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Article

Gastropod assemblages in the harsh environment of Mediterranean Dinaric karst intermittent rivers

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Abstract
Freshwater snails inhabit a wide range of freshwater habitats, including the intermittent ones, specific adaptations enabling them to survive the dry phase for an extended period of time. Despite an increasing scientific interest in biota occurring in intermittent freshwater habitats, our knowledge about environmental factors shaping freshwater gastropod assemblages in such habitats is still poor. Therefore, this study aimed to assess gastropod assemblage composition in four karst intermittent rivers in the Mediterranean during the lotic phase, compare gastropod taxa richness and abundance among the rivers, and determine their relationships with environmental variables. A total of six taxa was recorded, with each river harbouring a unique, species-poor (up to three species) assemblage. Gastropod assemblages were influenced by the physico-chemical water properties, especially the concentration of dissolved oxygen in water, conductivity, and chemical oxygen demand. Our results provide a basis for further research on freshwater snail assemblages in the Mediterranean karst intermittent rivers, as the need to protect these vulnerable ecosystems and develop adequate monitoring practices becomes imperative due to climate change and anthropogenic pressures.

Key words freshwater snails; temporary habitats; environmental variables; desiccation; aestivation.

Introduction

Freshwater gastropods, together with crustaceans and aquatic insects, play an important role in the macrozoobenthos of freshwater ecosystems. They inhabit a wide array of freshwater habitats, including underground aquifers and springs, streams, rivers, lakes, wetlands, but also drainage channels, temporary ponds, and other ephemeral and seasonal waters (Strong 2008). Many taxa are microhabitat specialists, associated with aquatic vegetation, wood, rocks, stones, and other solid surfaces or soft

sediment (Strong 2008). Accordingly, the composition and structure of freshwater gastropod assemblages are determined by various hydrological, physico-chemical and biological factors acting at different spatial and temporal scales (Savić *et al.* 2016; Bae & Park 2020). In both lotic and lentic environments, gastropod diversity is often constrained by waterbody-specific factors such as substrate composition, water velocity and chemistry (Lewis & Magnuson 2000; Bae & Park 2020). Limited dispersal capacity makes many freshwater gastropods highly sensitive to hydrological disturbance (Strong 2008; Bae & Park 2020).

Intermittent waterbodies, i.e. those that regularly undergo a partial or complete loss of surface water, are among the most hydrologically extreme freshwater habitats (Datry *et al*. 2014; Leigh *et al*. 2015). Gastropods inhabiting such waterbodies are highly exposed to the effects of drying, but specific adaptations enable them to retain water in their tissues and survive the absence of surface water for months or even years (Hubendick 1958; Alykrinskaya 2004; Poznańska *et al.* 2015a). The highest number of freshwater gastropod species occurring in intermittent habitats belong to pulmonate gastropods (Pulmonata). Since pulmonates have thin shells with no operculum, they bury themselves in the substrate at different depths to avoid desiccation (Alykrinskaya 2004; Gulanicz *et al.* 2018). They retract into their shells and secrete a thick mucous membrane or epiphragm, decreasing their metabolic rate and aestivating until the return of favourable environmental conditions (Nowakowska 2011; Poznańska *et al*. 2015a). During the dry period, some species remain on the soil surface, while others crawl under decaying vegetation and aestivate (Alykrinskaya 2004). Compared to pulmonates, prosobranch gastropods (Prosobranchia) inhabiting intermittent waterbodies have thicker shells with an operculum that completely closes the aperture of the shell and thus prevents water loss. Similar to pulmonates, prosobranchs aestivate during the dry hydrological phase burried into the sediment (Alykrinskaya 2004; Hayes *et al*. 2015; Glasheen *et al*. 2017).

