

Relationships of the *Cyprideis torosa* (Ostracoda, Crustacea) with Seasonal Occurrences, Carapace Type and Physicochemical Variables in Kocaya Delta (Türkiye)

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ABSTRACT

To understand the spatial and temporal continuing occurrence patterns and relationships of *Cyprideis torosa* to several physicochemical variables, monthly samples from seven stations were collected from Kocaya Delta (Bursa, Türkiye) between 2018 and 2019. Four (*Cyprideis torosa*, *Koencypris ornata*, *Candona* cf. *lindneri*, *Candona meerfeldiana*) of 14 ostracod taxa are new records for the ostracod fauna of Bursa province, where the total numbers of recent species increased to 33. *Cyprideis torosa* was the only dominant species found in almost all samples throughout the sampling. Based on the carapace type of the species, three groups can be divided as i) Type-1 (smooth carapaces), ii) Type-2 (noded carapaces), and iii) Type-3 (carapaces noded on one valve and smooth/rare on the other). Different occurrence patterns of the species with overlapping ecological ranges were observed among the stations. Except for station 1, all the types were encountered from other stations. Beginning from December 2018, nearly all populations had mostly Type-1 individuals until March. During April-May, individuals with Types-2 and 3 appeared to increase until October, while individuals in the Type-2 group were solely found from three stations (2, 3, and 5) in March and May 2018. There was a significant difference in salinity, magnesium, and calcium values among the stations ($P < 0.05$) but only total nitrogen, temperature, and calcium showed a medium correlation to carapace type. In all cases, populations with noded individuals were found in narrower ecological ranges for those variables than other populations with smooth individuals.

Keywords: Coding, seasonality, ecological tolerances, subfossils, recent distribution

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Introduction

The genus *Cyprideis* (Cytherideidae) includes about 31 species (Meisch et al. 2019). Of which, *Cyprideis torosa* with wider geographic distribution than other species (Karanovic 2012) has been found primarily on highly saline (euhaline), brackish or marine habitats (so-called “halophilic species” (Bronstein 1947)) and less frequently in freshwater habitats (Hartmann 1964). This is because the species shows broad tolerance ranges to salinity (Aladin 1993) and temperature values in several different

aquatic ecosystems such as springs (Gülen 1985) and small water bodies and irrigation canals (Akdemir and Külcöylüoğlu 2021). Also, live individuals of *C. torosa* have been recorded from streams (Külcöylüoğlu et al. 2020) and a lake (Lake Bafa) in Turkey (Akdemir et al. 2020) where electrical conductivity values were below 400 $\mu\text{S}/\text{cm}$, referring to freshwater conditions. *Cyprideis torosa* was also reported from several other inland water types (e.g., springs, ditches, pits, ponds and brooks) in Germany, where electrical conductivities ranged in 750 to

77400 $\mu\text{S}/\text{cm}$ (Scharf et al. 2017). Wouters (2017) - pointed out that species can be found from coastal zones of fresh, brackish, and marine habitats with high salinity values where the species was reported from 0.2 to 80‰ of salinity ranges in waters (e.g., see Bardawil inner lagoon) (Rosenfeld and Vesper 1977). Moreover, *C. torosa* can be active in waters with broad temperature ranges from 1.0°C (Ustaoğlu et al. 2012) to ca. 34.5°C (Bodergat et al. 2014). Dykan (2016) underlined that the species is highly abundant in density in a range of 0-25 °C temperature between 3 and 5 m depth at Northern Black Sea coasts. Additionally, laboratory experiments (see details in Jahn et al. 1996) also showed that at least 50% of *C. torosa* tolerated hypoxic (reduced oxygen of 70% air saturation) conditions along with very high (1 mM and 1.8 mM) hydrogen sulfide concentrations for three weeks. Hence, it is clearly seen that *C. torosa* is one of the most tolerant species to several environmental variables, which can explain its wide geographic distribution ranging from fresh to euryhaline coastal waters.

Cyprideis torosa is a polymorphic species with different populations, including individuals with noded or unnoded (smooth) carapace. Historically speaking, these two types were considered two other species and forms due to the presence (forma *torosa*) or absence (forma *littoralis*) of nodes on the carapace (see Sars 1928; Klie 1938; Elofson 1941). However, it was later pointed out that such difference was probably related to changes in environmental conditions (e.g., salinity) (Van Morkhoven 1962; Keyser 2005; Frenzel et al. 2012; Frogley and Whittaker 2016; Berndt et al. 2019). Moreover, finding both forms from the same sites has already been reported recently (e.g., Triebel 1941; Külköylüoğlu et al. 1993; 1995; Scharf et al. 2017; this study) and fossil forms (Nazik et al. 2008; Witt 2010; Tuncer 2020), supporting that the two forms belonging to a single species as *Cyprideis torosa* (Meisch 2000). Besides the presence of some morphological characters (e.g., length of carapace, posteroventral spine on the right valve, the shape of hemipenis and clasping organs, length of terminal claw and medial seta of the fourth segment of the first antenna) (Van Harten 1975; Wouters 2017), presence/absence of nodes has been commonly used for species identification both in fossil and live (recent) samples. There are plenty of studies (e.g., see Sandberg 1964; Kilenyi 1972; Vesper 1972a, b; Heip 1976a, b; Keyser and Aladin 2004; Keyser 2005; Wouters 2017) on the occurrence of the nodes. It was earlier considered that node formation might be a genetic response. However, as shown by the studies of Keyser and Aladin (2004) and Keyser (2005), the appearance of the nodes corresponds to decreasing

salinity levels during the molting stages due to osmoregulation. Therefore, nodes are most likely environmentally induced. This implies that individuals with nodes are more likely to be found in oligohaline habitats (<5‰ of salinity). Indeed, a few well-known long-term studies based on monthly samples (Vesper 1972a, b; Heip 1976a, b) and studies with seasonal samplings (e.g., Külköylüoğlu et al. 1993; 1995) provided supportive evidence for the previous works. These studies underlined that nodding might be related to the monthly occurrence of the species because of the monthly or seasonal influence of air temperature on the aquatic ecosystems.

