

Research Article

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Ecological Succession of Freshwater Ostracoda (Crustacea) in A Newly Developed Rheocrene Spring (Bolu, Turkey)

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Abstract: Six species of ostracod (*Candona neglecta, Heterocypris incongruens, Ilyocypris bradyi, Darwinula stevensoni, Pseudocandona compressa,* and *Psychrodromus olivaceus*) were collected from a newly developed spring between October 2001 and October 2004. The first 5 species have cosmopolitan distribution in the Holarctic region. The ratio of non-cosmopolitan to cosmopolitan species (called 'pseudorichness') was 0.2, suggesting dominance of cosmopolitan species. Among the species, *C. neglecta* displayed the highest tolerance to 6 different environmental variables, although its estimated optimum values varied. Except foor redox potential and salinity, optimum values for *H. incongruens* were the highest. High tolerance and optimum values seemed to provide more advantages for cosmopolitan species to increase their survival in a variety of habitats. Considering that this spring is newly developed, the ostracod species' composition may be demonstrating the first stages of ecological succession, in which the first invader animals can be cosmopolitan species due to their wide-ranging tolerance.

Key Words: Ostracoda, succession, spring water, ecology, cosmopolitan, pseudorichness

Yeni Gelişmekte Olan Bir Akarpınar Suyundaki (Bolu, Türkiye) Tatlısu Ostrakotlarının (Crustacea) Ekolojik Başarısı

Özet: Yeni oluşmaya başlayan bir kaynak suyundan Ekim 2001 ve 2004 tarihleri arasında altı Ostracoda türü (*Candona neglecta, Heterocypris incongruens, Ilyocypris bradyi, Darwinula stevensoni, Pseudocandona compressa, Psychrodromus olivaceus*) teşhis edilmiştir. İlk beş tür Holarktik bölgede kozmopolitan dağılım göstermektedir. Kozmopolitan olmayan türlerin kozmopolitan türlere göre bulunan (0.2) oranı (ki buna 'sahte zenginlik' diyoruz) kozmopolitan türlerin baskınlığını ifade etmektedir. Türler arasında, *C. neglecta*, optimum değerlerinin değişkenlik göstermesine rağmen, altı farklı çevresel değişkene diğer türlerden daha yüksek toleransı göstermiştir. Redoks potensiyeli ve tuzluluk hariç, en yüksek optimum değere *H. incongruens* sahiptir. Geniş tolerans ve optimum değerlere sahip olmak kozmopolitan türlerin farklı habitatlardaki yaşama şansını arttırması bakımından daha fazla avantajlı bir durumdur. Yeni oluşum gösteren bir kaynak suyunu ele aldığımızda, ki buraya ilk gelen hayvanlar geniş tolerans seviyesine sahip kozmopolitan türler olabilir, ostracod tür kompozisyonu ekolojik başarının ilk basamaklarını oluşturabilir.

Anahtar Sözcükler: Ostracoda, ardışıklık, kaynak suyu, ekoloji, kozmopolitan, sahte zenginlik

Introduction

Although the study of species succession has traditionally focused on plants, a few examples of animal succession do exist (e.g., see Günther, 1986). Reports of the living forms of freshwater ostracod succession are

even rarer (Löffler, 1990); however, research on the succession of spring-dwelling species (e.g., ostracods, gammarids, and bryophytes) can provide some understanding of the community structure and function of such habitats (Glazier, 1991; Gooch and Glazier, 1991;

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Külköylüoğlu, 1999a; Heino et al., 2005). Succession requires several steps (facilitation, tolerance, and inhibition) (Connell and Slatyer, 1977) and once the current state is known, future estimates can be predicted. The implications of this view can also be applied to ostracods because of their wide-spread distribution and diversity in a variety of habitats.