The Mediterranean area abounds in intermittent freshwater habitats, among the most common and hydrologically significant being intermittent rivers and streams (Datry *et al*. 2014; Skoulikidis *et al*. 2017), distinguished by three distinct hydrological phases: the flowing phase with continuous water flow, the non-flowing phase where flow cessation results in connected or isolated pools, and the dry phase characterized by the absence of surface water (Larned *et al*. 2010). The interchange of hydrological phases creates a mosaic of terrestrial, lotic, and lentic habitats, harbouring diverse aquatic and terrestrial biota (Stubbington *et al*. 2017; Rodríguez-Lozano *et al.* 2019; Vilenica *et al*. 2021, 2022), and contributing to the local and regional biodiversity of river networks. Moreover, these unique habitats provide many other ecosystem services, such as water supply, flood regulation, aquifer recharge, or have recreational value (Acuña *et al*. 2014; Kaletová *et al*. 2019). During the last decade, scientific interest in intermittent lotic habitats has been stimulated by an increase in their proportion worldwide (Magand *et al*. 2020; Vilenica *et al*. 2022, 2023), facilitated by climate change and water extraction for human activities (de Graaf *et al*. 2019).

Despite the increasing importance of understanding environmental drivers that shape macroinvertebrate assemblages in intermittent lotic habitats, exceedingly few studies have attempted to characterize freshwater gastropod assemblages in such environments. Furthermore, ecological studies aiming to relate gastropod assemblage composition with environmental factors have been conducted mostly in lentic habitats (Bae & Park 2020), much less in perennial lotic habitats (Savić *et al*. 2016) and very rarely in intermittent ones (Dmitrović *et al.* 2016), especially in the Mediterranean area. Therefore, the main objectives of this study were: i) to determine freshwater gastropod assemblage composition in four karst intermittent rivers in the Mediterranean, and compare species richness and abundance among the rivers, ii) to identify the main environmental variables that shape gastropod assemblages, and iii) to examine the relationships between individual gastropod taxa and environmental variables.

Material and methods

Study area

The study area is situated in the Dinaric Western Balkan ecoregion (ER5) in Croatia (Illies 1978). The region is characterized by a temperate humid climate with hot summers (Cfa, Köppen classification). The average temperature of the warmest month is above 22°C (Šegota & Filipčić 2003), the average annual air temperature is 14°C and the average annual rainfall is 1000 mm (Zaninović *et al*. 2008). Four

Mediterranean intermittent karst rivers of the Adriatic Sea basin were investigated within this study: the Krčić, Čikola, Miljašić Jaruga and Guduča rivers (Fig. 1).