As stated above, *C. torosa* has a wide geographic distribution (Sandberg 1964). According to Wouters (2002, 2003, 2017 and references in there), the species has been known from Africa, Asia, Europe and above the Arctic Circle (see Schornikov 2011). Hence, its occurrence may be questionable in Australia (De Deckker and Lord 2017). Furthermore, King and Kornicker (1970) and Heip (1976a) had already reported the species from several sites in North America, but Wouters (2017) indicated that the species reported there were synonyms, and *C. torosa* was not known from the Americas. Besides, Sandberg (1964), in his detailed work on the species, provided a list of *Cyprideis* species from the Americas but not *C. torosa*. However, Sandberg (1964, see p. 93) did not collect specimens from North America but used several materials obtained from the A. G. Davis Collection (British Natural History Museum) and juvenile valves from Kijkduin (Holland). In contrast, recently, Pint and Frenzel (2017) reported the species from Nevada (North America) and Chile (South America) while it was also reported from Texas (Külköylüoğlu et al. 2021a). Thus, considering all the studies above (and several others cited in there) and doubts about its occurrence in Australia suggest that the species almost exhibit cosmopolitan distribution in all continents except the poles.

Although a quantity of studies on the species' ecology, biology and distribution exists in the literature, there is no extensive and comparative study on its monthly occurrence patterns along with carapace type and distribution of fossil and recent populations of the species in Turkey. However, an important issue that the presence of the species with or without nodes can aid to (i) understand salinity and temperature changes and/or fluctuations in aquatic bodies, (ii) estimate and possibly reconstruct the past aquatic conditions sought in paleontological studies, (iii) compare levels of changes between the past and present water quality measurements, and (iv) create proxy models and scenarios for future aquatic conditions which can elaborate our understanding

about the possible impact of climatic changes. Therefore, the aims of the present study focus on three points to (1) accomplish the first monthly sampling of *C. torosa* along with its correlation to some environmental variables (e.g., salinity and temperature) in the Kocaçay Delta, (2) search relationship between occurrence patterns and carapace type, and (3) compare species distribution both in subfossil and recent populations in Turkey.

Materials and Methods

The sampling area (Figure 1) is located in Kocaçay Delta Floodplain Forest (ca. 42.000 hectares of surface area), which is known to be one of the essential floodplains in Turkey. Kocaçay stream

(aka Susurluk Stream) reaches the Marmara Sea after it receives water from several different aquatic bodies, such as Susurluk Stream and Lake Ulubat in the east of Karacabey District (Bursa province). As a result, it develops a large floodplain delta including three lakes (Poyraz, Arapçiftliği and Dalyan lakes, on the East and West of the stream, respectively), swamps, sand dunes, and floodplain (longoz) forest (Keçeli and Ursavaş 2019) where it emerges to the Marmara Sea.

Monthly samples were taken from seven stations (Figure 1) from the Kocaçay Delta (Bursa, Turkey) between 30 March 2018 and 04 April 2019. Water samples for chemical analyses were collected from each station in plastic bottles (1 lt). Chemical analyses were done after APHA (1998) methods.

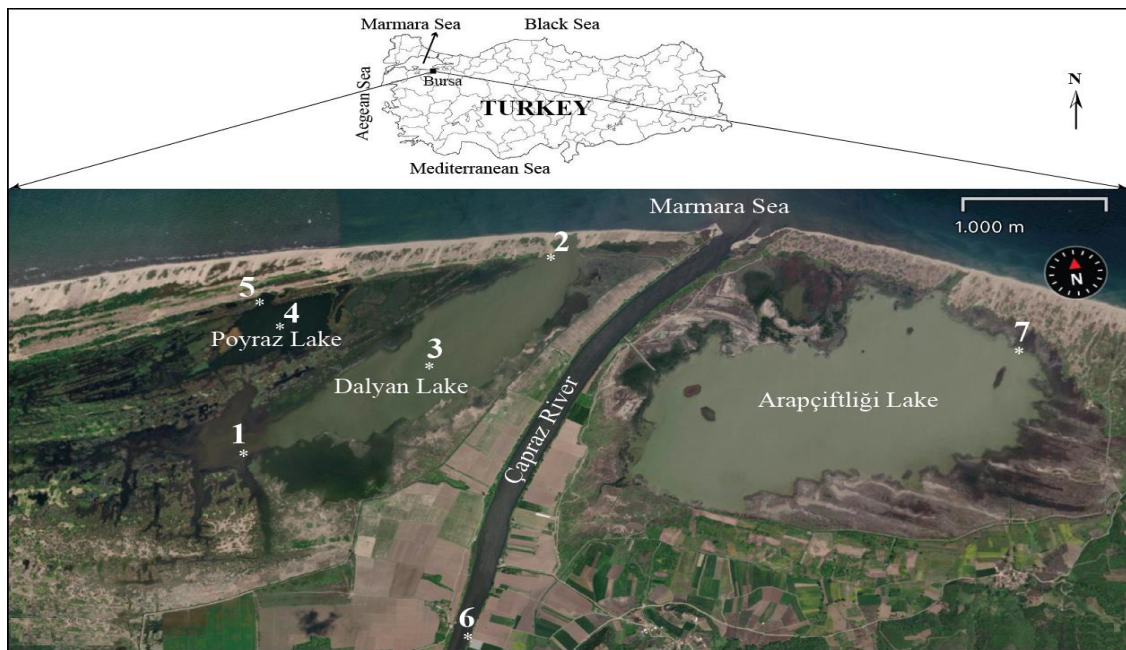


Figure 1. The seven sampling stations in Kocaçay Delta (Bursa, Turkey).