Springs are unique ecosystems in which constant conditions (e.g., chemical composition of water, temperature, pH, dissolved oxygen, etc.) provide organisms suitable conditions (Hynes, 1970; Odum, 1971; Glazier, 1991; Särkkä et al., 1997; Külköylüoğlu, 1999a,b; Külköylüoğlu and Yılmaz, 2006). Because such conditions can remain unchanged for hundreds of thousands of years (Gooch and Glazier, 1991), springs can provide unique data about endemism and zoogeography, demonstrating the patterns of post-Pleistocene colonization (Williams et al., 1990). Springdwelling organisms adapt (or acclimate) to these constant conditions (Glazier, 1998), and changes in water quality, coupled with species succession, can be deduced based on species composition (Külköylüoğlu, 1999a, 2005a; Külköylüoğlu and Yılmaz, 2006). Consequently, springs can be used as a key to past and present environmental conditions, from which future conditions can be estimated; however, spring habitats have been extensively disturbed by human activity, which has resulted in changes in habitat structure and function (Külköylüoğlu, 1999a; Smith and Wood, 2002; Devin et al., 2005). Such changes eventually demonstrate their influence on species composition and biological richness of habitats (Külköylüoğlu and Vinyard, 2000; Külköylüoğlu, 2005a). Although springs bear such important biological, ecological, geographic, and historical characteristics, relatively little is known about their use.

Ostracods are small microscopic aquatic invertebrates found in almost all kinds of aquatic habitats, from hot springs to cold waters (Külköylüoğlu and Vinyard, 1998). For example, *Thermopsis thermophila* was only found in the hot springs of the Great Basin area of North America, where water temperature reaches 55 °C (Külköylüoğlu et al., 2003). In contrast, a bisexual population of *Cavernocypris subterranea*, a crenobiont species, was reported from springs where temperature ranges between 9.6 and 17 °C (Külköylüoğlu, 1999a). Two other crenobiont ostracod species (Eucypris pigra, Scottia pseudobrowniana) can be found in cold spring waters or cool environments where temperatures reach 16 °C and can rarely reach 25 °C (Külköylüoğlu, 1999a; Shornikov and Trebukhova, 2001). All such examples underline that ostracods prefer certain kinds of conditions and can survive in such conditions as long as they do not exceed their tolerance range. This may support the idea that ostracod occurrence in springs can be related to their ecological succession; however, among the species, some generalist species (e.g., cosmopolitans) show wide geographical distribution, while some specialist species (e.g., non-cosmopolitans) have limited distribution. This is because individual species prefer different environmental conditions and their tolerance levels vary. Therefore, distribution of species may depend on their tolerances. If species show high tolerances to environmental variables, they are referred to euryoecious species (Fischer et al. 1997). Nonetheless, one must consider whether euryoecious species are cosmopolitan or vice versa (Külköylüoğlu, 2000). The implication of this approach raises several questions concerning the relationships between ostracods and their ecological importance. Such questions addressed in the present study include: Are cosmopolitan species (if not all) euryoecious or vice versa? Are cosmopolitan species good indicators of water quality? Do cosmopolitan species have high tolerances? If yes, what are the levels of tolerances? Which factor(s) is/are more important to their abundance? Basing such questions on present ecological conditions highlights the importance of ostracods in multi- and inter-disciplinary studies in which reconstruction of past environmental conditions can be estimated by means of using ostracods as indicator species (Boomer et al., 2003).

The concept of pseudorichness is based on the ratio of the number of non-cosmopolitan to cosmopolitan species (Külköylüoğlu, 2004a). Accordingly, increasing numbers of cosmopolitan species corresponds to low water quality or the first levels of species succession in a newly developing habitat, or both. Furthermore, this concept assumes that cosmopolitan species can better succeed in newly developing habitats because of their high levels of tolerance. Although the concept may help to understand the levels of succession, the hypothesis should be tested widely in different organisms found in a variety of habitats. Thus, in the light of these approaches, the goals of the present study were to (1) define ostracod species succession and composition in Hidayet Bey Spring, (2) understand the ecological preference and tolerance level of ostracods for 7 selected environmental variables, and (3) discuss the application of a new approach (pseudorichness), along with its relationship to cosmopolitan characteristics of species.

Material and Methods

Study area

Hidayet Bey Spring (lat 40°46′41′N, long 32°01′78′E, ca. 1010 m asl) is located on the northeast part of the shallow eutrophic Lake Yeniçağa (Bolu) (Figure 1). The spring has about 4 m² of surface area and a depth of about 20 cm. Materials were collected within this range between October 2001 and October 2004 (total: 21 months) (Table 1). The spring originated at the end of 1999 after drilling to a depth of 28 m to provide water for Lake Yeniçağa and its environs (personal communication by Hidayet Arık). Since then, at the head of the spring, water comes out of an iron pipe (60×15) cm) and flows through the lake after traveling about 120 m via a stream canal. Almost the entire surface area of the source is heavily covered by a cosmopolitan aquatic plant, Lemna cf. minor, which prevents light from penetrating to the muddy rust-colored bottom, possibly causing anoxic conditions for the organisms; only some species can survive there, such as Ostracoda, Isopods (Asellus sp.), Cladocera (Daphnia sp.), Copepoda (Cyclops sp.), and Arachnida (Acaria sp.).