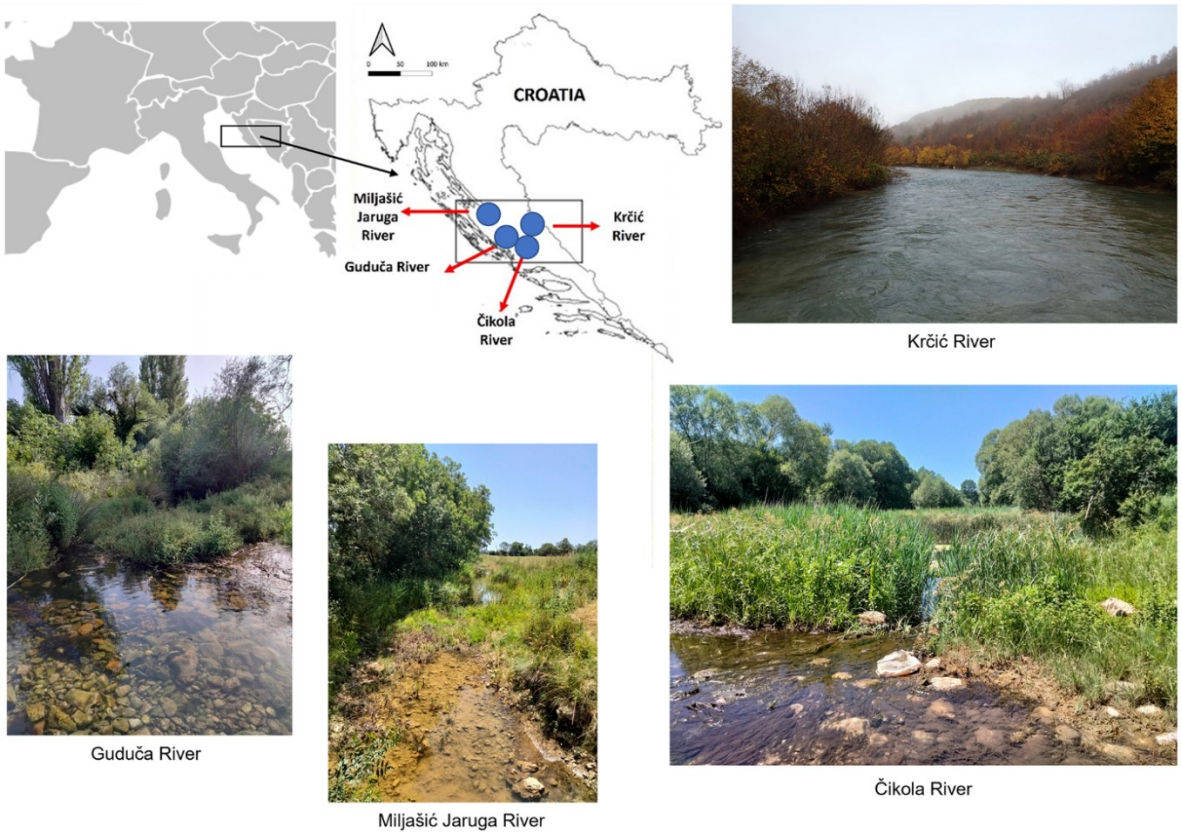

Figure 1. Map of the study area with photographs showing the examples of sampling sites at the four studied Mediterranean intermittent karst rivers, Croatia.

We sampled a total of 12 study sites, i.e. three sites per river (the first study site was closest to the river's source and the third one was farthest from the source). Detailed description of each river is given in Vilenica *et al*. (2021). At each study sites, four replicates were sampled at dominant microhabitats. Dominant substrate composition (substrate types covering more than 5% of the study site) consisted mainly of fine sediments (sand, silt, mud), lithal (stones, gravel), and aquatic vegetation (submerged and emergent). Detailed substrate composition of the study sites is presented in Vilenica *et al*. (2021).

Environmental variables

We conducted this study in April 2021, during the flowing (lotic) phase of all four rivers. At each study site, we measured the following physico-chemical water parameters: water body width and depth (using a handheld metre), water velocity (using the SonTek Flow Tracker), water temperature, dissolved oxygen concentration and saturation (using the WTW Oxi 330/SET oximeter), conductivity (using the WTW LF 330 conductivity meter) and pH (using the WTW pH 330 pH-meter). At each study site, these parameters were measured at four evenly spaced points in a transect from the shoreline to the middle of the river perpendicular to flow.

Moreover, at the same points, four replicate 1-litre water samples were taken from each study site for laboratory analyses of water chemical parameters (alkalinity, chemical oxygen demand, nitrite, nitrate, and orthophosphate concentrations) using standard analytical procedures (APHA 1992).

Freshwater gastropod sampling and identification

At each study site, macrozoobenthos (including freshwater gastropods) was sampled in April 2021 using a Surber sampler (25 cm x 25 cm, mesh size 500 µm). We collected four replicates at each study site, proportional to the microhabitats present (a total of 12 samples were collected at each river). Collected

samples were preserved in 70% ethanol in the field and were later sorted and identified in the laboratory. Gastropods were identified using standard identification tools (Glöer 2002, 2019). The voucher specimens are deposed at the Department of Biology, Faculty of Science, University of Zagreb, Croatia.

Data analysis

The Kruskal-Wallis H test with pairwise comparisons of average ranks *post hoc* tests were used to analyse differences in gastropod assemblage metrics (taxa richness and abundance) among the four intermittent rivers. Assemblage metrics were calculated for each study site at each investigated intermittent river.