Lovibond Senso multiprobe was used to measure water temperature ($^{\circ}\text{C}$), pH, dissolved oxygen (mg/L) and electrical conductivity (mS/cm) in situ. Ostracod samples taken from the littoral zones (stations 1, 2, 5, 6, 7) were collected from the shores (ca. 1 m^2 area with a maximum of 1 m depth) with a hand net (0.5 mm mesh size) and fixed with 70% alcohol in 200 ml plastic bottles. Other samples taken from the pelagic sites (stations 3 and 4) of the lakes were collected with Ekman bottom grab (152x152x152 mm in size) (ENVCO). This includes the samples collected from the uppermost sediment layer. These samples were filtered through a Retsch brand stainless sieve and separated from the sediment as much as possible. Then, samples were fixed in plastic bottles with 70% alcohol in situ. In the laboratory, all individual samples were separately washed under the tap water through three standard sieved sieves (0.5, 1.0, 2.0 mm

of mesh size) and fixed with 70% ethanol for future studies. We used a stereomicroscope (Olympus SZ-STLA) to sort specimens from the sediment and dissect them in lactophenol solution. Individual samples were examined with fine needles (no: 000) and covered with a cover slide while related information (gender, dimensions, sampling date, site name etc.) was noted on each of them. Whenever possible, taxonomic identification at the species level was made under a light microscope (Olympus BX-51). A taxon is left as "sp." if lacking undamaged and adult individuals. The carapace and valves of dissected species were kept on micropaleontological slides. We followed the taxonomic keys of Meisch (2000) during identification. All samples were placed in the Limnology Laboratory, Department of Biology, Bolu Abant İzzet Baysal University, Bolu, Turkey. The measured values were compared among

the stations with the non-parametric t-test with equal variances (significant if $P < 0.05$). To comprehend possible relationships among carapace type (Type-1 (smooth carapaces), Type-2 (both carapaces noded), and Type-3 (both carapaces noded on one valve and smooth on the other), abundance values (numbers of live adult individuals) and measured physicochemical variables explained above, we used Spearman correlation analysis (0-0.33 low, 0.33-0.66 medium, >0.66 strong correlation) with binary data and ternary plots obtained from the PAST 4.03 program (Hammer et al. 2001).

Results

A total of 10 recent (extant, living) and four subfossils (dead valves and carapaces) ostracod taxa (*Neglecandona angulata*, *C. cf. Lindneri*, *C. meerfeldina*, *Candona* sp., *Cypria* sp., *Cyprideistorosa*, *Cypridopsis* sp., *Eucypris* sp., *Heterocypris salina*, *Ilyocypris* sp., *Koencypris ornata*, *Limnocythere* sp., *Plesiocypridopsis* sp. and *Potamocypris* sp.) were reported from the present study. Four reported taxa (*C. torosa*, *K. ornata*, *C. cf. lindneri*, and *C. meerfeldiana*) increased the number of documented recent species up to 33 in the Bursa province. *Cyprideis torosa*, the most frequently occurring dominant species, was observed in almost all samples throughout the sampling period (but see a few exceptions) (Figure 1, Table 1). Based on the carapace type of the species, three groups can be separated as i) Type-1 with smooth carapaces, ii) Type-2 with noded carapaces, and iii) Type-3 with carapaces noded on one side and smooth on the other or nodes are smaller on the left valve than right one. Different occurrence patterns were observed among the stations (Table 1). While one live female and three subfossils (carapace and valves) of *C. torosa* with all smooth carapaces were found at station 1, populations with all three types of carapaces were randomly encountered from other stations. Live individuals were found in wide ranges of salinity (0.21-28.89 mS/cm) and water temperature (6.03-34°C), corresponding to the known ranges (Table 2). There was a significant difference in the values of salinity, magnesium (Mg), and calcium (Ca) among some stations ($P < 0.05$), while no significant difference was found for other variables. These differences were especially apparent between two stations (1st and 6th stations) located far from the Marmara Sea. Spearman correlation analyses exhibited medium but insignificant correlations for water temperature, Ca and total nitrogen with carapace type. At the same time, none of the variables examined here revealed a

significant correlation with the abundance values (Table 3). Carapace type tends to show variations among the seasons from November until April, and almost all populations had mostly smooth carapaces. During April-May, individuals with Types-2 and three carapaces appeared to increase until the end of October. In all cases, populations with noded individuals were found in narrower ranges for those variables than those with smooth, smooth, and noded individuals. At the same time, the first rank was changed between the smooth and smooth-noded populations at different sites and sampling times (Table 1). A comparison of the fossil and recent populations showed that the distribution and reports of fossil forms were wider than current *C. torosa* populations in Turkey (Figure 2, Appendix). Overall, electrical conductivity (referring to salinity) seems more effective on the species occurrence and abundance than Mg and Ca alone (Figure 3). Results suggest that the occurrence of nodes on the carapace can be affected by both temporal and spatial conditions.