Sampling and Measurement Procedures

Seven major water variables (pH, standard hydrogen electrode (SHE [mV]), dissolved oxygen (DO [mg/l]), water temperature (t(w) [°C]), percent oxygen saturation (%Sat), electrical conductivity (EC [μ S/cm])), and salinity (Sal [ppt]) were measured (between 10:00 AM and 1:00 PM) in situ before sampling. A mercury thermometer was used to measure ambient temperature. An eighth major water variable, total dissolved solids (TDS [mg/l]), was calculated by multiplying conductivity values by 0.65 when pH and redox potential values were measured with a Hanna model HI-98150 pH/ORP meter (20 °C). SHE

was calculated from redox potential field data (*Eh*). Other variables were measured with a YSI-85 model oxygentemperature meter. Elevation and coordinates were recorded with a global positioning system (GPS Garmin-45).

Samples collected from the source with a hand net (250 μ m mesh) were fixed in 70% alcohol in glass bottles (250 ml). In the laboratory, all materials were washed in 4 standardized sieves (2.0, 1.0, 0.5, and 0.25 mm mesh, consecutively). Species identification followed Kempf (1997) and Meisch (2000), and was based on adult individuals.

Statistical analyses

Non-parametric Spearman's rank correlation analysis was used to show the correlations between 7 environmental variables and the number of species. Oneway analysis of variance (ANOVA), along with the F-test (α = 0.05), were applied to reveal significance levels between the number of adult species found and selected environmental variables. Species tolerance ($t_{\rm k}$) and estimated optimum ($u_{\rm k}$) levels of 7 environmental variables for the 3 most abundant ostracods were calculated from the following equations:

where y_{ik} and $_i$ are the abundance of each taxon (k), and the value of each environmental variable (*x*) in the sample *i*, respectively (ter Braak and Barendregt, 1986; Birks et al., 1990; Külköylüoğlu and Dügel, 2004).

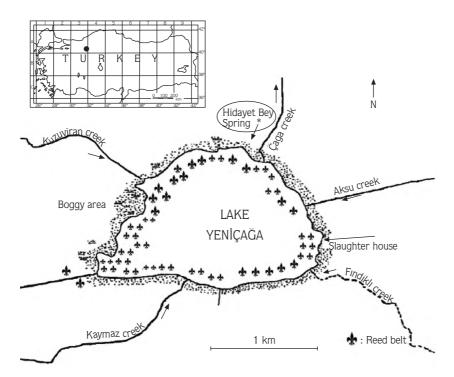


Figure 1. Location of (*) Hidayet Bey Spring near Lake Yeniçağa (Bolu).

Results

Mean dissolved oxygen in Hidayet Bey Spring was 2.88 mg/l and mean water temperature was a relatively cool 13.2 °C (range: 10.2-18.1 °C) (Table 1). The spring had a small number of ostracod species compared to similar habitats, as only 6 species (Candona neglecta, Heterocypris incongruens, Ilyocypris bradyi, Darwinula stevensoni, Pseudocandona compressa, and Psychrodromus olivaceus) were recorded between October 2001 and October 2004. The first 5 (maybe all) species have cosmopolitan distribution in the Holarctic region, and relatively high tolerances (Table 2). Thus, the level of pseudorichness (non-cosmopolitan/cosmopolitan species = 0.2) of the spring was low. Significant differences were observed in the mean number of species and environmental variables (P < 0.05, F-test). Spearman's rank correlation analyses (Table 3) showed that some of the variables were significantly correlated to each other at the 0.05 level. The most frequently occurring species, Candona neglecta, displayed the highest tolerance to 6 different environmental variables. Findings suggest that the ecological preferences of the 3 most abundant species (C. neglecta, H. incongruens, and P. olivaceus) were reflective of their tolerance levels and cosmopolitan characteristics. Overall, results imply that cosmopolitan species (e.g., some ostracods) may be used as indicators of the first levels of ecological succession in a newly developing habitat, as is the case in Hidayet Bey Spring.