The Spearman correlation coefficient was used to analyse the relationship between the gastropod assemblage metrics as well as each gastropod taxon and environmental variables measured in the four intermittent rivers.

The relationship between gastropods and environmental variables was tested using the redundancy analysis (RDA), using data of six taxa and nine environmental variables (those that differed significantly among the four rivers according to Vilenica *et al.* (2023)). Prior to analysis, gastropod abundances were log(x+1) transformed. The relationship between taxa composition and environmental variables was tested using a Monte Carlo test with 499 permutations ($p<0.05$).

All data sets were tested for normality using the Shapiro–Wilk W test Statistica 13.0 (TIBCO SOFTWARE INC. 2017). The Kruskal-Wallis H test with pairwise comparisons of average ranks *post hoc* test and Spearman correlation coefficient were performed in Statistica 13.0 (TIBCO SOFTWARE INC. 2017). RDA and Monte Carlo test were performed in the CANOCO package version 5.11 (ter Braak & Šmilauer 2012).

Results

Freshwater gastropod assemblages

In the four Mediterranean intermittent rivers, a total of six taxa was recorded (Table 1). Four taxa were identified to the species level and two to the genus level since all specimens were juvenile (*Radix* sp. and *Stagnicola* sp.). Significantly higher gastropod taxa richness (Kruskal-Wallis H test with Multiple comparisons *post hoc* test, $H = 18.46$, $p<0.001$) and abundance ($H = 19.87$, $p<0.001$) were recorded in the Miljašić Jaruga River compared to the Krčić River, where no gastropods were documented (Table 1, Fig. 2). The other two rivers, Čikola and Guduča, harboured intermediate values of assemblage metrics (Fig. 2). *Stagnicola* sp. was the most abundant, and *Radix* sp. and *Radix labiata* the least abundant (Table 1). None of the recorded taxa were shared among the rivers (Table 1).

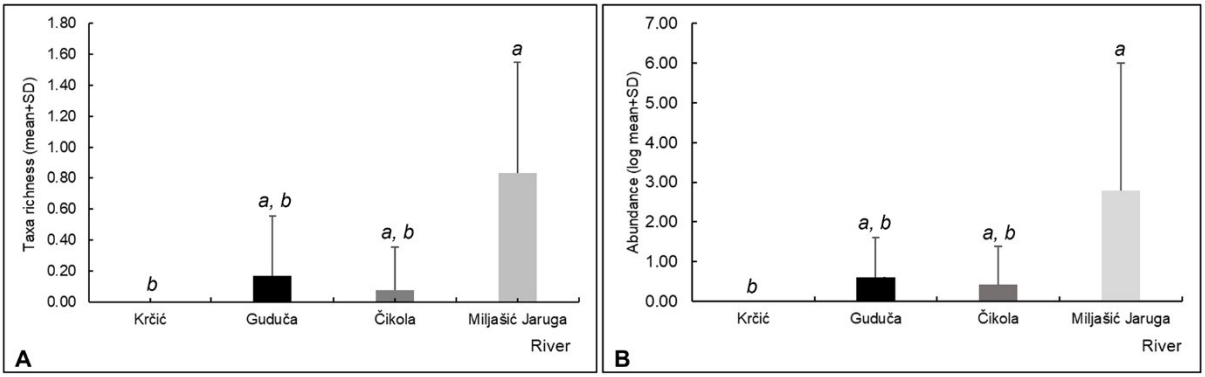

Figure 2. Freshwater gastropod assemblage metrics in four intermittent rivers in the Mediterranean, Croatia: a) taxa richness and b) log-transformed abundance shown as mean with standard deviation (SD).