Discussion

Co-occurrence and salinity

With the additional reports, the number of non-marine ostracods in Bursa province increased to 33 species. This number is more than many other provinces of similar size in Turkey (Külköylüoğlu et al. 2021b). However, it is still considered an underestimation since previous reports are based on random or primarily one-time sampling efforts, and there is no extensive study on the ostracod fauna of the province. Meanwhile, looking at the abundance of individual species, it is seen that *C. torosa* is the only dominant species encountered, along with nine other recent taxa (Table 1). Of which, four candonids (*N. angulata*, *C. meerfeldiana*, *C. cf. Lindneri*, *Candona* sp.) were the most accompanying taxa, with *C. torosa* followed by others (*Cypria* sp., *Heterocypris salina*, *Eucypris* sp., *Potamocypris* sp., *Plesiocypridopsis* sp.). It is already known that some of these taxa can be found in fresh to saline habitats together with *C. torosa* (Meisch 2000; Scharf et al. 2017; Pint and Frenzel 2017; McCormack et al. 2019). However, a comparison of the abundance values amid taxa portrayed that *C. torosa* was generally overnumbered (>98%) during our study. Plotnikov et al. (2021) reported that *C. torosa* was



Figure 2. Distribution of fossil (*) and recent (▲) *Cyprideis torosa* in Turkey (see Appendix for the references).

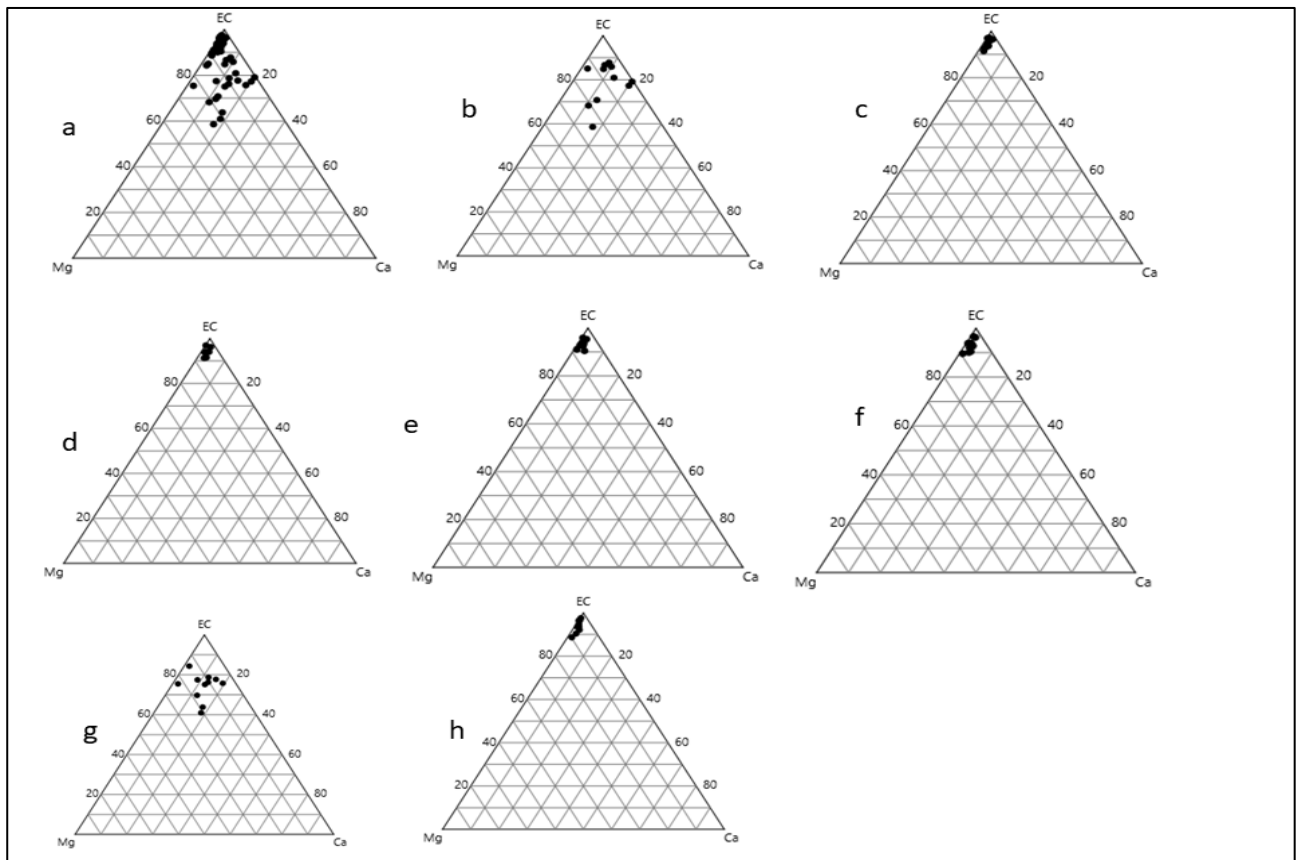


Figure 3. Ternary plots with percentage values show relationships among Ca, Mg and EC for all data (a) and stations 1-7 (b-h).

Table 1. Monthly distribution of *Cyprideis torosa* among seven stations (St No). Abbreviations: m (adult male), f (adult female), S (smooth individuals), N (noded individuals), NS (noded + smooth individuals) carapaces. Recent (extend, live individuals), Subfossil (surface sediment samples) (adult carapace or valves), Rec Juv (live juveniles) and Fos Juv (subfossil juveniles/only carapace or valves).