Discussion and Conclusions

I. bradyi, D. stevensoni, and *P. compressa* were the least frequently occurring species in Hidayet Bey Spring. Among them, the first 2 were encountered only once during the entire study period and have cosmopolitan characteristics, while *P. compressa* is common primarily in the Holarctic region. In contrast to *I. bradyi* and *D. stevensoni*, not much is known about the ecology of *P. compressa*. Tolerance and optimum values of these species were not calculated because they were observed infrequently, but earlier studies indicate that these species can be found in a wide range of habitats (Table 1). Although limited, the 3 most abundant species (*C. neglecta, P. olivaceus, H. incongruens*) collected from Hidayet Bey Spring also provide useful information about species ecological succession. For example, *C. neglecta*, a

Table 1. Sampling dates and values of 7 major variables in Hidayet Bey Spring. Codes include pH, standard hydrogen electrode (SHE (mV)), dissolved oxygen (DO (mg/l)), water temperature (t(w)), percent oxygen saturation (%Sat), electrical conductivity (EC (μS/cm)), salinity (Sal (ppt)), and 6 ostracod species *Candona neglecta* (Cn), *Heterocypris incongruens* (Hi), *Psychrodromus olivaceus* (Po), *Darwinula stevensoni* (Ds), *Pseudocandona compressa* (Pc), *Ilyocypris bradyi* (lb).

Date	рН	SHE	DO	t(w)	%Sat	EC	Sal	Species
10.14.01	7.49	189.34	4.26	13.4	42.2	599	0.3	124Hi, 3Po
11.11.01	7.35	192.15	3.98	12	37.3	603	0.3	7Hi
12.23.01	7.28	196.42	3.99	10.2	35.8	454	0.2	
04.28.02	7.31	189.66	2.17	16.9	23.3	279	0.1	
05.31.02	7.54	183.38	0.32	18.1	3.6	210	0	1Ds, 8Cn, 1Pc
06,28.02	7.76	175.69	2.85	14.4	28.5	616	0.3	1Hi
07.30.02	7.42	184.88	1.28	15.8	26.6	640	0	2Hi
07.30.03	7.04	213.85	1.9	14.3	17.7	715	0.3	1Pc
08.29.03	7.31	210	2.17	13.3	19.7	612	0.3	9Cn
09.01.03	7.29	199	3.91	12.2	32	598	0.3	1Cn
10.31.03	7.5	184.58	3.42	11.8	31.2	678	0.3	_
11.30.03	7.41	189.54	2.56	11.7	23.6	664	0.3	5Cn
12.27.03	7.43	188.58	5.05	11.8	46.5	619	0.3	11b, 17Cn
03.31.04	7.53	181.88	3.39	11.8	30.4	617	0.3	1Cn
04.30.04	7.15	206.57	2.91	13.2	27.6	618	0.3	2Po
05.29.04	7.23	200.81	1.49	13.9	16.3	593	0.3	
06.24.04	7.13	199.42	2.59	12.5	28.6	596	0.3	2Cn, 2Po
07.28.04	7.15	203.84	2.08	13.4	18.9	581	0.3	7Cn, 16Po, 1Pc
08.28.04	7.32	197.62	3.38	12.5	32.3	598	0.3	11Po, 3Cn
09.25.04	7.25	199.19	3.99	12.7	38	604	0.3	_
10.29.04	7.14	209.05	2.95	12.3	29.3	600	0.3	5Cn, 8Hi, 114Po
Mean	7.33	195.02	2.88	13.2	28.7	575.9	0.26	1.14
Min.	7.04	175.69	0.32	10.2	3.6	210	0	0.0
Max.	7.76	213.85	5.05	18.1	46.5	715	0.3	3.0

Table 2. Estimated optimum (uk) and tolerance (tk) values for 7 variables for the 3 most abundant species. Abbreviations are given in Table 1.

Species		рН	SHE	DO	t(w)	%Sat	EC	Sal
Cn	uk	7.35	195.72	2.96	13.21	27.68	556.16	0.26
	tk	1.04	10.00	1.58	2.07	14.47	141.3	0.1
Po	uk	7.16	207.08	2.91	12.47	28.63	597.96	0.3
	tk	0.07	4.24	0.36	0.37	3.91	6.31	0.0
Hi	uk	7.46	190.55	4.08	13.33	40.65	601.02	0.29
	tk	0.09	5.17	0.55	0.54	4.3	11.28	0.04