Freshwater gastropod assemblages and environmental variables

Gastropod taxa richness and abundance were positively correlated with conductivity (Spearman correlation coefficient, $R=0.55$, $p<0.001$; $R=0.56$, $p<0.001$), alkalinity ($R=0.46$, $p<0.01$; $R=0.48$, $p<0.001$), concentration of dissolved oxygen ($R=0.43$, $p<0.01$; $R=0.47$, $p<0.001$) and water temperature

(R=0.37, p<0.01; R=0.38, p<0.01), while negative correlations were recorded with water velocity (R=-0.53, p<0.001; R=-0.54, p<0.001) and pH (R=-0.39, p<0.01; R=-0.42, p<0.01).

Table 1. Freshwater gastropod taxa recorded in the four Mediterranean intermittent rivers, Croatia.

Taxa/River	Krčić	Guduča	Čikola	Miljašić Jaruga
Acroloxus lacustris (Linnaeus, 1758)			2.7	
Ancylus fluviatilis O. F. Müller, 1774		2.7		
Bithynia tentaculata (Linnaeus, 1758)				13.3
Radix labiata (Rossmässler, 1835)				1.3
Radix sp.		1.3		
Stagnicola sp.				602.7
Mean abundance (individuals/m^2)	0	4.0	2.7	617.3
Taxa richness	0	2	1	3

Bithynia tentaculata abundance was positively correlated with conductivity (R=0.46, p=0.001) and concentration of dissolved oxygen in water (R=0.34, p<0.05). Negative correlations were recorded between the species' abundance and water velocity (R=-45, p=0.001) and nitrates (R=-0.44, p<0.05). *Stagnicola* sp. abundance was positively correlated with concentration of dissolved oxygen (R=0.53, p<0.001), alkalinity (R=0.44, p<0.01), conductivity (R=0.42, p<0.01), and water temperature (R=0.30, p<0.05), while it was negatively correlated with pH (R=-0.38, p<0.01) and water velocity (R=-0.42, p<0.05). Other gastropod taxa did not show significant correlations with physico-chemical water parameters (p>0.05).

The results of the RDA ordination of freshwater gastropod taxa and environmental data are shown in an F1 × F2 ordination plot (Fig. 3). The distribution of gastropod taxa is highly related to axes 1 and 2; eigenvalues are 0.45 and 0.06, showing a taxa-environment correlation of 51.6%. Monte Carlo permutation test indicated that species-environment ordination was significant (first axis: F-ratio = 32.47, p=0.002, overall: trace = 0.54, p=0.002). Axis 1 is related to dissolved oxygen concentration (R=0.58) and conductivity (R=0.44), and axis 2 to chemical oxygen demand (R=−0.33), indicating that these were the most important parameters in explaining patterns of the gastropod assemblages.

