gulf of Mexico, North Atlantic Ocean	Mullin and Onbé (1992)
	23–26	–	2–6		–	Inland Sea of Japan	Mullin and Onbé (1992)
	16–32	7.3–37.2	1–14	125 μm/1100	1980–1991	North Pasific Ocean	Tang et al. (1995)
	21.2–28.5	24.7–35.6	1–14	200 μm/4383	2000	Gulf of Guanabara, South Atlantic Ocean	Marazzo and Valentin (2004b)
	–	–	–	125 μm/∼500	1998–1999	Tolo Harbour, North Pasific Ocean	Wong et al. (2004)
	14.8–28.2	31.1–35.7	1–10	200 μm/350	2005–2008	Gulf of Ubatuba, South Atlantic Ocean	Miyashita et al. (2010)
	10.4–24.2	**21.9–27.3**	**1–9**	**200 μm/637**	**2004–2008**	**Sea of Marmara, Turkey**	**This study**

CRediT authorship contribution statement

Dalida Bedikoğlu: Laboratory work, Data analysis, Methodology, Conceptualization, Writing - original draft. **I. Noyan Yilmaz:** Sampling design, Conceptualization, Methodology, Writing - review & editing. **Nazli Demirel:** Supervision, Conceptualization, Data analysis, Funding acquisition, Writing - review & editing, Writing - original draft.

Declaration of competing interest

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

Acknowledgements

The present study is part of a M.Sc. thesis entitled "Reproduction strategy of dominant Cladocera species of the Sea of Marmara" by Dalida Bedikoğlu.

Funding

This work was supported by the Scientific Research Projects Coordination Unit of Istanbul University, Turkey [Grant number: FYL-2019-33563].

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