Date	St No	Carapace	Recent	Subfossil	Rec Juv	Fos Juv
30.03.2018	1					
30.03.2018	2	S	1			
30.03.2018	3	S	4f			
30.03.2018	4	S	1m1f	8		
30.03.2018	5	N	1f			
30.03.2018	6					
30.03.2018	7					
04.05.2018	1					
04.05.2018	2	N	2m16f			
04.05.2018	3	N	6m1f	1		
04.05.2018	4	NS	>100	>100		
04.05.2018	5	NS	3m9f	>100		
04.05.2018	6	NS		2		
04.05.2018	7	NS	7m18f	1		
28.05.2018	1	S				
28.05.2018	2	S		2		
28.05.2018	3	S	1m			
28.05.2018	4	S	1m3f		2	
28.05.2018	5					
28.05.2018	6					
28.05.2018	7	S		1		
02.08.2018	1					
02.08.2018	2	S	2			2
02.08.2018	3	S	1m4f		1	
02.08.2018	4	S	3f	1		
02.08.2018	5	NS	>100	>100	>100	>100
02.08.2018	6	NS		1	1	
02.08.2018	7	NS	>100	>100	>100	>100
05.09.2018	1					
05.09.2018	2	NS	10m35f	1	1	
05.09.2018	3	NS	8m11f	1	1	
05.09.2018	4	S	3f	20	1	
05.09.2018	5	NS	>100	>100	>100	>100
05.09.2018	6	NS	1f	1	2	
05.09.2018	7	NS	>100	>100	>100	>100
29.09.2018	1					
29.09.2018	2	NS	8m28f	1	5	
29.09.2018	3	NS	3m2f	1	4	
29.09.2018	4	NS	8m49f	>100	>100	

Table 1. Continued.

Date	St No	Carapace	Recent	Subfossil	Rec Juv	Fos Juv
29.09.2018	5	NS	>100	>100	>100	>100
29.09.2018	7	NS	>100	>100	>100	>100
24.10.2018	1	S	1f	2		
24.10.2018	2	S	7m9f	1	1	
24.10.2018	3	S	17m53f	>100	>100	
24.10.2018	4	NS	2m6f	>100	>100	
24.10.2018	5	NS	31m40f	>100		>100
24.10.2018	6	S		1		
24.10.2018	7	S	27m42f	>100	>100	>100
20.12.2018	1	S		1		
20.12.2018	2					
20.12.2018	3	S	2m3f	5		
20.12.2018	4	S	2m8f	>100	>100	
20.12.2018	5	S		2		
20.12.2018	6	S		1		
20.12.2018	7					
17.01.2019	1					
17.01.2019	2	S		3		
17.01.2019	3	S	2m38f	2		
17.01.2019	4	S	7m4f	>100	>100	
17.01.2019	5	S	4m3f	9		
17.01.2019	6	S		1		
17.01.2019	7					
20.02.2019	1					
20.02.2019	2	S	5m5f	1	1	
21.02.2019	3	NS	10m40f	1	>100	
22.02.2019	4	S	>100	>100		
23.02.2019	5	S	2f	2		
24.02.2019	6					
25.02.2019	7	S		11		
04.04.2019	1					
04.04.2019	2					
04.04.2019	3	S	2m9f	1		
04.04.2019	4	S	2m1f	2		
04.04.2019	5	N		1		
04.04.2019	6					
04.04.2019	7	S	4m2f	2		

Table 2. Mean, maximum (MAX) and minimum (MIN) values (n = 77) of 13 variables for *Cyprideis torosa* with noded, nodes + smooth, and smooth carapaces. Abbreviations: DO (dissolved oxygen, mg/L), EC (electrical conductivity, mS/cm), water temperature (T°C), salinity (Sal, ppt), phosphate (PO₄-P), total phosphate (TP), nitrite (NO₂-N), nitrate (NO₃-N), total nitrogen (TN), and suspended solid matters (SSM) (all units are in mg/L unless otherwise indicated).

	DO	pH	EC	T°C	Sal	Mg	Ca	PO ₄ -P	TP	NO ₂ -N	NO ₃ -N	TN	SSM	<i>C. torosa</i>
MEAN	7.13	8.18	12.82	17.08	7.44	694.33	254.59	0.055	0.138	0.0140	0.167	3.531	35.35	Noded
MAX	9.80	8.51	18.06	19.60	10.67	875.52	384.77	0.171	0.209	0.0490	0.403	4.827	46.70	
MIN	5.10	7.84	3.89	15.18	2.05	228.69	24.05	0.010	0.077	0.0010	0.073	2.197	22.30	
MEAN	7.06	8.42	16.47	24.18	9.92	937.83	342.58	0.102	0.326	0.0260	0.229	5.425	70.33	Noded+ Smooth
MAX	11.90	8.79	44.70	34.00	28.89	3112.96	801.60	0.369	1.253	0.2010	1.099	16.370	175.30	
MIN	3.40	7.93	0.64	13.20	0.31	82.69	68.14	0.006	0.054	0.0001	0.027	1.595	13.40	
MEAN	7.45	8.25	10.41	15.76	6.26	555.23	197.85	0.071	0.203	0.0090	0.263	3.220	54.67	Smooth
MAX	10.80	8.83	28.30	30.17	17.42	2315.24	673.34	0.277	0.587	0.1350	1.738	5.893	215.30	
MIN	1.90	7.37	0.442	6.03	0.21	2.43	12.02	0.003	0.050	0.0006	0.038	1.925	11.20	

the most common species with long-term tolerance to salinity increase in the Aral Sea. These authors found different occurrence frequencies of the species between Large Aral (salinity range 8-13 ppt) and Small Aral (salinity range 0-3 ppt). The species was the last survivor during the salinity increase in the lake. However, they argued that increasing salinity could even cause the extinction of *C. torosa* in Large Aral but the species present in Small Aral, implying that even *C. torosa* has some upper limits of salinity tolerance.

During the present study, there are, however, variations of the species occurrence pattern among the stations. For example, one possible explanation for such an occurrence may be that station 1 receives a water discharge from a small creek (Figure 1). Besides, it is also faced with a seasonal sea water intrusion when the sea water level rises over the narrow coastal barrier into the lake area (Dalkıran N., pers. comm). Thus, one may argue that this water back up from the creek may reduce salinity (also referring to electrical conductivity) at that sampling point lower than *C. torosa* prefers. However, the species can tolerate wide salinity (and temperature) values. In a microcosm study, Frenzel et al. (2012) showed highest numbers of reproductive rates at the salinities ranged from 3 to 8 psu (Practical Salinity Unit = ppt) while noded valves being most abundant below 2 psu were also found up to 7 psu.