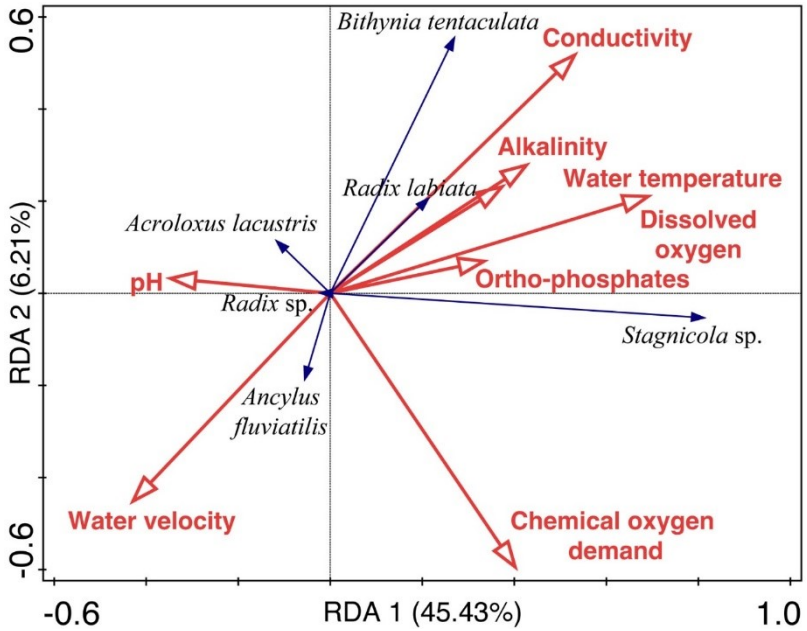

Figure 3. Redundancy analysis (RDA) ordination biplot showing the relationships between freshwater gastropods (blue arrow symbols) and environmental variables (red arrow symbols) in four intermittent rivers in the Mediterranean, Croatia. Environmental variables: Water temperature (°C); Concentration of dissolved oxygen in water (O_2 mg L^{-1}); pH; Conductivity (µS cm^{-1}); Water velocity (m s^{-1}); Concentration of ortho-phosphates in water (mg P L^{-1}), Chemical oxygen demand (mg O_2 L^{-1}), Alkalinity (mg $CaCO_3$ L^{-1}).

Discussion

The results of this study show that the studied intermittent rivers harbour low freshwater gastropod taxa richness and abundance, which was expected due to the harsh hydrological conditions. Previous studies showed that species richness and abundance are generally much higher in perennial than in the intermittent rivers within the same region (Beran 2011, 2016; Vučković 2013). For instance, abundance of some of the recorded taxa, such as *B. tentaculata* and *R. labiata,* were several hundred times higher in the perennial Krka River (3312 individuals/m^2 and 112 individuals/m^2, respectively), mainstream of the Čikola and Guduča rivers (Vučković 2013), compared to the results obtained within this study.

The highest freshwater gastropod taxa richness and abundance recorded at the Miljašić Jaruga River is most probably the result of the river's uniform morphology along its whole course, with microhabitat composition consisting predominantly of fine sediments, xylal and dense aquatic vegetation. Individual patches of muddy sediment, especially of those among the dense emergent vegetation, tend to stay moist during the dry hydrological phase, allowing gastropods to burrow themselves easily into the sediment for aestivation. Moreover, dense emergent vegetation and its dead parts provide a suitable shelter for individuals that have not burrowed themselves into the sediment. For both pulmonates and prosobranchs, finding a suitable microhabitat as a refuge is often crucial for their survival in harsh environmental conditions, including the periodic fluctuations of water level (Lajtner *et al*. 2022), which is particularly important if the period of desiccation is long. Although we have not recorded any freshwater gastropods in the Krčić River, a previous study by Dorić (2016) reported *Galba truncatula* (O. F. Müller, 1774), *A. fluviatilis* and *Gyraulus* sp. (the latter two represented by empty shells), caught in pitfall traps in the riparian habitat of the Krčić River, close to the water's edge. These aquatic taxa were probably trapped during an increase in water level, when the pitfall traps were submerged. Those findings suggest higher taxa richness (i.e. eight) of the studied intermittent rivers, highlighting the necessity for further systematic research.

All gastropod taxa recorded are generalists, with various adaptations that enable them to survive in hydrologically challenging habitats, such as those related to respiration, life cycle duration and desiccation coping mechanisms, e.g. microhabitat selection (Alykrinskaya 2004; Poznańska *et al*. 2015a, b). The recorded gastropods are widely distributed in Europe (Glöer 2002) and inhabit both lothic and lenthic habitats (Glöer 2002; Moog 2002). Some of them are widely distributed in lotic habitats where they occur along the whole river course, between crenal/rhithral and potamal river sections (e.g. *A. lacustris* and *B. tentaculata* occur between hyporhitral and hypopotamal zone; *A. fluviatilis* occurs between hypocrenal and epipotamal). Some taxa have more restricted longitudinal distribution and are typical for crenal and rhithral regions (such as *R. labiata*) or for potamal zones (such as *Stagnicola* sp.). Moreover, all taxa recorded in this study can also be found in littoral zones of lentic habitats, where for some of them (*A. lacustris*, *Stagnicola* sp.), lentic habitats are the preferential habitat type (Moog 2002). All pulmonates recorded in studied intermittent rivers are hermaphrodites and semelparous with the life span of approximately one year, and the reproduction most often occurring in the spring (Jakubik 2012). Such life cycle type could be beneficial for their survival in hydrologically challenging environments such as intermittent rivers. *Bithynia tentaculata*, a prosobranch snail, is a dioecious and iteroparous species. Iteroparous snails mostly reproduce in spring, however, in cases where conditions are unfavourable, mature individuals may postpone reproduction until environmental conditions improve. Such reproduction pattern is also frequent in species that live in isolated freshwater reservoirs, where competition for food resources and habitat is higher, and survival of parent individuals increases the chance of survival of the whole population (Jakubik 2012).