	Sn	DO	EC	Sal	pН	SHE	Sat	T(w)
Sn	1	-0.1	-0.14	0.09	0.12	-0.6	-0.3	0.16
DO		1	0.11	0.37	0.16	-0.18	0.09*	-0.68*
EC			1	0.37	0.16	-0.09	0.12	-0.25
Sal				1	-0.23	0.34	0.27	-0.39
pН					1	-0.93*	0.21	-0.09
SHE						1	-0.25	0.05
Sat							1	-0.60*
T(w)								1

Table 3. Non-parametric Spearman's correlation analysis of 7 environmental variables and number of species (Sn), where n = 21. (*) Correlation is significant at the 0.01 level (2-tailed). Abbreviations are given in Table 1.

cosmopolitan species (at least in Holarctic region), is one of the most common species found in various types of aquatic bodies (Külköylüoğlu, 2000, 2003, 2005a,b; Meisch, 2000) and is one of the most reported species in freshwater habitats, both living and in fossil form. For example, *C. neglecta*, along with 5 other ostracods, was reported as the dominant form in Late-Glacial ostracod assemblies and in ancient Lake Duvensee in Northern Germany (Günther, 1986); however, over the course of time, due to several factors, such as changes in climate, lake ground water levels, and inflow, the succession of species changed in Post-Glacial layers, favoring *Candona* species and bountiful *Metacypris cordata*.

Danielopol et al. (1993) studied Lake Mondsee, a deep pre-alpine lake, and reported that C. neglecta was among 3 species to have disappeared last from the lake during eutrophication. The species has high levels of tolerance to different variables; for instance, it was reported to tolerate warm waters with relatively low oxygen (below 3 mg/l) in summer (Meisch, 2000). One recent study of a mesotrophic reservoir enriched with continuous nutrient input (Külköylüoğlu, 2005b) showed that C. neglecta tolerated a wide range of changes in water temperature (3.66-27.91 °C). Külköylüoğlu and Yılmaz (2006) reported the species from a helocrene spring. Occurrence of the species was negatively correlated to water temperature, with the highest tolerance level (tk = 3.8), and optimum estimates to DO (uk = 9.08) and pH (uk =7.79). Mezquita et al. (2005) conducted an extensive study, combining data collected from different types of water bodies of the Iberian Peninsula, and showed similar results for dissolved oxygen (uk = 8.8, tk = 2.3), water temperature (uk = 10.7, tk = 1.6), and pH (uk = 7.42,

tk = 0.36). Similarly, among the 63 ostracods, C. *neglecta* showed higher tolerance to water temperature (tk = 4.60) in freshwater bodies of West-Pomerania in Germany, where the species was among the group observed in colder and deeper aquatic habitats (Viehberg, 2005). In the present study, C. neglecta was common within relatively low DO values (0.32-5.05 mg/l). This implies that C. neglecta has a relatively greater range of tolerance, even in anoxic conditions, than previously known. Indeed, according to Table 2, C. neglecta had the highest tolerance levels, not only to DO and temperature, but also to pH, Eh, EC, and %Sat in Hidayet Bey Spring. These results support that *C. neglecta* is a euryoecious species with high tolerance levels to different environmental variables. Hence, overall, the present study's results support its broad geographical distribution as a cosmopolitan species, which appears to be an advantage for its progressive succession in a variety of habitats. Indeed, this is supported by a study of the Late Glacial lacustrine environment in the southern Baltic Sea (Germany) in which C. neglecta was reported to be one of the species known to succeed, based on continuous core samples (Viehberg, 2005).

The second most abundant species in the present study was a cosmopolitan species, *H. incongruens.* Shornikov and Trebukhova (2001) stated that it prefers heavily polluted water bodies. According to earlier studies (Külköylüoğlu, 2000, 2004a, 2004b), this species can be found in environments with wide ranging variables, including temperature (6.0-29.0 °C), pH (6.00-9.83), DO (1.0-14.5 mg/l), and EC (56.0-2580 μ S/cm). Results of the present study correspond to those of previously reported ranges; for instance, *H. incongruens* was found

in environments with low DO (1.28-4.26 mg/l) and high EC (599-640 µs/cm). The species also displayed higher optimum estimates to several variables, such as pH, DO, water temperature, %Sat, and EC (Table 2). Most recently, in the environs of Buenos Aires (Argentina), Laprida (2006) collected the species from very alkaline (pH = 8.0-12.8) and salty (TDS = 2395-4435 mg/l)water. These are, to date, the highest pH range and TDS values (implying salinity) for this species. If this is true, H. *incongruens* has much broader tolerance levels to salinity in alkaline waters, in which it can increase its succession. Nonetheless, this needs to be confirmed by more studies. Overall, like *C. neglecta*, *H. incongruens* is a euryoecious species with a wide range of tolerance to different variables in different aquatic habitats. Compared to C. neglecta, however, H. incongruens is known to have a much broader geographical distribution. Unlike C. neglecta, generally speaking, H. incongruens can be found even in a small pit filled with water. Thus, this may increase its earlier succession in extreme conditions. Species with high tolerances should not necessarily be better competitors, but such ability obviously increases their chances for survival in fluctuating habitats or newly developing habitats.