Furthermore, the authors reported smooth valves above the limit 7 psu. Accordingly, their study showed a similar trend for both males and females. In our case, however, salinity ranges between station 1 (0.16 and 0.69 ppt) and station 6 (0.21 and 0.47 ppt) overlap. Therefore, an insignificant level of salinity range does not explain why *C. torosa* was relatively abundant in station 6 but station 1.

Pint and Frenzel (2017) recently proposed a flowchart for paleoenvironmental

interpretation based on species dominance. Hence, if the dominance of the species is more than 90%, the habitat can be characterized as hypersaline or with oxygen deficiency. In contrast, dominance with less than 90% refers to fresh to brackish waters. Although their application is suggested to use fossil occurrences of the species, it can also be used to determine habitats with present conditions. We collected *C. torosa* from the stations (but cf. station 1) with more than 90% of dominance almost all year round. This finding suggests that the delta is of hypersaline conditions, but this does not support oxygen deficiency due to a relatively high mean oxygen value (ca. 7.16 mg/L).

Table 3. Results of Spearman correlation analyses between the numbers of living adult *C. torosa* (NumInd) and carapace type (Car. Type) with 12 variables. Bold numbers show medium but not significant correlations for T°C, Ca and TN. See the text and Table 2 for the units. "NumInd" represents the calculated values after abundances.

Variable	NumInd	Car. Type
DO	-0.045	-0.150
pH	0.190	0.158
T°C	0.119	0.389
Salinity	0.237	0.234
Mg	0.235	0.291
Ca	0.223	0.342
PO ₄ -P	0.092	0.067
TP	0.147	0.189
NO ₂ -N	0.135	0.033
NO ₃ -N	0.061	-0.102
TN	0.258	0.429
SSM	0.249	0.075

Mg, Ca and nodding

This explanation above may have a value since salinity, Mg and Ca measurements were significantly (t-test, $P < 0.05$) different between stations (1st and 6th) and others (2-5, 7th) where the species exhibited seasonal occurrence patterns with high abundance. No significant difference ($P > 0.05$) was found for other variables. Station 6 is located on the Çapraz River, which flows continuously through the Marmara Sea, but intrusion from the sea occurs seasonally. Thus, its water is mixed all the time, where both smooth and smooth-noded individuals were collected during the study. Both elements are necessary for the carapace formation, while Ca is generally higher than Mg in the carapace. However, with a few exceptions, the Mg values of the stations were found to be almost always much higher than Ca during the present study. These differences were apparent between two stations (1 and 6) which were the furthest in the distance to the Marmara Sea. Indeed, we found *C. torosa* from the known ranges of these variables obtained in the literature. What is, however, the imperative is to associate species' frequent occurrences amid the stations with or without (or both) noded carapaces. As mentioned, carapace morphology seems to be related to salinity (and temperature) changes in waters that noded individuals tend to be found more commonly in freshwaters than brackish or saline waters. In addition to these variables, however, previous studies (Keyser 2005; Frenzel et al. 2012) pointed out that node formation might also be correlated to deficiency of Ca level, suggesting that the numbers of nodes can be increased in the waters with low Ca. Although the correlation was medium and not significant (Table 3), our results support the opposite of this view that the mean Ca level (197.85 mg/L) was the lowest among other groups where there were only individuals with smooth carapaces (Table 2). While working on another species (*Limnocythere inopinata*) in Lake Van (Turkey) known with Ca limitation (0.105 to 0.087 mmol/L) (Reimer et al. 2009), a similar finding was outlined by McCormack et al. (2019) that node formation may be influenced by several other factors that Mg may be one of them. Our values are much higher than these and may seem good enough to build a carapace structure. However, this does not explain the absence (except one female) of *C. torosa* at station 1, although its chemical composition is similar to station 6, where the species was relatively higher in numbers and occurrences.

Several studies (Meisch 2000) showed that some species and/or genera could be associated with lower salinity ranges. For example, finding members of the genus *Candona* from station 1 may support this view due to their freshwater habitat preferences with low

salinities (Neale 1988; Karanovic 2012), but we still need to find out why *C. torosa* was not found and/or was not common there. This question is essential because some taxa reported here (e.g., *Heterocypris salina*, *Eucypris* sp., *Plesiocypridopsis* sp., *Cypridopsis* sp.) are already known to survive in wide ranges of salinity, temperature and/or pH values (Delorme 1991). As indicated in their excellent review, Dettman and Dwyer (2012) underlined that several other factors can influence carapace chemistry and structure. Hence, there is no single explanation for the relationships between the formation of nodes on the carapace and Mg, Ca and/or Mg/Ca in waters. On the other hand, Figure 3 suggests that its electrical conductivity is more closely related to species occurrence/abundance than Mg and Ca alone. Moreover, our results with Mg and node formation support a similar explanation for Ca, where individuals without nodes were solely found below the mean (555 mg/L) of Mg level.

Temperature, seasonality and nodding

Herman et al. (1983) showed that *C. torosa* has one generation, and several factors can affect its life cycle and occurrences effectively. For example, salinity increase can be directly intimated with temperature. This is the case for *C. torosa*. Heip (1976a, b), after more than four years of continuous work, illustrated that the adults' abundance and occurrence were triggered and closely related to water temperature above 15°C. Our results support this approach with a few exceptions in some months (see Table 1) where adults are high in numbers below this proposed temperature level. For example, there were more adults at station 3 during January and February 2019, when the water temperature was 6.03 and 13.2°C, respectively. In contrast, a medium correlation between water temperature and species abundance was not significant. Nevertheless, this does not change the general view proposed by Heip (1976a) that the numbers of adults increase with increasing temperature (and salinity), but this should be investigated in detailed studies.