Gastropod assemblages in the studied Mediterranean karst intermittent rivers were primarily influenced by higher concentration of dissolved oxygen in water, higher conductivity and lower chemical oxygen demand. Accordingly, highest taxa richness and abundance were recorded at the Miljašić Jaruga River, characterized by increased oxygen content and conductivity, most probably resulting from dense macrophyte vegetation, high share of fine sediments and inflow of nutrients from surrounding agricultural fields (see also Vilenica *et al*. 2023). Some previous studies showed the importance of oxygen concentration and stable substrates for freshwater snails in lotic habitats (e.g. Savić *et al*. 2016).

Some of the taxa recorded showed significant correlations with the measured environmental variables. For instance, association of *Stagnicola* sp. and *B. tentaculata* with higher oxygen

concentration and *Stagnicola* sp. association with higher water temperature is in line with biological requirements of many freshwater snails (Tanveer & Kahn 1989; Savić *et al*. 2016; Olkeba *et al*. 2020). Their positive association with higher conductivity values could be related to the preference for muddy substrates or calcium concentration in water that can lead to higher conductivity values at a particular habitat. Muddy substrates could provide refuge during the dry hydrological period (Alykrinskaya 2004; Nowakowska 2011; Poznańska *et al*. 2015a; Gulanicz *et al*. 2018), while calcium concentrations in water above 5 mg/L represent a general requirement for freshwater snails (Lodge *et al*. 1987). Negative association of limnophile/limnobiont *Stagnicola* sp. with water velocity can be explained by its habitat preference, i.e. these snails primarily inhabit littoral zones of lentic habitats (Schmidt-Kloiber & Hering 2015, 2023). On the other hand, the negative association of this taxon with higher pH values is in contrast with the results of some other studies that have shown positive correlations between gastropod population densities and pH values (Økland 1983; Herrmann *et al*. 1993*;* Lewin & Smolinski 2006; Savić *et al*. 2015). However, since all the studied rivers have slightly alkaline pH values, those correlations should be discussed with caution. Although *B. tentaculata* is known not to have a specific water velocity preference (Schmidt-Kloiber & Hering 2015, 2023), in our study it was negatively associated with water velocity, but this association could be indirect and related to some other environmental variable, such as the preference for microhabitats associated with lower water current. Moreover, unlike most other freshwater snails which are shredders, grazers and detritus feeders, *B. tentaculata* is primarily an active filter feeder (Moog 2002), thus it could benefit from habitats with lower water velocity, especially in eutrophic environments where phytoplankton is abundant (Brendelberger & Jurgens 1993). Negative association of this species with nitrate concentration in water corroborates the results of previous studies (Russel-Hunter 1978; Savić *et al*. 2016).

Conclusions

This study revealed rather low gastropod taxa richness and abundance in the studied Mediterranean karst intermittent rivers. Their assemblages and dominant taxa were highly influenced by the physico-chemical water parameters, which differed according to the river morphology and microhabitat composition. Higher assemblage metrics were recorded in the rivers encompassing microhabitats with fine substrates and xylal that can provide refugia during the dry hydrological phase. This study is among the first focusing exclusively on ecological and habitat requirements of freshwater snails in intermittent rivers in the Mediterranean, and as such it represents a basis for future research, especially in the light of climate change and increasing anthropogenic pressures on freshwater ecosystems.

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