The third most frequently occurring species was P. olivaceus, for which ecological data is least abundant among the species reported herein. It is generally reported from springs and/or spring-related ponds and pools with cool to moderate temperature (Gülen, 1985; Baltanás et al., 1993; Nagorskaya and Keyser, 2005). This is supported by other reports. For example, according to Mezquita et al. (2005) and Külköylüoğlu and Yılmaz (2006), optimum and tolerance levels of the species to water temperature (10.9 and 1.8, and 10.97 and 3.8, respectively) are similar. These results also correspond with the present study (Table 2), during which P. olivaceus was encountered in water with a narrow range of temperature (12.3-13.4 °C) (Table 1). In addition, P. olivaceus usually prefers well oxygenated waters (DO: 11.28-7.26 mg/l) (Külköylüoğlu, 2004a; Külköylüoğlu and Yılmaz, 2006); however, according to the present study, it appears that *P. olivaceus* can tolerate very low levels of oxygen (DO: 2.08-4.26 mg/l). In different types of aquatic bodies of the Iberian Peninsula, Mezquita et al. (2005) calculated the tolerance and optimum levels of the species to DO as 0.8 and 9.1, respectively. Accordingly, Külköylüoğlu and Yılmaz (2006) reported that the tolerance and optimum estimates of the species in different types of springs in Bolu (Turkey) were 2.43 and 8.84, respectively. Compared to these studies, the present study (Table 2) observed relatively low tolerance and optimum values, 0.36 and 2.91, respectively. Nevertheless, the present results show that *P. olivaceus* can tolerate low %Sat and that it prefers cool freshwater habitats with low salinity.

Compared to similar springs, the ratio-or so called pseudorichness-of the number of non-cosmopolitan (1) to cosmopolitan (5) species (0.2) was relatively low in Hidayet Bey Spring. There are 2 possible reasons for such a low ratio. Firstly, it may be related to when the spring was established; considering that its waters first came out of the ground 6 years ago, this may not be enough time for species establishment. As such, ostracod species succession may be in its early stages in this spring. Indeed, Connell and Slatyer (1977) stated that empty spaces (e.g. in our case Hidayet Bey Spring) could first be occupied by opportunist species with broad dispersal powers and rapid growth to maturity. Such characteristics are known in cosmopolitan ostracods, which are widely distributed, grow fast, and tolerate a wide range of environmental variables. This, therefore, implies that empty aquatic habitats can first be occupied by cosmopolitan species. Although there are several ways (e.g. facilitation, tolerance, and inhibition) to determine which species can replace these early occupants (Connell and Slatyer, 1977; Sousa, 1979), the effects of different factors (biotic and/or abiotic) are important over time as well. For example, species with high tolerance levels and high competitive ability may dominate a spring with stable ecological conditions in the long-term. Indeed, Connell (1978) proposed that in recently disturbed communities only a few early colonizing species prevail; therefore, after a long period of time, even diversity remains low, but these few species are long-lived and competitively dominant. This should be supported by long-term studies, but it also requires detailed knowledge about species composition and their ecological preferences.

Secondly, Hidayet Bey Spring had a small number of species due to its ecological conditions, in which speciesspecific adaptation can be favored for species establishment. In extreme conditions, generalist ostracods (e.g. cosmopolitans) will have more advantages than specialists in the short term; however, if species adaptation is succeeded, the species may be considered a specialist for these kinds of conditions. Consequently, species with higher tolerance levels may increase their chances for survival.

Results of the present study seem to support the second possibility for which there is a lack of information concerning the life histories of many ostracod species and habitat establishments of individual species. If 5-6 years are sufficient for ostracod species succession, then the second option of a small number of species is better supported; however, both views are still contentious due to the lack of knowledge about ostracod ecological succession. Finally, although the idea of pseudorichness is useful, a prominent question remains–which factors (biotic and/or abiotic) have greater effects on species succession (and how)?

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