On the other hand, relating the temperature to monthly occurrences of the nodding, it is valuable to indicate that adults without nodes mostly begin at the end of the fall season (November) until the spring season (April). Similarly, the individuals without nodes (but with a few exceptions) were reported all year round from a eutrophic lake, Lake Küçükçekmece (Turkey) (Külköylüoğlu et al. 1993). In another monthly study, however, Külköylüoğlu et al. (1995) reported a similar pattern of the noded and smooth individuals of *C. torosa* from a brackish water lake (Lake Büyükçekmece) (now the lake is freshwater characteristics due to separation from the

Marmara Sea in 1985) in summer (June) and winter (December) seasons. In both studies, authors failed to measure the salinity values of the lakes. Külköylüoğlu et al. (1995) underlined that node formations might be a critical issue for the species because it probably helps the species movement on the sediment in freshwater conditions while the species may not need the nodes in saline waters due to lifting force. Unfortunately, these authors did not ask a specific question about the study's correlation between nodding and salinity.

Additionally, these explanations may not represent the true nature of the correlation between node formations and water chemistry. However, they help to deduce an understanding of it. Nevertheless, as shown in previous studies (see above), node formations are possibly a response to environmental factors.

pH, alkalinity and nodding

Alkalinity was suggested as an influential factor in the carapace structure and formation of nodes (Van Harten 2000; McCormack et al. 2019); for instance, De Deckker and Lord (2017, p.4) stated that "...It is unfortunate that neither *Vesper* nor *Heip* measured alkalinity of the waters during their long investigations of the life cycles of *torosa*, and this needs to be examined in the future to understand ostracod shell composition better. Alkalinity, combined with ionic analysis of the ambient waters, will lead to identifying the calcite saturation nature of the waters in which ostracods moult and grow." We did not measure alkalinity during the present study, but pH values were calculated. Moreover, we know that water pH and alkalinity are not the same, but they are closely related (Boyd et al. 2017). This relationship implies that increasing pH values (>7, referring to alkaline waters) means high alkalinity. In a very comprehensive work by Boyd et al. (2017), this relationship in waters is provided as pH = 6.6, alkalinity = 1 mg/L; pH = 7.3, alkalinity = 5 mg/L; pH = 7.6, alkalinity = 10 mg /L; pH = 8.3, alkalinity = 50 mg/L. This information may be applied to the studies; for example, *C. torosa* was reported in the waters of Terschelling Island, where pH values were measured between 7.5 and 8.5 (Scharf and Hollwedel 2010). The implication is that alkalinity was at least ten or more in the island's waters. During the present study, we have a total of 77 pH measurements. There are only 16 of 77 cases where pH values were below 8.0. Of these, there are only three cases (pH = 7.84, 7.92, and 7.96) where we identified live *C. torosa* (the first two with noded individuals and the last with smooth individuals, respectively). In comparison, we found no ostracods or only valves/carapaces in six and seven cases (mostly

smooth and noded-smooth individuals but no single population with solely noded individuals found), respectively. The remaining cases (61 of 77) include pH values ≥ 8.0 . Adapting the equations of Boyd et al. (2017), we may link the pH values (now referring to alkalinity values above) to the nodding on carapaces. The mean pH values (8.14-8.47) among the stations did not show a significant difference, but it can be inferred that the species may prefer waters with alkalinities above 10 mg/L or even 50 mg/L. This can be helpful to information provided here for the first time that such a view may be used in fossil forms for understanding past environmental conditions in paleontological studies.

Fossil vs Recent (live) forms

In Turkey, *C. torosa* was reported from Early Miocene (Ilgar and Nemeč 2005) corresponding to the previous records (cf. Van Harten 2000; Witt 2010; Wouters 2017). When we compare dispersion of the fossil and live species reported so far (Figure 2), the numbers of fossil records from about 24 provinces (aka cities) are higher than living specimens in 20 provinces. With a few exceptions (Figure 2), living forms have been mostly coupled with fossil records reported from nearby the west and northwest coastal zones (around the Marmara Sea) of Turkey. Although there are extensive studies in some provinces (e.g., Sinop, Çankırı, Eskişehir, Elazığ, Konya), which include about 1000 water samples, there are only surface sediment samples of (subfossils) *C. torosa* populations reported from them. The last four of these cities (and more others, see Figure 2) are far away from the seas and are located within Anatolia, where fossils were found in several different water bodies. Two other similar proxies can be worth discussing: First, *C. torosa* with smooth and noded individuals were reported from Holocene samples of Lake Sevan (Armenia) (Wilkinson et al. 2005). The lake is at 1900 m asl and has no connection to the seas. The authors pinpointed those smooth forms were encountered in a Holocene sequence more than noded forms, implying that the lake salinity had increased during at least the last 5000 years or late Holocene. Second, similarly, in Germany, Scharf et al. (2017) reported Quaternary fossils of *C. torosa* from 32 of 45 inland sites far away (more than 200 km) from the Baltic and the North seas. The opposite situation is also true for live populations with a few cases. There can be at least three possible ways to delineate this situation (1) lack of studies, (2) unsuitable habitats for the species, and (3) no time for the species migration yet. On the other hand, we believe that such a map showing overlapping ranges of fossil and live forms can help

us understand species distribution since the Early Miocene in Turkey.

Overall, in conclusion, as stated above, alkalinity was not directly measured in situ, so we cannot explain its correlation with the nodding of the carapace. However, combining salinity and/or alkalinity with other environmental and biotic variables may be a better way to apply them in future studies. Indeed, total nitrogen (and phosphorous) portrayed a medium correlation ($P > 0.05$) to the species abundance among the stations. Consulting Figure 1 and the site description above, one can recognize agricultural activities or so-called “human activities” around the study area. According to Chen et al. (2015), the global distribution of TN and TP values in lakes can be found between 0.526 mg/L and 0.014 mg/L. Our mean values are all higher than these (cf. Table 2). This implies possible sources of nitrogen and phosphate and their compounds reaching the sampling sites due to human activities. *C. torosa* can overcome all these artificial inputs due to its high tolerance ranges. As indicated by Frenzel et al. (2012), *C. torosa* can be used as a suitable indicator species because the populations inhabit or prefer a wide range of salinities. For example, individuals of the athalassic populations from stable water bodies can be used to describe continuous and detailed water bodies.

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Conflict of interest

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

All authors contributed to the study conception and design. Material preparation, data collection was performed by Enis Akay and Nurhayat Dalkıran. Ostracod samples preparation and analyses were provided by Okan Külköylüoğlu and Mehmet Yavuzatmaca. The first draft of the manuscript was written by Okan Külköylüoğlu and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Appendix

List of provinces in Turkey where the fossil and recent forms of *Cyprideis torosa* were reported. Also, references used in these lists are provided below.

Fossil forms

Adana (Nazik and Gökçen 1995; Şafak 2003; Avşar et al. 2006; Darbaş et al. 2008; Darbaş and Nazik 2010), Antalya (Alçiçek 2007), Aydın (İlhan and Öner 2019; İlhan 2020), Balıkesir (Leroy et al. 2002; Nikolaou et al. 2016; Parlak and Nazik 2016; Darbaş and Demircan 2017; Vardar and Öner 2017), Çanakkale (Atay and Tunoğlu 2002; Atabey et al. 2004; Çağatay et al. 2006; Meriç et al. 2019), Çankırı (Yavuz et al. 2017), Denizli (Şafak 2010; Karayığit et al. 2015; Tuncer et al. 2016; Rausch et al. 2019; İlhan et al. 2020;

Rausch et al. 2020), Edirne (Sakınç et al. 2000), Tekirdağ (Sakınç et al. 2000), Elazığ (Koç-Taşgın et al. 2012), Eskişehir (Bassiouni 1979; Tunoğlu et al. 1995), İzmit (Gülen et al. 1995; Matzke-Karasz and Witt 2005; Kırıcı-Elmas et al. 2021), Hatay (Boulton et al. 2007; Meriç et al. 2012a; Tekin et al. 2019), İstanbul (Şafak et al. 1999; Meriç et al. 2000; Çevik Üner and Özkar Öngen 2009; Witt 2010; Şekeryapan 2011; Meriç et al. 2013; Şafak 2016; Doğan et al. 2020), İzmir (Meriç et al. 2012b; Berndt 2014; Yümün et al. 2016; Stock et al. 2019; Stock et al. 2020), Kahramanmaraş (Şekeryapan et al. 2016), Karaman (Ilgar and Nemec 2005), Konya (Karakas Kadir 1998; Beker et al. 2008), Malatya (Nazik et al. 2008), Mersin (Melis et al. 2015; Şafak and Nurlu 2018; Şafak 2019), Muğla (Gül et al. 2019), Sakarya (Kerey et al. 2004), Sinop (Şekeryapan 2011), Sivas (Koçyiğit 1989) and Yalova (Matzke-Karasz and Witt 2005; Rückert-Ülkümen et al. 2006).

Recent forms

Adana (Külköylüoğlu et al. 2005; Perçin-Paçal 2011; Ustaoglu et al. 2012; Bodergat et al. 2014), Adapazarı (Altınsaçlı and Griffiths 2002; Altınsaçlı 2003; Altınsaçlı 2004; Altınsaçlı et al. 2014), Afyonkarahisar (Altınsaçlı and Mezquita 2008), Aksaray (Altınsaçlı 2004), Aydın (Sarı et al. 2001), Balıkesir (Kubanç and Altınsaçlı 1990; Altınsaçlı and Griffiths 2002), Bursa (Altınsaçlı 2004; Perçin-Paçal 2019), Çanakkale (Kılıç et al. 2000; Kubanç and Kılınçarslan 2001; Altınsaçlı and Griffiths 2002; Ustaoglu et al. 2012), Denizli (Altınsaçlı and Mezquita 2008), Hatay (Perçin-Paçal 2011; Akdemir and Külköylüoğlu 2021), Edirne (Altınsaçlı 2004; Altınsaçlı et al. 2018; Perçin-Paçal 2019), İstanbul (Kubanç 2003; Külköylüoğlu et al. 1993; Altınsaçlı and Yılmaz 1995; Külköylüoğlu et al. 1995; Altınsaçlı and Griffiths 2002), İzmir (Kubanç and Altınsaçlı 1990; Altınsaçlı and Griffiths 2002; Altınsaçlı 2004), Kırklareli (Kılıç 2 2001; Altınsaçlı 2001; Altınsaçlı and Griffiths 2002; Özuluğ and Yaltalier 2008), Kocaeli (Kılıç 2001; Altınsaçlı and Griffiths 2002; Altınsaçlı et al. 2014), Muğla (Özuluğ and Kılıç 2002; Altınsaçlı 2004; Altınsaçlı et al. 2015a, b; Yavuzatmaca 2019; Akdemir et al. 2020), Muş (Külköylüoğlu et al. 2020), Rize (Kılıç 2001; Altınsaçlı and Griffiths 2002), Samsun (Kaleli 1993; Altınsaçlı and Griffiths 2002; Ustaoglu et al. 2012; Yavuzatmaca 2020) and Sinop (Kaleli 1993; Altınsaçlı and Griffiths 2002; Yavuzatmaca et al. 2017).

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